Introduction

All the fascinating complexities of life including the human mind are the results of millions of years of Darwinian evolution by natural selection. Evolution occurs when morphological, physiological, cognitive and behavioral traits have genetic basis and vary across individuals (Dawkins, 1986; Lewontin, 1974). Behavior is a major target and driver of evolutionary change (Duckworth, 2008), but studying behavioral evolution poses fundamental challenges. Most behavioral traits are causally distant from the genome, and display high degree of both plasticity and individual variability (Dingemanse, Kazem, Réale, & Wright, 2010; West-Eberhard, 1989).

Ever since Fodor (1983) mind, cognition and brain organization are viewed as modular (Bertolero, Yeo, & D’Esposito, 2015; Meunier, Lambiotte, & Bullmore, 2010; Sternberg, 2011). In classical ethology, behavioral organization has been viewed as hierarchically modular (Hogan, 2009, 2015; Toates, 1998). The behavioral phenotype is modular too. For example, many studies reveal correlations across various behavioral domains (Sih, Bell, Johnson, & Ziemba, 2004) which give rise to consistent personalities in animals of various taxonomic groups similar to human personality (Budaev & Brown, 2011; Dingemanse, Kazem, Réale, & Wright, 2010; Gosling, 1999; Reale, Dingemanse, Kazem, & Wright, 2010). These correlations can be caused by common genetic, physiological, developmental, neurobiological or cognitive mechanisms (Arnold, 1992; Budaev & Brown, 2011), but can also be the result of ecological adaptation (Budaev & Brown, 2011; Reale et al., 2010; Wilson, Clark, Coleman, & Dearstyne, 1994). Consistent correlations across different cognitive domains can point to modularity in the underlying architecture of the cognitive processes (Rabaglia, Marcus, & Lane, 2011). Modularity constrains and facilitates evolutionary adaptation of cognitive and behavioral traits (Andersen, Jørgensen, Eliassen, & Giske, 2016; Clune, Mouret, & Lipson, 2013; Giske et al., 2014). This agrees with the emerging views on modularity in biological systems (Lorenz, Jeng, & Deem, 2011; Wagner, Pavlicev, & Cheverud, 2007), where evolved adaptive architectures are found across many organizational levels from the genome to cognitive mechanisms.

In spite of the growing empirical evidence for the importance of the integrated phenotype (McGlothlin & Keterson, 2008; Murren, 2012), most mathematical and optimization models of animal behavior in evolutionary ecology ignore these proximate complexities. By a broad assumption that the phenotypic traits are unconstrained, the tradition in evolutionary ecology has been to model fitness consequences of specific behaviors directly (Emlen, 1966; Fisher, 1930; Houston, Clark, McNamara, & Mangel, 1988, but see Pierce & Ollason, 1987). This assumption, called “the phenotypic gambit” (Grafen, 1984), is justified as a starting point but becomes increasingly unrealistic when studying cognition and behavior in a novel, changing and stochastic environment (Fawcett, Hamblin, & Giraldeau, 2013; Giske et al., 2013, 2014).

In cognitive science, psychology and neurobiology, the approach based on cognitive architecture has experienced an immense success...
Cognitive architecture is defined as an “overall, essential structure and process of a broadly-scoped domain-generic computational cognitive model, used for a broad, multiple-level, multiple-domain analysis of cognition and behavior” (Sun, 2004). It is a basic framework for the organization of cognition and behavior that can be extended in various ways to build more detailed and specific computational models of these phenomena that focus on particular research problems and purposes (Anderson, 1983; Duch, Oentaryo, & Pasquier, 2008; Lucentini & Gudwin, 2015; Samsonovich, 2012). The adaptable cognitive architecture (Fig. 1) is the main feature of the BICA challenge: development of a general-purpose computational equivalent of the human mind (Samsonovich, 2012).

Building blocks of AHA

Overview

The cognitive architecture provides a general meta-model that could be implemented in specific computer algorithms, usually involving a procedural agent-based “machinery” (Sun, 2009). The architecture in AHA consists of simple generic units that are combined and extended to build more specific adaptive evolutionary models. It is implemented at an intermediate level of functional modules and their connecting pathways: it works above the level of individual neurons but below symbolic or other high-level representations. In the Online Supplement we provide a brief overview of the most important theoretical concepts that provide the major building blocks for the AHA architecture: the survival circuit, emotion, motivation, global organismic state, arousal, attention and prediction-oriented cognition with elementary subjective simulation.

