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RESEARCH ARTICLE

ONE Function for the Anterior Cingulate Cortex and General AI: Consistency Curation

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Abstract
Control is essential in all complex systems serving any purpose, and cognitive control is claimed to fill a pivotal role for the cognition of natural agents. The Anterior Cingulate Cortex (ACC) is a neural structure, widely believed to be involved in cognitive control. In the human brain, the ACC undoubtedly takes a center position and features several peculiarities. It has been implicated in a wide range of tasks ranging from sensing pain and autonomic regulation to high-level executive functions like error monitoring and abstract control. A sketch how this seemingly irreconcilable plurality can be understood as manifestations of only one general process working in diverse contexts on different content is presented and also how this constitutes evidence for a specific cognitive architecture. Going beyond extant proposals for ACC function, the here presented one recommends an embedding into a very general overarching model of cognition. Discrepancy monitoring highlights deviations between predictions derived from memory content and current activations. A process doing this has recently been proposed as central to the 'Ouroboros Model' under the title of 'consumption analysis'. It is claimed that ONE functional account centered on consistency checking and, based thereupon, the overall minimization of discrepancies ("consistency curation and cultivation") can parsimoniously explain the plentitude of reported observations for the ACC, thus shedding new light on the neural computations, which form the foundations of cognition and, finally, consciousness. A specific "natural" reconciliation of various current conceptualizations and theoretical models is offered, which points out promising directions for future modelling efforts and attempts to harness the findings generally for artificial intelligence.

Keywords: cingulate cortex, agranular, von Economo neurons, monitoring, conflict, discrepancy, attention, bias, predictive coding, consumption analysis, Ouroboros Model.

Introduction

The anterior cingulate cortex (ACC) is part of the cingulate cortex, a large medial region encircling the corpus callosum. It is connected widely to the prefrontal and parietal cortex as well as to motor and visual systems. ACC, here mainly seen as Brodmann's areas 24, 32, and neighboring, is one of the central network hubs in the human brain according to several definitions (van den Heuvel and Sporns, 2013; Chaudhuri et al., 2015). The ACC is characterized by a lack of a granular layer IV. Together with the insular cortex, ACC is home to a peculiar class of neurons, in the observed relative quantities only found here in the human brain, i.e., spindle cells or Von Economo Neurons (VENs). Going much beyond what is possible to describe in a short position paper, it seems that the anterior insular cortex (AIC) serves similar functions as the ACC. In particular, AIC has also been hypothesized to work as comparator (Allen et al., 2016a). While four main subdivisions for the anterior cingulate cortex have been suggested as serving executive, cognitive, emotional and evaluative functions, extensive evidence of significant overlap between regions activated during pain, negative affect, and cognitive control points towards an integrated adaptive control hypothesis with the ACC involved to a large extent in aversively motivated action (Shackman et al., 2011).

Essential to a function centered on comparing new with old content and doing this similarly for real compared to envisioned representations, distinguishable main networks have been found lately in human individuals, differing in their inclusion of hippocampal circuits and exhibiting interdigitated lay-outs in several cortical areas including neighbors of the ACC (Braga & Buckner 2017).

In a self-reflective and self-consistent manner following the Ouroboros Model, an overall sketch is first attempted here before subsequently filling in details (Thomsen, 2010).

Documented functions of the anterior cingulate cortex

The anterior cingulate cortex has been observed being involved in markedly different contexts. There is ample evidence for the ACC taking part in cognition, decision making and emotional functions as well as in the regulation of physiological processes, such as blood pressure and heart rate. Among the key functions ascribed to the anterior cingulate cortex are:

- Control
    - Anticipation and preparation before (difficult) task performance
    - Attention
    - Error detection
    - Learning
    - Conflict monitoring
- (Regulation of) Emotions
    - Stress
    - Appraisal
    - Bias
    - Curiosity
- Pain
- Consciousness

Directly underpinning these functions, particular anatomical features have been found in the ACC.

- Anatomic peculiarities
    - No granular layer
    - Von Economo Neurons (VENs)
    - Asymmetry

Without any claim to completeness, selected findings are briefly presented in the following one after the other in an attempt to develop a coherent perspective and to build up the case for an encompassing conceptualization. Such is briefly outlined with the Ouroboros Model in the second section of this paper; and how this could match with previous proposals and prevailing theories of cognition and consciousness is delineated towards the end. While it is clear that only a coarse sketch can be presented here it is intended to self-consistently offer a fresh integrative view as well as pointing out promising starting points for more detailed investigations and future utilization.

Control

It seems that one common theme, which is linked with the Anterior Cingulate in many tasks, can be captured under the heading of 'control' (e.g., Paus, 2001). Here, this is understood as the truly central function of directing resources and actively steering the behavior of an actor aiming to achieve some goal. There is a direct connection to cybernetics' use of the term as a meaningful first step in any direction presupposes sensing the current status in a given context. The simplest control circuits keep some parameter in a predefined range by checking for deviation/discrepancy and actively steering against any divergence, thus constraining that controlled parameter to its allowed range. More advanced control systems steer effectors depending on the current status and the intended condition. The ACC has been claimed to be important for interpreting outcome information with respect to the current task context to guide action selection (Walton and Mars, 2007). The observed ACC activation is specific to the detailed conditions and overall context (Braem et al., 2016).

Anticipation

The ACC has often been implied in anticipatory activity (e.g., Murtha et al., 1996). Enhanced activation has been reported during preparation for difficult tasks, and, especially when a new task-set is demanded with changed requirements, often after a 'reset' ensuing a previous attempt, which did not suffice to reach a goal. Focusing on the actually relevant features is essential for avoiding interference and errors. This can be seen as filtering and noise-suppression, i.e., highlighting content and concentrating on it. Strong and clear anticipation for a simple stimulus has been found to enable fast visual awareness of its presence (Railo et al., 2015). ACC activity varies with changes in response expectancy; it has been proposed that it is strongly related to the process of response selection, which determines subsequent action (e.g., Gajewskia et al., 2008; Scheibe et al., 2009). Reversible inactivation of the ACC impairs prospective memory, i.e., the anticipation of upcoming correct response locations, as well as selective visual attention, i.e., there is increased distraction by task-irrelevant stimuli (Kim et al., 2016).

