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Towards an animal model of consciousness based on the platform theory

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Abstract

The evolution of intellectual capacities has brought forth a continuum of consciousness levels subserved by neuronal networks of varying complexity. Brain pathologies, neurodegenerative, and mental diseases affect conscious cognition and behavior. Although impairments in consciousness are among the most devastating consequences of neurological and mental diseases, valid and reliable animal models of consciousness, that could be used for preclinical research are missing. The platform theory holds that the brain enters a conscious operation mode, whenever mental representations of stimuli, associations, concepts, memories, and experiences are effortfully maintained (in working memory) and actively manipulated.

We used the platform theory as a framework and evaluation standard to categorize behavioral paradigms with respect to the level of consciousness involved in task performance. According to the platform theory, a behavioral paradigm involves conscious cognitive operations, when the problem posed is unexpected, novel or requires the maintenance and manipulation of a large amount of information to perform cognitive operations on them. Conscious cognitive operations are associated with a relocation of processing resources and the redirection of attentional focus. A consciousness behavioral test battery is proposed that is composed of tests which are assumed to require higher levels of consciousness as compared to other tasks and paradigms. The consciousness test battery for rodents includes the following tests: Working memory in the radial arm maze, episodic-like memory, prospective memory, detour test, and operant conditioning with concurrent variable-interval variable-ratio schedules. Performance in this test battery can be contrasted with the performance in paradigms and tests that require lower levels of consciousness. Additionally, a second more comprehensive behavioral test battery is proposed to control for behavioral phenotypes not related to consciousness. We hope that the ideas presented here could serve as a guidance for the decryption of the neurobiological basis of consciousness.

Key words: Platform theory of consciousness, behavioral phenotyping, neural correlates of consciousness, composite score, disorders of consciousness, animal consciousness, behavioral test battery

1. Introduction

Although there are numerous definitions of consciousness, such as an experience, sensation, perception, mental time travel, theory of mind, awareness of something, awareness of awareness, self-consciousness, -knowledge, -recognition, and -detection, to name a few only (see Zeman, 2001 for review), it is commonly accepted that consciousness, whatever its nature or content is, should be the product of activity within a neuronal network. Therefore, the definition of consciousness developed by neurologists, as well as their methods to measure the brains activity, became especially important in consciousness research (Corballis, 2013; Zeman, 2001).

In neurology, consciousness is commonly thought to be a phenomenon that humans possess during their waking state (Teasdale and Jennet, 1974). Furthermore, different states of consciousness have been proposed that roughly include waking, rapid eye movement - and slow-wave sleep, unconsciousness/anesthesia (e.g., induced by drugs), minimally conscious state, vegetative state or coma, and brain death (Baars et al., 2003; Dehaene and Changeux, 2011). Disorders of consciousness include various conditions consist of the minimally conscious state, persistent vegetative state, mild locked-in syndrome, akinetic syndrome, and chronic coma.

In conclusion up to date there is no consensus regarding the meaning of the term consciousness. The definitions are exceptionally broad and range from the simple processing of sensory information (perceptions), memory related cognitive functions (mental time travel) up to metacognitions (awareness for self, others, time, and things). The current definitions of different states of consciousness by neuro- and electrophysiological approaches are even less helpful in trying to corner the volatile phenomenon of consciousness. The notion that the level of consciousness should be highest during waking and lowest during brain death will obviously not help much to understand the nature of consciousness or to provide mechanistic insight into this phenomenon. Electrophysiological recordings of neuronal activity either from the scalp or from within the brain are equally too inaccurate mass phenomena to distinguish between the simple sensory stimulus transmission, perception, and conscious processing of information. We have proposed a hypothetical psychological and neurophysiological theoretical framework that can help to resolve these conceptual

118 issues and provides an operational definition of consciousness that can be used for
119 empirical studies with both humans and animals (Dere et al., 2021).