The adaptable cognitive architecture (Fig. 1) is the main feature of an evolutionary agent-based model system—the AHA model—that includes the environment and populations of agents that evolve by natural selection. The environment includes various objects, such as food items that serve as the source of energy and predators that prey on agents. Each agent is a whole virtual organism with a unique genome, simple hormonal system, physiology, neurobiology and behavioral repertoire.

Overall, control of behavior in the organism is achieved through an evolved balanced dialogue between ancient and continuously adapting programs linking perception, cognition and behavior. The central component of AHA architecture is the survival circuit (LeDoux, 2012, see Online Supplement) integrating multiple sources of perceptual information into a unitary internal state. The internal state depicted by the survival circuit is categorical but also has a continuously graded activation level or motivation. The agent has several survival circuits that encapsulate different emotional states: fear, hunger, thirst, reproductive drive etc. These internal states trade priority with each other by competing through lateral inhibition so that only one becomes the global organismic state (GOS). The level of motivation for this state becomes the arousal of the agent. The global organismic state exerts an arousal-attuned top-down attention modulation effect suppressing all perceptions that are not linked to the current GOS.

The life cycle of the agent involves a constant flow of perception → action: adaptive decision making and naturalistic behavior in the model environment. However, most perceptions will not lead to any action. The GOS determines which behavioral action is to be executed. Actions, defined structurally (Hogan, 2015), are selected from a fixed repertoire through various behavior selection paradigms (see below). Agents that survive and successfully secure resources (grow) over the life cycle can pass on their genetic information to the next generation. The offspring genome is subject to genetic recombination and random mutations. Over repeated generations, the genetic algorithm leads to evolutionary adaptation of the agents and the gene pool (Banzhaf & Eeckman, 1995; Huse, Strand, & Giske, 1999; Ruxton & Beauchamp, 2008; Strand, Huse, & Giske, 2002).

The AHA model uses nonparametric functions that are based on nonlinear interoperation (Ioannou & Pittilides, 2008; Szabados & Vertesi, 1990). This makes it sufficiently generic, free of specific theoretical assumptions, and hopefully well-suited for a range of data-driven models. We have implemented AHA as a programming framework written in object oriented Fortran (see the Online Supplement for more details) provided as open source at http://ahamodel.uib.no.

The survival circuits: Perception and motivation

The perception mechanism allows the agent to obtain information about its own physiological states, physical properties of the environment, as well as various spatial objects. In the simplest implementations perception does not require recognition. In more complex models object recognition can be implemented by connectionist modules mapping fuzzy perceptual patterns into specific sensory signals (see Albantakis, Hintze, Koch, Adami, & Tononi, 2014; Strand, Huse, & Giske, 2002). Sensory signals that are fed from the agent perception are mapped to the neuronal response by the agent’s individual genome. The relationship between the perceived sensory stimulus P and the resulting neuronal response R (see Fig. 1) is defined by additive sigmoidal functions (see Online Supplement, 2.1). Since the work of Cybenko (1989), the sigmoidal function is widely used for input-to-output mappings in the neural networks (Brette et al., 2007; Churchland & Sejnowski, 1992; Lytton, 2002), for example nonlinear perceptual stimulus integration (Gollisch & Herz, 2012), stimulus categorization (Mysore & Knudsen, 2012) and gain modulation (Brozović, Abbott, & Andersen, 2008). AHA extends this by combining several sigmoidal functions, which can represent more complex combinations of sigmoidal, concave, convex or nearly linear relationships (Andersen et al., 2016; Eliassen et al., 2016; Giske et al., 2013, 2014).