Attention

Flexibly shifting the focus and allocating cognitive resources to where they are required most urgently can be taken as prime function of attention, which is especially demanded when routine stimulus → response associations turn out as not sufficient for successful performance. Very coarsely, attention can automatically be drawn to a feature, a specific location or object by a salient stimulus (bottom up), and it can be allocated (top down) as a result of internal (cognitive, often conscious) processing. Anticipations guide attention, e.g., bias sensitivity, for specific features while attenuating responses to disturbances from outside the actually relevant (feature-) area; i.e., signal / noise is enhanced. In accordance with this two-faced characteristic, attention not only directs activity, it is also an immediate consequence of many (alerting) processes. The ACC has been reported to form part of a distributed attention network in the human brain (e.g., Bush, Luu and Posner, 2000). "Attention for action in context" has been suggested as most adequate description of ACC functions (Luu and Pederson, 2004). ACC activity predates excitation of neurons in the locus coeruleus, which in turn causes changes in pupil diameter as a response to surprise and cognitive effort (Joshi et al., 2016). Lesions of the ACC have (surprisingly) small effects. Monkeys with ACC lesions were little impaired in updating their choices; they displayed difficulties in sustaining a correct response in a changing environment and took into account only the immediately preceding information (Walton and Mars, 2007). Relating to a vastly generalized facet of attention, ACC has been hypothesized to supply a "global energizing factor", which stimulates action and decision making. When the anterior cingulate cortex is severely damaged, this can result in akinetic mutism (Holroyd and Yeung, 2012). Dorsal ACC and lateral prefrontal cortex appear to play critical roles in acts of volition (Mulert et al., 2005; Gmeindl et al., 2016); activity there is reduced during hypnosis (Jiang et al., 2016).

Detection of errors & surprise

A role for the ACC in the detection of errors during task performance has been reported in a large number of studies (e.g, Bush, Luu and Posner, 2000). There is overwhelming evidence, which links a centrally sensed evoked scalp potential observed after the commission of an error "ERN" or "N2" to activation in the anterior cingulate cortex (e.g., Falkenstein et al., 1990; Gehring et al., 1993). A potential very similar to the error negativity is evoked at longer latency when subjects are told that they have made a mistake (e.g., Holroyd, Dien and Coles, 1998). Some activation in the anterior cingulate cortex can be detected even when an individual is not aware of his error or conflicts but awareness increases that activity (Luu and Pederson, 2004). The anterior cingulate cortex signals not only deviations to the negative but also to the positive: better than expected outcomes also activate the ACC (Ferdinand et al., 2012; Shenhav et al., 2013). In well-known oddball experiments, ACC activation is quite generally observed when an expectation, e.g., in a stream of stimuli, is violated; this can be simply described as surprise (Crottaz-Herbette and Menon, 2006). Looking in detail, the evoked potentials for new versus deviant items in a sequence are similar but differ in their fine timing and topographies (Noyce and Sekuler, 2014).

Reward based learning theory

Errors need not be only seen as negative; they can trigger immediate correction or improvement and, on a longer time scale, also learning. Thus, they point and pave the way for better performance in the more distant future. Reward based learning theories see the anterior cingulate cortex as serving these needs (Ridderinkhof et al., 2004). Effort, which is amplified after an error, is linked to enhanced ACC activation. There are significant individual differences in attitudes and in activations evoked by errors (Moser et al., 2011). Regions in the dorsolateral cingulate cortex were found to be especially involved in the implementation of fast adjustments in a close coupling to lateral prefrontal cortical areas (Garavan et al., 2002). Errors have to be remembered in order to avoid their repetition. Memorized values in turn inform decision making. The anterior cingulate cortex has been claimed as essential for the selection of actions, being also a main target of dopaminergic inputs from the ventral tegmental area (VTA) of the brain reward system, active for previously pleasurable memories (Paus, 2001). In the other direction, the ACC appears to first signal some results to the reward system, to the amygdala and also to the hippocampus for establishing distinct memory entries (Parkinson et al. 2000; Pourtois et al., 2010; Brunce et al., 2013; Thomsen, 2017). Later on, for memory retrieval, direct reverse connections will contribute relevant information like concerning context and expected rewards for a task-set for its new handling by the ACC (Holroyd and Coles, 2002; Rajasethupathy et al., 2015).

Detection of conflicts

Reliably sensing conditions under which errors are likely to occur is essential for avoiding them. ACC activity has also been observed during correct responses under conditions of increased response competition in the same region as in cases when errors actually occurred (e.g., Carter et al., 1998;

Botvinick et al., 2001). ACC activity is intensified and prolonged in conflict trials that require revision of a prepared response plan (e.g., Gajewskia et al., 2008). When there are conflicting response tendencies at the same time the anterior cingulate cortex appears to determine which should be followed (e.g., Holroyd et al., 2004). Conflict, quite generally, has been found to induce negative affect (Braem et al., 2016).

Cognitive Dissonance

When people are confronted with information that is inconsistent with their beliefs they feel cognitive dissonance. Holding two or more contradictory beliefs, conflicting ideas, or values at the same time causes mental stress and discomfort, which has been described long before any involvement of dorsal anterior cingulate cortex in these conditions had been observed (Festinger, 1957; van Veen et al., 2009). Disgust or watching unfairness, which activate similar ACC areas, might be characterized as falling into a related category (Corradi-Dell`Acqua et al., 2016). ACC activation from “low level” conflicts is diminished if subjects engage in the affirmation of “high level” values (Proulx et al., 2012).