120 According to our platform model, conscious cognitive operations, first of all, require the
121 presence of a state of alert and responsive waking. This is a prerequisite for performing
122 conscious cognitive operations that are usually subsumed under the umbrella term
123 executive functions. Second, consciousness itself is not a state, but bound to
124 conscious cognitive operations performed on mental representations of stimuli,
125 associations, concepts, memories, and experiences. Conscious cognitive operations
126 require the maintenance of mental representations in a working memory workbench.
127 This conception implies that consciousness starts and ends with these conscious
128 cognitive operations. Conscious cognitive operations can vary with respect to their
129 complexity and processing demand. The anticipation or imagination of a future event
130 (for example a job interview) and the development of a strategy to master the tasks
131 and possible problems that might be associated with this anticipated event, require
132 more processing capacities as compared to the detection of similarities and differences
133 between two types of objects (for example to decide which of two detergents one
134 should buy). Likewise, the first operation will also be associated with a higher load on
135 working memory and will require much more sophisticated cognitive operations.
136 Comparative studies suggest strong inter-individual and between species variation in
137 working memory capacity and executive functions (Kolata et al., 2005; Kolata et al.,
138 2007; Breeden et al., 2016; Dere et al., 2019; Dere et al., 2021). Therefore, it is
139 reasonable to assume that different animal species possess qualitatively and
140 quantitative different levels of consciousness (Breeden et al., 2016; Dere et al., 2019).
141

142 According to the platform theory of consciousness (described in more detail below),
143 consciousness is not a state of the brain itself, but is rather related to what the brain is
144 operating on, or actively manipulating (Dere et al., 2021). Consciousness is bound to
145 sophisticated and complex cognitive operations, that require large processing
146 resources of the brain. Furthermore, consciousness is something that the brain is
147 allotting to mental representations of stimuli, associations, concepts, memories, and
148 experiences that are effortfully maintained in working memory and actively
149 manipulated in a central executive/online platform. Therefore, a great deal of our daily
150 activities (taking a shower, preparing breakfast, driving, etc.) run with a mental state
151 that does not require consciousness as defined above. Proof for this conception comes

from classical work that shows that the acquisition of motor and cognitive skills is only effortful in the beginning, in terms of attention, execution, and control demands. Skill acquisition has also been shown to require substantial amounts of processing resources. In contrast, after sufficient training, the accomplished performance is no longer effortful and runs essentially as an automated script or habit. Skill acquisition is also associated with strong neuronal activation in the prefrontal cortex, basal ganglia and cerebellum. This activation declines in the course of training and, in the case of the prefrontal cortex, is even absent when the execution or performance becomes automatic (Haier et al., 1992; Raichle, 1998).

According to this view, consciousness is associated with an effortful cognitive process that is used to produce an innovative and creative output, to solve problems, plan for the future, or to realize goal-directed behaviors. This conception implies that awake and behaving humans, who are guided by habits or automatic motor programs, can be (in the above sense) totally unconscious (Dere et al., 2021).

Consciousness is likely to have developed slowly and gradually in the course of human, animal, and possibly plant evolution (Butler, 2008; Gardiner, 2012; Irvin, 2020). It is also conceivable that this evolution is still in progress. Consciousness, at least in its rudimentary forms, emerged with the development of a central nervous system that allowed the organism to perceive, encode, and maintain entero- and/or exteroceptive stimuli beyond their presence, in order to overcome simple reflexive behavior that is simply generated in response to a perceived stimulus.

We have proposed that consciousness is tightly bound to the ability to maintain mental representations (in the above sense) in working memory and more importantly to actively manipulate them (for the reasons specified above). *The degree of consciousness of a species is likely to be related to the amount of information that can be maintained in working memory and the complexity of cognitive operations and manipulations that can be performed on these mental representations.* This novel conception of consciousness might explain the "consciousness gap" that probably exists between humans and animals and stands in sharp contrast to the classical consciousness literature, their nomenclature, and conceptions that will be briefly reviewed in the following (Dere et al., 2021).

Traditionally, very different phenomena including experiences, sensations, perceptions, mental time travel, theory of mind, awareness of something, awareness of awareness, self-consciousness, -knowledge, -recognition, and -detection (Zeman, 2001 for review) have been put forward as manifestations or proof of consciousness. According to the platform theory of consciousness, these phenomena and processes are not the same thing as consciousness but can be the content of consciousness. The focus of consciousness can be directed to a great variety of problems and questions. The result of these conscious cognitive operations can be for example knowledge about the own existence as an entity that is different from the rest of the world or the knowledge about the difference between "what I know" and "what others know". These types of insight are end products of conscious cognitive operations and are stored as semantic concepts with self-references. They can't be equated with consciousness. In conclusion, rather than searching for human-like consciousness in animals, we here suggest a series of behavioral tasks to demonstrate conscious cognitive operations in animals. In fact, our definition of consciousness, as it is outlined above should be applicable to humans, animals, and artificial intelligence.