Outputs from different neuronal response functions that contribute to the same survival circuit are integrated (Fig. 1), giving a single value of motivation (M) for each circuit. This initial motivation value (primary motivation Mf, Fig. 1) can be modulated by genetic or non-genetic factors (e.g. hormones influenced by age or life cycle stage of the agent), resulting in the final motivation (Mf, Fig. 1). Reproductive motivation can for example be suppressed in young agents allowing accumulation of an internal hormone-dependent reproductive factor without raising reproductive motivation.
Affective competition and the global organismic state

Once the final motivation values \((M_f, \text{Fig. 1})\) are calculated for all survival circuits, they compete with each other to become the next GOS of the agent. If no incoming motivation is strong enough, the previous GOS is retained. Competition between the incoming motivations and the current GOS is based on a dynamic threshold (for details see Online Supplement), which is an inverse convex function of the current arousal level \(G\). Briefly, if the current arousal is low, a relatively high competing motivation is required to win competition with the current GOS. Conversely, when the current GOS arousal is high, just a marginally higher incoming motivational value is enough to become the next GOS (see Online Supplement 2.2 for details). This makes it relatively easy to switch the internal state when the arousal is high, but more difficult when it is low, providing for continuity of the internal state. The dynamic threshold reduces dithering-like switching between different behavioral actions (see Bryson, 2000; Lewis & Canamero, 2016; McFarland & Sibly, 1975) which is considered maladaptive for both animals (Barnard, 2004; McFarland & Sibly, 1975) and artificial agents (Lewis & Canamero, 2016). This issue is common in decentralized bottom-up architectures (Bryson, 2000), for example, a robot trying to satisfy several needs simultaneously could keep dithering without guaranteed gratification of any of these needs. In spite of behavioral persistence, the agent should be able to switch its internal state easily when a high arousal GOS is confronted with a high-incentive stimulus, e.g. if a very hungry or aggressive animal suddenly sees a predator in proximity.

When the current GOS is not outcompeted by an incoming motivation, the old GOS is retained, but the arousal level is reduced (arousal dissipation). Maintaining a high level of neuronal activity is energetically costly (Ames, 2000; Niven, 2016) and involves synaptic depression due to neurotransmitter exhaustion leading to habituation (Christoffersen, 1997). This will also prevent the agent from getting stuck on a specific GOS as it will ultimately be encouraged to switch to a different state. The combination of the GOS dynamic threshold mechanism and spontaneous dissipation of repeated arousal state results in substantial continuity of the dominant internal state and can produce agents with various degrees of behavioral flexibilities (Landsrød, 2017).

Attention control

The GOS at time \(t\) modulates the agent’s perception at the next time step \(t + 1\). Each of the perception signals that is not associated with the current GOS is suppressed by the attention modulation factor (see Online Supplement 2.3). This mechanism provides an effective top-down control of perception that dynamically depends on the current GOS. For example, a frightened agent in a highly aroused state would obtain weakened perceptual signals of food and hence not be distracted from its anti-predator response.
Coping with novelty and uncertainty

Coping with novelty is a special problem in both behavioral ecology and robotics. Although a live organism and robot (Oudeyer, Kaplan, & Hafner, 2007) can use intrinsic exploratory activity to learn from the environment, this would not work when it is suddenly confronted with a totally novel context for which no information—and no expected utility—is available. Confronting an animal with a novel environment is frequently used to test coping strategies and personality because such a test often reveals a wide range of individual differences (e.g. Budaev & Brown, 2011; Sih et al., 2004). In AHA, the agent can adaptively deal with such situations through the so-called hope function. Briefly, the expected utility of the novel option is constructed from the pattern of the last perception memory (see Online Supplement 2.4). This can facilitate adoption of the novel option by the agent in situations of diminishing returns. By changing the parameters of the hope function it is possible to produce a range of strategies from novelty avoiding to novelty seeking, which provides a mechanistic tool to model novelty bonuses (see Kakade & Dayan, 2002).

Decision making and action selection

The GOS determines which behavioral action shall be executed. AHA allows various behavior selection paradigms (Bryson, 2000; Seth, 2007; Tyrrell, 1993). In the simplest case the GOS fully dictates the action. For example, if the agent is in the hunger state and there is at least one food item in perception, “eat the nearest food item” action is executed. If the agent perceives no food in its vicinity, a Gaussian random walk can be executed to search for food. Because a long walk puts the agent into a novel environment, the walk size could be determined by the hope function mechanism: If local food availability is diminishing, the expected utility of a longer walk would increase. Thus, the agent could optimize its exploration/exploitation ratio by producing Lévy-like movement patterns known to facilitate finding of rare but clumped food in stochastic environment (Bartumeus & Catalan, 2009; Reynolds, 2015, 2018; Wosniack, Santos, Raposo, Viswanathan, & da Luz, 2017).