Ironic rebound

Tasks demanding somewhat self-contradictory effort like thought suppression appear to offer a particularly effective way of provoking cognitive conflict or dissonance. Many studies have shown that "ironic rebound" arises after individuals strived to suppress particular thoughts, attitudes, beliefs, or emotions (Wegner, 1989). The fact that suppressed cognitions and feelings resurface, even more intensely than before, has been explained by a two component model of cognitive control. While a "monitor" is hypothesized trying to detect the suppressed content, an "operator" inhibits them. According to Wegner, Wenzlaff, and Kozak (2004), the anterior cingulate cortex might underpin the operator, by facilitating the inhibition of unsuitable cognitions or emotions. The important point would be that "monitoring" necessitates a comparison and some inevitable type of activation to start with. Not only has this been described by Sigmund Freud (1900), there are also recent reports that suppressed thoughts often surface in dreams (Wegner et al., 2004).

Emotions and their regulation

Committing errors is unpleasant, probably more so than a mere feeling of inconsistency. The amygdala, which is amongst others tightly connected to the ACC and insula, has been strongly implicated for mainly negative emotions, in particular for the formation and the storage of memories associated with emotional events (e.g., Etkin et al., 2011). In a rare case where ACC and amygdala activation could be studied intra-cranially, activity elicited by novel stimuli in the ACC always preceded amygdala activation (Pourtois et al., 2010). Later on, memorized emotional tags are employed in decision making (e.g., Paus, 2001). In addition to first establishing an emotional tag, and thereafter using memorized evaluations for decisions and action, the ACC appears to be involved also in regulating emotion in a manner following the same lines as for steering other behavior (Compton et al., 2008). This implies second-order emotions and subsequently second-order coping and behavior adaptation. Cells in the anterior cingulate have been found to signal rewards, both, for experienced and for fictive outcomes (Hayden et al., 2009). Successful (and more so for difficult) conflict resolution has been demonstrated to provoke positive affect (Schouppe et al., 2015). Beyond the involvement in temporary emotions, the long-term trait of subjective happiness was found to be correlated with grey matter density in rostral ACC (Matsunaga et al., 2016).

Appraisal and Bias

Appraisal theories claim assessments, i.e., appraisals along certain selected dimensions, as essential and ground-laying components of emotions (Moors et al., 2013). Affect delivers (often valid) information for an agent on the one hand side (Schwarz and Clore, 1983), and, on the other, at (about) the same time, emotions bias perception and direct action to relevant directions (Ciompi and Panksepp, 2005). Positive mood induces preparatory activity in the ACC, actually biasing problem solving towards creative insight solutions (Subramaniam et al., 2008). The ACC and frontoinsular cortex are the two areas, which have been found to be consistently activated by different types of jokes (Watson et al., 2007).

Curiosity

Differing in at least the non-definitiveness or -permanence of its objects from more genuine affects, curiosity often is also considered an emotion fueling motivation. It has been linked to gaps in knowledge and understanding (Loewenstein, 1994). Humans and animals actively seek to reduce uncertainty, which is experienced as disturbing. This goes as far as humans' inherent desire to resolve uncertainty can actually induce them to perform specific actions despite expecting direct negative consequences (Hsee, 2016). Induction of perceptual curiosity has been shown to activate the ACC (Jepma et al., 2012).

Pain, Pleasure and Empathy

One can claim that errors and conflict are painful and that consistency monitoring is the seamless and natural expansion of checking for bodily integrity and the wellbeing of any agent; the ACC has been implicated in a network sensing pain and also coping with it (Hsieh et al., 1999). There is evidence for at least some overlap between cingulate and insular areas devoted to nociceptive and empathic pain (Zaki, et al., 2016; Corradi-Dell`Acqua et al., 2016). Consistently, a very popular pain killer has been found to attenuate error evaluation; especially a reduction of PE, the positive potential usually following ERN, has been observed (Boldt and Yeung, 2015; Randles et al., 2016). Recently, empathy reduction as side effect has been reported in subjects consuming the same common pain killer (Mischkowski et al., 2016). While the ACC has earlier been implied as part of the "pleasure system" in the brain, - subjects implanted there with electrodes kindle themselves - , consensus in the meantime appears to see exciting the ACC as producing “want-” rather than genuine pleasurable states (Berridge et al., 2015).

Consciousness

Curiosity, emotions, pain, pleasure and empathy are usually tightly associated with awareness and conscious perception, and, in particular, the ability of a subject to report about it. Furthermore, evidence has been found for a close relationship between conscious effort and anterior cingulate cortex activity (Mulert et al., 2005). Patients with diverse disorders of consciousness showed diminished ACC activity during the perception of self-related stimuli (Quin et al., 2008). As just one more exemplary hint at clinical aspects, it has been suggested that dysfunction in attention-deficit/hyperactivity disorder (ADHD) is linked to decreased connectivity between the dorsal anterior cingulate and the precuneus (Castellanos et al., 2008). Dorsal cingulate cortex and the precuneus, both, are close neighbors to the ACC (Cavanna 2007). Their activity has been reported to tightly correlate with consciousness; functional integrity of Posterior Cincgulate Cortex connectivity appears necessary for maintaining consciousness of the external environment (Herbet et al., 2014).

Anatomical peculiarities

Studies in monkeys indicate that the ACC is widely connected to prefrontal, orbitofrontal, insular and anterior temporal cortices as well as to the amygdala, hypothalamus and various thalamic nuclei (Öngür and Price, 2000). Similar to many areas in the human brain, a hierarchical ordering is observed in the medial prefrontal cortex with a rostro-caudal gradient of abstraction in correspondence to the connected regions (Zarr and Brown, 2016). Compared to other areas, the anterior cingulate cortex exhibits some features, which are not found at all outside this region, or not found in similar extensions or configurations.

Agranular

Conventionally, the anterior cingulate cortex is seen as constituting a less advanced version of cortical circuitry as the ACC does not have a granular layer IV. Interestingly, it shares this feature with the neighboring motor cortex, and it has been hypothesized that ACC actually is an evolutionary late extension, optimized for specific tasks providing output from the top of a processing hierarchy (Allman et al., 2001). Efferent connections of the ACC connect to superficial layers 1 and 2 in eulaminate cortex, which indicates modulatory influence there (Barbas, 2015).

Von Economo Neurons, Spindle Cells

There is no doubt that spindle cells, Von Economo Neurons (VENs), are a recent addition to cerebral circuitry, restricted to humans, apes and a few more animals owning large brains (Allman et al., 2001). The cell bodies of VENs are about 4 times as voluminous as more common pyramidal neurons, which suggests that they bear large, rapidly conducting axons. They are also characterized by much more locally restricted dendritic arbors. The first feature can be interpreted as enabling the rapid transmission of strong signals over long distances, whereas the second perfectly fits with the accurate sensing of tightly localized activations and also with a special computational relatively simple function (Watson et al., 2006).

ACC Connectivity

In a pattern of wide functional connectivity of the ACC, negative correlations for activities have been found between ACC and some subcortical circuits (Margulies et al., 2007). Cingulate cortices have been claimed to occupy central positions in a wide-ranging and coarse default mode network (DMN) and in a salience network. Here, it shall be highlighted, that not only exciting but also dampening influences are exerted by the ACC; in particular, the cerebellum appears to be inhibited by ACC activations.

Laterality, source of hemisity

While many monitoring processes can run in parallel, ultimately, overall control for any consistent behavior has to be somehow bundled in one entity. On an anatomical level, the ACC seems to offer a good candidate basis as it is one of very few structures in the brain, which exhibit consistent differences in the two hemispheres with the dominant one containing significantly more neurons; this has been taken as support for a concept of hemisity (Morton, 2013). The idea here is that the dominant executive system, the basis for the 'will' of an individual, must physically reside in one hemisphere.

ACC Functions from the point of view of the Ouroboros Model

In order to elucidate the participation of the ACC in each of the highlighted functions, the main tenets of the Ouroboros Model will first be introduced briefly in the following. In a fully self-reflective and self-consistent approach adhering to the principles of the Ouroboros Model, the aim here is to initially outline a coarse but overarching sketch on a conceptual level before delving into more intricate details and finally elaborating mathematical formalizations, quantitative simulations and some utilization (for implementations) in the future.

The Ouroboros Model

The Ouroboros Model has been introduced recently in an attempt to explain a wide range of findings pertaining to cognition and consciousness of natural and also artificial agents (Thomsen, 2010-2015). The Ouroboros Model offers a widely applicable "algorithmic backbone"; it has its starting point in, and it puts its focus on, every-day (human) experience and commonsense reasoning. There are only two basic ingredients, which are claimed as responsible in their proper combination for the core of all (human) perception, cognition and action including, e.g., memory retrieval and problem solving:

- Action- and memory structure (organized into schemata as basic building blocks)
- Cyclic iterative processing (with 'consumption analysis' as the main process in a loop)

The decisive novel step is to explicitly "make the wheel turn", i.e., the results of one processing cycle are dynamically used to actively control the next iteration, steering an overall advantageous course over time comprising the incessant autocatalytic generation of new memory content, self-guided to where the need arises.

Action and Memory Structure

The Ouroboros Model holds that memory entries (like for episodes or actions) are organized into cohesive chunks called schemata; these are distinct combinations of features, which have been experienced at least once before as belonging together (Thomsen, 2010).

New entries as a record of any current activation are preferentially committed to memory at times marked as important by consumption analysis. Building blocks include whatever representations are active at the time when such a 'snapshot' is taken, comprising sensory signals, as well as abstractions, i.e., previously laid down representations encompassing also features relating to probable transients and causal structure, just as prevalent emotions and longer lasting moods. At subsequent occasions, newly bound structures will be employed in the same way as earlier established schemata. Only in extreme cases these 'snapshots' will be full-fledged "core dumps" of the type proposed for flashbulb memories (Brown and Kulik, 1977).

A rather well-defined parcellation of memory content is held as most important for the proposed processes, which work on this very basis; it allows the confined activation of complete entries from only fragments of the original content, i.e., pattern completion, the generation of anticipations and relevant predictions, and, at the same time, an activated frame enables straightforward monitoring of current activity in the light of previous experience. From a finite set of building blocks practically unlimited diverse concepts can assembled.

Directly relevant to questions of experience and self-consciousness, such snapshots of all related and strong activity in a brain will also contain and link features of the actor herself. These can span many levels of abstraction, including bodily signals, emotions, motivations, as well as personal goals; somatic markers are but one example, while qualia and higher order thoughts follow suit (Harnad, 1990; Damasio, 1996; Rosenthal, 1997; Thomsen, 2011b).

Cyclic Iterative Processing

The Ouroboros Model is built around a self-reflective and self-referential recursive process with alternating phases of data-acquisition and -evaluation, comprising the main steps: ... anticipation, action / perception, evaluation, and new anticipation, .. . These steps are concatenated into full repeating cycles evolving over time. In the picture and words of medieval alchemists, the serpent called the Ouroboros devours its own tail (Thomsen, 2010). Anticipation can be seen as lying at the very heart of the Ouroboros Model.

A central monitor-process termed 'consumption analysis' is intermittently checking how well expectations triggered at one point in time fit with successive activations.

The outcome of this monitoring, a universal form of consistency checking, generally marks discrepancies and leads to impacts on various (time-) scales: locally, it highlights “open slots”, i.e., attributes that belong to the one selected schema (task set) but are not yet confirmed by currently available input, and, more globally, it provides feedback for an actor on how matters develop as a basis for autonomously directing future steps and the meaningful allocation of (attentional) resources.

In the conception of the Ouroboros Model, an overall recursive process progresses in real time in a piecewise and predominantly serial fashion while concatenating stages, which are often intrinsically parallel, into one principal loop (Thomsen, 2010). The overall process obtains a self-organized direction and prioritization towards what is currently experienced as relevant and also expected to be so in the future. Consumption analysis delivers also a global measure for the goodness of fit between anticipations and the actual status, and, amongst others, it not only triggers the allocation of attention, but gives rise to emotions, determines what is put into (long-term) storage and calls for conscious stronger engagement in cases where automated responses or habits do not suffice (Thomsen, 2011). This directly opposes any "echo chamber" effect: the emphasis is on widening the mind frame and not on ingraining prejudices.