In more complex models, the action selection procedure within a GOS can involve competition between several potential actions that best optimize certain criteria (see also Arkin, 1998; Brooks, 1991). This could involve prediction-oriented mechanisms, e.g. predicted reward or arousal and also predicted response in other agents. Each survival circuit can have its own action selection implementation that is activated if this circuit is the GOS. Thus, AHA allows various hierarchical organizations with competing units at each level.

Dual-process framework

The dual process theories of mind postulate two basic modes of operation: autonomous/reflective and predictive/reflective (Anderson & Lebiere, 2003; Irlbacher, Kraft, Kehrer, & Brandt, 2014; Vaughan et al., 2016). A similar distinction is made in the animal learning and cognition literature, e.g. between associative and cognitive (goal-directed) responses (Dickinson, 1985, 2012; Toates, 1997). Various arbitrary combinations of these two modes can be implemented in AHA, e.g. a fixed stimulus-response reaction for fear and a complex selection of optional food items to minimize expected hunger.

Elementary self-awareness and neural reuse

One possible prediction-oriented action selection paradigm is based on what we call elementary self-awareness. It is defined here as the ability of the agent to assess its own internal state and use this information for decision-making and action selection. In AHA, emotions that are activated by specific survival circuits represent such internal states. The emotional arousal represents a common subjective currency for decision-making. Thus, the agent selects and executes the action that optimizes the expected emotional arousal (see Online Supplement sect. 2.5 for more details). Consequently, prediction of the environment by the agent is mediated by prediction of the agent’s own internal state. This reduces a virtually infinite number of possible environmental states and parameters to a small set of internal subjective variables. In effect, decision making is simplified due to grossly diminished combinatorial complexity: now the agent does not need to calculate utility expectations over all possible environmental factors and their effects on all its internal states. In AHA, this computational challenge is moved from individual learning to adaptive evolution of the population gene pool. We propose that subjective prediction mediation may provide one solution to the computational complexity issue in decision making theory (Bossaerts & Murawski, 2017).

The notion of elementary self-awareness in AHA is intimately linked to specific action rather than abstract information processing: it involves computationally simple subjective simulations of the affective value of such actions. Conceived in this way, elementary self-awareness would not require complex dedicated neural structures. Instead, it reuses already existing survival circuits that conduct affective compuation (neural reuse, see Anderson, 2010). However, it adds a relatively simple component for reentrant1 activation of the existing survival circuit. Thus, AHA is consistent with the emerging view that components of awareness and consciousness may not require complex dedicated brain machinery and could emerge even in organisms with simple nervous systems (e.g. Barron & Klein, 2016).

Computational example: Can simple self-awareness evolve?

We illustrate the feasibility of the AHA framework by a model of elementary self-awareness. The model is similar to the fish system developed by (Giske et al., 2013, 2014). The source code and detailed documentation are described in (Budaev, 2018). A population of plankton-eating fish lives in a vertically stratified environment where their food performs diel vertical migrations (moving upwards in the water column at night and downwards during the day). Pelagic water masses have strong and predictable vertical gradients of light intensity that affect both prey encounter rate and predation risk. All interactions in this model are local and based on vision. That is, predators and prey have no knowledge outside of their limited visual sensory range. Visibility of an object (visual range) is a function of its size, contrast and illumination level (Aksnes & Urte, 1997). For both the fish and its prey, the risk of being detected by a predator increases with light intensity and prey size. Competition for food and dilution of risk could make opposing effects on the profitability of staying close to conspecifics. This simple system provides physical gradients, environmental dynamics and stochasticity.

To find food, the fish must follow the constantly changing vertical distribution of its prey. The energy gained from feeding is spent on activity and basic maintenance with surplus energy allocated to growth and reproduction. If a fish does not eat, it will quickly die from starvation. The neurobehavioral system of the fish is built according to the above architecture and has three survival circuits: hunger, fear and reproduction. It also has a behavioral repertoire including various movements (including vertical migrations) immobility, escape, long-range migration and feeding on plankton. Behavior selection at each time step minimizes the expected negative emotional arousal by reentrant assessment as described above. All behaviors are selected on this basis, i.e. the agents act based on elementary self-awareness. Trading between feeding, predator avoidance, avoidance of competing conspecifics and attraction to conspecifics to dilute risk would involve

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1 Reentrant processes involve repeated activation loops across neuronal ensembles and are thought to underlay conscious experiences (see Baars, 1995; Edelman, 2004).
adaptation. Thus, it represents a viable tool for the study of adaptive mechanisms that shaped cognition and subjective phenomena through evolution.