Comprising and actively combining diverse characteristics, the Ouroboros Model can be seen as schema-, i.e., model-based as well as data-, i.e., input- or event-driven, and also as value-guided, as values and goals are just examples of peculiar high-level schemata. Bottom-up and top-down activity unfolds incrementally in iterative cycles progressing in time, this interplay implementing, effectively, Bayesian mechanisms and performance (Thomsen, 2010).

How the Ouroboros Model could fit with the reported functions of the Anterior Cingulate Cortex

In the light of the above it seems obvious to see the ACC as the substrate for the working of consumption analysis. Not only do especially diverse discrepancies lead to activations but also this triggered activity exerts control over many other areas (e.g., Gajewski et al., 2008). In the following, the different facets of ACC function are commented as manifestations of the Ouroboros Model under the same headlines **[examples]** as in the previous lay-out section.

"Consistency Curation" in the ACC can be seen as control on the basis of "time-stamped carbon copies": actual incoming percepts (or activated memory traces) are compared with a currently selected schema, goal or plan and associated anticipations and expectations derived from previous experience. Gaps and deviations of all possible types with respect to an active schema direct attention to details or reset the whole context in a hierarchically staged series of escalation steps; in conditions, where an expected change is already implemented (during task switching), no extra ACC activation is observed **[Anticipation, Attention, Control]**.

According to the Ouroboros Model, for solving a task, first a schematic anticipation is activated, similar to what has been described more than a century ago by Otto Selz (1913). This biasing of suitable schemata will be more pronounced with increasing task difficulty, e.g., when (response-) conflicts are looming large and preparation before a (difficult) task is required **[Anticipation]**.

Matching an expectation with incoming activation, i.e., 'consumption analysis', highlights discrepancies and open slots; the Ouroboros Model holds that to these, (attentional) resources are allocated by enhancing the representations for anticipated features **[Conflict monitoring, Attention, Bias]**.

If the results turn out as not satisfactory, i.e., discrepancies are exceeding a threshold, this causes stronger activation and possibly a "reset" **[Error detection]**.

Discrepancies between expectations and available material can be of very diverse character; filling-in an open slot might fail, there might be no fitting material or also overflow. Checking for deviations will include a time-dimension, possibly quantified, and also (inherited) emotional tags as attributes of schemata, – just as any other features, going much beyond simple single attribute occurrence. "Surprise" is seen by the Ouroboros Model as a generalization of "error", i.e., in particular, not necessarily with negative connotation **[Surprise]**.

Activations pertaining to the agent herself are nothing special in this respect; they just (self-referringly) comprise features with that special content, thus laying the ground for self-reflectivity and full self-consciousness at the top **[Consciousness]**.

The Ouroboros Model posits that episodes marked as special (positive as well as negative) are preferentially submitted to memory; the ACC has indeed been found poised to mediate signal transfer into and out of the hippocampal formation (Thomsen, 2017) **[Control, Learning]**.

Not only feedback for the endpoints and extremes in this process are of interest **[Pain, Pleasure]**, but also how overall activity progresses towards a resolution and how deviations are resolved (i.e., **[Cognitive Dissonance]** signaled and reduced) contains very valuable information **[(Regulation of) Emotions, Stress, Appraisal]**. Important matters will draw more resources, the faces and behavior of conspecifics providing prominent examples **[Empathy]**. "New" emotion signals are continuously computed from a measure how well expectations based on old memories are met at any particular point in time, while "inherited" affective tags form an integral part of previously established schemata **[Feeling]**.

With limited resources available and under severe time constraints, full harmony between anticipations and the results actually achieved will hardly ever be reached for real-time performance. "Left overs" are accumulating, and one prime function of (dream-)sleep has been proposed as taking care of these **[Ironic rebound]**.

There will always be open slots, and agents differ in their background, interests, biases and acceptance thresholds for triggering diverse actions in order to reduce the associated tension **[Curiosity]**.

Discrepancy monitoring can be seen as "cognitive" extension of a very fundamental function, which ensures that a body is not taking harm by moving in a way, which does not work **[Pain]**.

The Ouroboros Model is centered on consumption analysis, and the underlying structure "at the (/one) top of the brain" (the ACC) focused on comparing activations and biases would expectedly be different than the neural substrates involved in intermediate steps **[absence of granular layer]**.

For the detection and distinct identification of deviations and differences, an appropriate sensing neuron should base its triggering on a tightly confined (cortical) input (region); from the claim that the comparison extends widely over diverse content it follows that discrepancies subsequently have to be communicated fast to probably far-away cortical areas **[Von Economo neurons (VENs)]**.

Antithetic and/or complementary to the specific modulation of cortical areas would be interpolating and averaging; an observed negative correlation between ACC activity and the cerebellum thus dovetails with the tenet of the Ouroboros Model that sees the cerebellum as general purpose interpolator (Thomsen, 2014) **[connectivity]**.

Here, it shall be stressed that there is another way in addition to structural dominance in one spot to ensure overall consistency, as an alternative or, most likely, in addition: instead of a location in physical/topological brain-space, the seemingly indispensable "top unity of command" can be tied to specific points in time in a process-centered account, and something similar might be said concerning the "unity of consciousness" as experienced by healthy subjects (Thomsen, 2011b). Taking the time-dimension into proper account allows to accommodate the finding that there appear two distinct brain mechanisms involved in conscious versus subliminal error detection; (Charles et al., 2013; Crottaz-Herbette and Menon, 2006) **[Asymmetry, Consciousness]**.

With wide-spread activation, as hypothesized being essential for conscious action (High Personality Activation, HOPA), more and diverse areas of the cingulate cortex sense a deviation between anticipations and actual performance (Thomsen, 2011b). One can argue that finding a stepwise change in error negativity for unconscious versus conscious error response just highlights the difference between “local” and “global” excitation in a human brain, the latter including posterior areas producing PE, likely corresponding to the awareness/involvement of an actor (Charles et al., 2013; De Cul et al., 2009; Jahn et al. 2014). The Ouroboros Model sees consciousness as developing and manifesting itself over longer times in shades of grey; — for one and the same individual at different occasions and conditions, and also to (strongly) varying degrees in different species. This does not preclude a sharp transition between states (modes) of an actor at any given occasion (Sergent and Dehaene, 2005) as the first relates to a maximum available capacity/capability whereas the second to a nonlinear transition from partly / local to global activation to the extent possible (Bayne and Hohwy, 2013). There is evidence for switching between modes after crossing a threshold, similar as has been found for simple perceptual decisions when accumulating sensory evidence (Kang et al., 2017).

It is important to note that the quasi-global activation hypothesized by the Ouroboros Model as ground laying for consciousness, HOPA, is still an orderly and constrained one, in some contrast to increased rather indiscriminate global functional connectivity, which has been found to correlate with LSD-induced ego dissolution (Tagliazucchi et al., 2016). After psilocybin infusion, decreased alpha activity has been observed in human subjects in the precuneus and posterior cingulate cortex (Carhart-Harris et al., 2014) **[Consciousness]**.

A unifying model of the medial prefrontal cortex as action-outcome predictor, the "predicted response-outcome" (PRO) model, which comes relatively close to the comprehensive view advocated by the Ouroboros Model, has been proposed recently by Alexander and Brown (2011). Their construct of 'negative surprise' is claimed to occur for cases in which actions do not produce the expected outcome when comparing many associated features in parallel, — all of them connected in a delimited schema according to the Ouroboros Model. This group found distinct regions signaling the violation of expectancies and their degree (Jahn et al. 2014). ACC processing had before been claimed to yield at least two qualitatively different types of prediction errors: as a Bayesian surprise signal and a signed prediction error, i.e., an evaluation outcome (Ide et al. 2013).

Links to Selected other Models of Cognition and Consciousness

Predictive Coding

Predictions and how they are met lies at the heart of the Ouroboros Model; a comparison with other accounts putting their emphasis on predictions thus is obvious. "Predictive Coding" is the brand name of a whole family of models receiving a lot of interest lately. The common hypothesized main claim of these models is that rather than forwarding positive signals for the occurrence of any specific feature, the decisive ingredient is error back-propagation. According to these models, activity in higher areas predicts excitation in lower ones, and mainly, even only, the deviation between this prediction and the actual activation ("the residual prediction error") is transmitted in the forward direction between cortical areas (e.g., Friston, 2010). An associated "free energy principle" has been proposed as unifying basis for cognition.

While standard predictive coding posits inhibitive feedback from higher to lower tiers in the coding hierarchy, it is possible to achieve basically the same with excitatory feedback links (Spratling, 2008); seemingly contradictory predictions by more standard predictive coding accounts and other well-known biased competition models can in fact be harmonized as different implementations of the same abstract mathematical idea. Predictive coding has its way of dealing with (perceptual) uncertainty: "error-precision". The claimed function can be seen as in principal similar to the output of consumption analysis directly reflecting a goodness of fit as hypothesized by the Ouroboros Model when concentrating on relevant attributes.

Currently favored predictive coding accounts with their posited reciprocal connections between stages in a strict encoding hierarchy offer clear progress over a one-directional linear feedforward chain of feature detectors. But, they still stress a (bi-)linear succession of processing stages. The layout of the Ouroboros Model is offering additional benefit to predictive coding by expanding the structure from a primarily linear extension to its full possible breath. Conceptually, splitting that stream in two and separating the branches in time for cyclic succession, allows for wide iterations, with higher levels able to also directly impact lower ones (in addition to more local feedback connections); this adds tremendous flexibility. Cyclic activity unfolds over time, and the natural picture is one of iterations: activity at any one point in time building on the (recent) history and easily incorporating many other relevant (or influential) factors in parallel.

The point of the Ouroboros Model is, that, in addition to local effects of habituation and feedback, activity is globally coordinated and inhibition (as well as positive biasing) is primarily updated and effective after a full iterative cycle, including, in particular, the output of consistency checking as far as it has been completed at a specific point in time. Goodness of fit is calculated in intervals, taking into account all current activations. This can explain results interpreted as supporting standard predictive coding and at the same time why no separate populations of "error-neurons" as postulated are found. Not properly inhibited, subliminal activations can be smuggled in: e.g., unconsciously elicited disgust thus will influence an assessment by diminishing positive evaluations and the confidence in them, while strengthening doubt if already prevailing (Allen et al., 2016b).

Searching for canonical computations performed by the cerebral cortex, feedforward selectivity and recurrent gain control are emerging (Miller, 2016). In order to avoid run-away excitation, input is claimed to best be attenuated leaving only some residual net excitation. Competition between neutrons of the same stage certainly helps in sharpening responses.

Brains without doubt adhere to a general efficiency principle avoiding unnecessary energy use and associated cost; still, forward-directed signal- and evidence-transfer as ground laying function seems more natural than focusing almost exclusively on errors, which often cannot tell much, especially not for new percepts or in completely new situations. The observation and necessity of communicating evidence in a forward direction has been pointed out repeatedly over time. "Error" is a relative concept, which presumes some "correct" reference frame, context. To really expel a tacitly assumed homunculus or "Lufthaken", it would be required to explain why and how neurons know that they represent (conflicting) alternatives (Botvinick et al., 2001). The Ouroboros Model does exactly this when contrasting memory-derived expectations with current actual activations.

Quenching, i.e., a top down signal, which silences a predecessor stage, will be required primarily for detector / input- stages; there are temporal receptive windows, and a hierarchy of times is observed: ACC features the longest (Chaudhuri et al., 2015).