**General discussion**

The major paradigm in psychology, ethology and neuroscience is that behavior is just a series of responses to stimuli (Edelman, 2016; Heisenberg, 2014). There is, however, a growing recognition that much of the behavior is in fact generated endogenously (subjectively) by the animal, has intrinsic spontaneity and indeterminacy (Brembs, 2011; Maye, Hsieh, Sugihara, & Brembs, 2007), and could often be based on internal predictive models involving the subjective state (Dickinson, 2011, 2012) even in animals with simple nervous systems (Dyer, 2012; Giurfa, 2013; Haberkern & Jayaraman, 2016; Loukola, Perry, Coscos, & Chittka, 2017; Menzel & Giurfa, 2001; Srinivasan, 2010; Webb, 2012). For example, recent evidence indicates that even seemingly hard-wired phototaxis in *Drosophila* involves quite complex value-driven computations dependent on the internal state of the animal (Gorostiza, Colomb, & Brembs, 2016). This suggests that environmental stimuli "modulate" rather than "elicit" behavioral actions, and that perception is an active process, as emphasized by the Bayesian active inference framework (Clark, 2015; Pezzulo, Rigoli, & Friston, 2015; Seth, 2013; Seth & Friston, 2016). AHA is consistent with such an "agency" perspective. Indeed, the behaviors of AHA organisms is generated endogenously as the survival circuits trade priority internally, and are modulated (rather than fully caused) by the environmental stimuli.

**Internal architecture**

A major problem of naturalistic behavior in a stochastic environment is the combinatorial explosion (Bryson, 2000; Railsback & Harvey, 2013): the agent cannot recalculate every possibility at any time and environmental condition, rather sensible architectural constraints on perception, decision making and action must be imposed (Bossaerts & Murawski, 2017). Mapping unconstrained stimuli to a specific response does not scale up to realistic environments and quickly reaches an almost intractable computational complexity, thereby making strictly bottom-up "behaviorist" approach untenable (Tsotsos, 1995). More generally, the frame problem of the computational theory of mind illustrates how non-modal, unencapsulated processes are computationally infeasible (Shanahan & Baars, 2005). A surprisingly similar emphasis on the importance of internal architecture and phenotypic constraints can be found in the study of behavioral ecology and evolution beyond the "phenotypic gambit" (Andersen et al., 2016; Giske et al., 2013, 2014; Rubin, 2016; Springer, Crespi, & Swanson, 2011). The cognitive architecture in AHA mechanistically implements active perception and internal subjective evaluation thereby providing a unifying framework for the study of cognition and behavior in an ecological and evolutionary perspective. Furthermore, it emphasizes the importance of subjective phenomena in behavior of even simple organisms.

**Subjective phenomena**

Subjective phenomena are 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 subject (Searle, 2002; Zahavi, 2005). Subjective phenomena have long been an anathema in psychology and neuroscience, especially when non-human species were concerned (Baum, 2005). Even though the study of subjective phenomena have been revitalized in psychology and neuroscience (e.g. Barrett, Mesquita, Ochsner, & Gross, 2007; Searle, 2000), they are largely ignored in animal behavior, behavioral ecology and evolution. However, we are now in a position to recognize the importance of subjective phenomena not only in humans, but also
in many non-human species (Baars, 2005; Boly et al., 2013; Butler & Cotterill, 2006; Dawkins, 2015; Edelman & Seth, 2009; Gallup, 1985; Griffin, 1993; Rogers, 1997; Schönfeld, 2006) and even implement them in artificial agents (Goto & Hayashi, 2008; Reggia, 2013).

Elementary self-awareness that builds on reuse of existing neural circuits for simple forms of internal reinertant simulation provides the simplest foundation for subjective experience that can be found in organisms with more complex nervous systems. For example, consciousness is thought to build on reinertant neural activations (Baars, 1995; Edelman, 2003, 2004). Thus, AHA provides the starting point for further models that implement the main properties of conscious experiences such as qualia with unity and continuity (Searle, 2000, 2002). In doing so, it links elementary building blocks thought to produce subjective experiences with fitness and evolutionary adaptation of the integrated phenotype.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at https://doi.org/10.1016/j.bica.2018.07.009.

References