Generally, progress can be expected from advances in imaging methods, which can finely distinguish the extent of activations, their signs (excitatory versus inhibitory) and also their timing. A good prediction based on a well-established schema, according to the Ouroboros Model, would result in relatively limited activation because only few dedicated neurons with clear response assignments are needed. Representations sharpened by expectation would require less overall (gamma) activation but could still transfer the same amount of information as available from a wide population excited in the absence of specific guiding top-down information (Kok et al., 2012; Zhang et al., 2015). This is about what has been found as "prediction suppression" (Crottaz-Herbette and Menon, 2006).

In the real world, any actor has to face dynamic changes happening all the time. It is important to keep track of the development, i.e., by noting what has already been sensed, used and classified, contrasting this with novel percepts. In order to avoid getting stuck in repeated considerations of one and the same input, consumption analysis effects also the tagging of stuff already exhaustively dealt with. This is very important at many levels and will be implemented via inhibition of the respective earlier stages leading to a suppression of their continued response. This implements well-known "inhibition of return"; misapprehended, this could be interpreted as error feedback. Repetition suppression and expectation suppression of early sensory areas both are related to enhanced coding efficiency. They interact but can be separated among other things on the basis of their timing; the second occurring later and being obviously the effect of more distant top-down influences (Crottaz-Herbette and Menon, 2006; Grotheer and Kovács, 2016). On a global scale, whenever an error is detected this first needs encompassing inhibition of current activity before a new bias can be disseminated (Shen et al., 2015).

Amongst others, three problems for the predictive coding theory of attention have been raised by Ransom and Fazelpour (2015), who argue that predictive coding fails to model endogenous feature-based attention, that it is unclear how non-perceptual forms of attention like to one’s thoughts might be accommodated, and, that it does not explain the influence of affectively silent objects. According to the Ouroboros Model in short, ACC activation can highlight whatever is coded (as a feature or action) in a brain, not necessarily only perceptual attributes; many complete objects and features taking part in schemata will have associated importance/emotional (relevancy-/saliency-) tags "inherited" from previous encounters, which assure their strong impact on the ongoing processing as one possibility, and/or, also, if not anticipated as part of the active schema, as they will stand out from the expected, and they will activate the ACC. The same applies for novelty in general. Curiosity has been shown to be a strongly motivating drive accompanied by ACC activation, quite contrary to a naive prediction of standard predictive coding that an agent would prefer to quietly sit in a dark room (e.g., Froese and Ikegami, 2013). An approach maximizing predicted information gain in a Bayesian framework to direct curiosity-driven exploration of an embodied agent in action-perception loops has been claimed to stand in stark contrast to the free energy hypothesis (Little and Sommer, 2011) but is, in fact, efficiently outlined with the Ouroboros Model.

Behavior in Time

Most of the time, the world is changing, and this has to be taken into account by any agent. The Ouroboros Model emphasizes a global frame and its compartmentalization into schemata, which include also slots for timing(-)attributes. On this basis, an orderly process of consumption analysis unfolds in time in iterative cycles. "Funneling" all activity in a healthy human brain through a global consistency checking stage, comprised mainly by the ACC, appears to dovetail nicely with what is known about its function.

There is electrophysiological evidence that ACC activation modulates prior probabilities as part of a preparatory process (Scheibe et al., 2009). When there is an expectation, an attended stimulus will be processed preferentially whereas unattended stimuli, not being part of that activated schema, will be suppressed (Todorovic et al., 2015). In the light of the Ouroboros Model, expectation and attention are about the same, the labels just referring to different stages of cyclic processing, i.e., more generally at the outset and directed at specific relevant slots during later cycles, respectively. The ACC has been found to effectively adjust the distance to the decision threshold in a context according to the current amount of available predictive/relevant information (Domenech, 2010). Not only are specific slots in a schema biased, the mere announcement of potentially changing respond-demands provokes changes in medial frontal activity in the absence of errors or response conflict (van Noordt et al., 2015). Neural signatures of subjective value comparison during decisions requiring reward─effort trade-offs in the ACC have been documented recently (Klein-Flügge et al., 2016).

In a large-scale dynamical model of the macaque neocortex based on quantitative connectivity data a hierarchy of timescales naturally emerges: sensory areas show brief, transient responses to input (appropriate for fast sensory processing), while association areas integrate inputs over time and exhibit persistent activity (suitable for decision-making and working memory) (Chaudhuri et al., 2015).

Brains are teeming with periodic signals at a wide span of frequencies. Object binding by fast gamma synchronization is an early prominent example (Gray et al., 1989). Gamma oscillations have been claimed to be nested in slow theta rhythms (Lisman and Idiart, 1995.) In a 'match-and-utilization-model' MUM, gamma-band activity spaced in time at theta-synchronous intervals has been proposed to, firstly, accompany the comparison of memory content with stimulus-related information, and, thereafter, promote the utilization of signals derived from that comparison (Herrmann et al., 2004). These ideas have been elaborated for visual search where the slow oscillation, interpreted as reflecting top-down influences, initially is reset and synchronized to the fast gammy cycles representing individual items (Sauseng et al., 2010; Sauseng et al., 2015;). Quite similar processes, basically swapping fresh sensory signals for their reinstatement from memory entries, have also been proposed (Nyhus and Curran, 2010; Zhang et al., 2015). Synchronized gamma and theta cortical activity will enhance the coupling to the hippocampus and long term episodic memory (Colgin 2015; Bunce et al., 2013). Externally produced prediction errors, like endogenous ones, have been shown to promote one-shot learning (Maryott et al., 2011). An interpretation of the ERN as related to ongoing EEG processes, rather than being a discrete and separate response, has gained wide support; in particular, frontal midline theta rhythms have been found to reflect alternative activation of prefrontal and anterior cingulate cortices in humans (Asada et al., 1999; Luu et al, 2004; Cavangh and Frank, 2014; Voloh et al., 2015). Particularly in preparatory states, medial prefrontal cortex showed a phase-lead relative to parietal areas (Phillips et al., 2014). Surprise disrupts cognition engaging the same fronto-basal ganglia suppressive mechanism as active in outright action-stopping (Wessel et al., 2016). In a simple oddball task where both, functional Magnetic Resonance Imaging (fMRI) and Event Related Potentials (ERP) methods with high time-resolution were employed, primary sensory regions have been found to generate a small mismatch signal about 50 ms prior to feedback from the ACC and a large signal 60 ms thereafter (Crottaz-Herbette and Menon, 2006).

How the above could be implemented in neural circuitry is the subject of ongoing research. A promising example has been presented by Luduena and Gros (2013), who show that in an unsupervised feedforward neural network following an anti-Hebbian learning rule a comparator-function can emerge under strictly local rules through self-organization, which can signal the grade of similarity between unrelated input streams even in the presence of noise.

Conclusion and Outlook

The Ouroboros Model, at the moment, delivers a still very coarse-grained picture but roughly consistent with all of the above (--and, where not, these would be exactly the points to direct attention to). A schematic frame has to be valid for a rather long time, enabling the filling-in of attributes; top-down (preparatory stage-setting) signals are therefore associated with lower frequencies (Theta). Individual components, comprised themselves of contributions from diverse neural, e.g., sensory, populations bound by fast gamma oscillations, can be understood as bottom-up (feedforward) signals. Contrary to repeated proposals in the literature, theta oscillations and embedded ERPs are seen as effecting control and not merely indicating a need for control (Cavangh and Frank, 2014).

If (response) conflict cannot be solved quickly, this will manifest in increasing ACC activation in successive cycles, i.e., enhanced mid-frontal theta-band activity as well as functional connectivity (Carter et al., 1998; van Driel et al., 2015). From the point of view of the Ouroboros Model, it is expected that announcing a conflict trial leads to enhanced activity of the proposed consistency curation stage, i.e., the anterior cingulate cortex.

Recent results provide strong evidence that the dorsal anterior cingulate cortex drives behavior by means of spatiotemporal spike coding; downstream receivers are unlikely to act as simple neural integrators, which just sum up their input (Logiaco et al., 2015).

The following would be a condensed sketch of activity during cognition along the lines of the Ouroboros Model / neural activity with a focus in ACC during cognition in a healthy (human) brain:

1. For an arbitrary start, fast gamma activity is evoked locally by a sensory signal in an early cortical area. Theta recurrent activity is kindled, and through the ACC this biases a whole schema from memory, enhancing the chance of additional local fast oscillations in areas, which represent all expected associated features, for this context or task set.
2. Consumption analysis is implemented in the ACC comparing expectations (arriving top down) and actual available input (arriving bottom up).
3. In case the anticipated slots are easily filled (expectation suppression) and activity proceeds as expected, consumed constituents are inhibited (inhibition of return), and new input is selected.
4. If gaps cannot immediately be adequately closed, for these, open slots' biases will increase until eventually a threshold is reached and a reset is triggered. Especially evident for motor acts, ongoing activity has to be interrupted. Thereafter a new schema has to be selected and put into force (ERN, goto1.).
5. Forward and backward messages are transferred at different phases of the overall theta cycle, and their combined synchronized gamma and theta excitation gates memory retrieval and also the storage of new entries.
6. With priors specified as coherent schemata and posteriors resulting from the inclusion of actual activity, a Bayesian interpretation of the input and also choice of action is achieved; interpretation- as well as prediction-errors are minimized.

7. Repeating these actions in successive iterative cycles with nested frequencies will show up as oscillatory activations in a healthy brain.

Emphasizing cognitive processing in iterations as the Ouroboros Model does, some fundamental complication arises immediately: when cutting a full circle open in twain to obtain a linear succession of steps, it is possible to pick out quite different points as beginnings or ends, yielding in turn dissimilar perspectives and seemingly contradictory interpretations, e.g., preparatory versus monitoring activity as essential tasks of the ACC. “Earlier” and “later”, in a well-defined sense, depends on the point of view. Still, fully respecting the progression of stages in time, no problem with circularity arises.

The added value of the Ouroboros Model compared to other conceptualizations mentioned above lies in cross disciplinary integration: starting with very simple and few ingredients, i.e., memory compartmentalized in schemata and a self-referential incremental control process, it appears possible to explain very diverse finding in many widely different fields in a common framework. Concerning neural computing, promising directions (as a first step, for future modelling efforts) are highlighted.

Prediction error minimization is essential for the survival of living beings, and also very important for artificial agents. The Ouroboros Model offers a principled account for very diverse activities based on bootstrapping from simple associations and a very general process of discrepancy-use and future avoidance. It can be seen as a "globalized" version of predictive coding with a strong emphasis on iterative and self-steered progressing of behavior implementing Bayesian optimization, applicable to whatever type of content. No real fundamental distinction exists between sensory percepts or memory representations, including ones of the agent herself. Also in this sense, the Ouroboros Model is akin to standard predictive coding accounts being able to apply its explanation-pattern self reflectively also to interoceptive inference (Seth, 2015).

Consistency curation and discrepancy minimizing entails, first, consistency checking, and, second, steering behavior such as to reduce short-term gaps and inconsistencies, as well as trying the best for avoiding already known problems in the future. Optimum for this control task, all relevant aspects concerning the environment, the actor, her goals and motivations, emotions, plans… are taken into account. Comprehensive monitoring and directly employing its results for actual control are hypothesized to be implemented to a large extent in the ACC.

Work on the Ouroboros Model in general and also on the role of the cingulate cortex is in progress. Following a fundamental self-reflective and self-consistent approach, a first coarse but overarching schematic sketch (like theta biasing from the ACC) has to be filled-in with more fine-grained and quantitative details in subsequent iterations (like more local gamma oscillations); collaborations to this end are most welcome. Implementations in soft- and hard-ware would then be the next step harnessing the results for neural inspired computing and for general intelligence of artificial agents. On top of this come medical aspects; a deepened functional understanding of a central hub in the human brain will almost certainly open new perspectives and enable novel ways for the successful treatment of associated ailments

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