2. Neural correlates of consciousness

The phenomenon of consciousness has been addressed by philosophers and thinkers for thousands of years. The heyday of consciousness research, that we are experiencing today, probably already began with the Greek philosopher Plotinus (205-270), who formulated a layer model of consciousness based on a subjective self that was thought to enable the experiencing of the internal- and external world (Hutchinson, 2018). The nature of consciousness and how it arises from brain activity (the so-called "mind-body problem") is still an unresolved question in the neurosciences and related disciplines, although several promising approaches, including the platform theory, have been developed to tackle this problem.

Currently, the focus of research is directed towards the search for the neurophysiological and neuroanatomical correlates of consciousness (Crick and Koch, 1998). However, it should be considered that these studies used traditional definitions of consciousness, which of course limits their validity. The discussion of the following studies should be read with that knowledge in mind. In what follows, the term

consciousness has been put into quotation marks, when it refers to a traditional definition of consciousness.

Neuropsychological data from healthy individuals and patients with disorders of "consciousness" (Giacino et al., 2018), electroencephalogram and functional brain imaging studies, as well as electrophysiological studies including single cell and local field potential recordings have discovered neurobiological substrates and mechanisms proposed to be potential correlates of "conscious" experiences. The neural correlates of "consciousness" that have been postulated range from thalamic gamma synchronization (in response to the conscious recognition of a visual stimulus) to widespread endogenous activity of large parts of the brain observed within the "hot zone complex", which includes temporal, parietal, and occipital areas, or the "default mode network", that comprises the medial prefrontal cortex, posterior cingulate cortex/precuneus, and angular gyrus (Engel et al., 2001; Koch et al., 2016a; Koch et al., 2016b; Sormaz et al., 2018; Von der Malsburg, 1995). Furthermore, "aware wakefulness" has been shown to be correlated with an increase in neuronal activity in the precuneus and the posterior cingulate cortex (measured with functional magnetic resonance imaging), while during drug-induced "unconsciousness", specifically anesthesia, a decreased activity was observed in these cortical regions (Mashour and Alkire, 2013).

A positron emission tomography study by Långsjo et al. (2012) attempted to correlate neural activation associated with "consciousness" with changes in cerebral blood flow. Neurons that become active and fire action potentials have an increased demand in oxygen and glucose provided by the arterial system. Neuronal activation thus leads with a certain delay to a regional increase in blood flow. The authors searched for brain structures that become activated when an individual regains "consciousness". The fading of the effects of an extremely potent anesthetic drug (propofol) was assessed with the emergence of a motor response to a spoken word. This response was found to be associated with the activation of a brain network involving subcortical and limbic regions that became coupled or synchronized with parts of the frontal and inferior parietal cortices. The authors proposed that a wide brain network, including the brainstem, thalamus, anterior cingulate cortex, and frontoparietal cortex, is likely to represent the minimal neural correlates of "consciousness" (Långsjo et al., 2012).

These findings suggest that frontal, medial and posterior cortical regions serve as "consciousness" control centers, that are driven by subcortical-thalamic and limbic networks.

3. Neural correlates of animal consciousness

The evolution of intellectual capacities in the animal kingdom has brought forth a continuum of consciousness levels in different species accompanied by neuronal networks of different morphology, cytoarchitecture, connectivity and complexity (Gazzaniga, 1998). However, it is still a matter of debate whether neurobiological factors like brain size and morphology can entirely explain cross-species differences in cognitive functions, such as mental time travel, that require high levels of consciousness (Dere et al., 2018a; Dere et al., 2019).

According to the platform theory (Breeden et al., 2016; Dere et al., 2019; Dere et al., 2021), mental time travel is among the conscious mental operations that require increased working memory capacity and high levels of information processing and computation resources. Mental time travel into the past and future requires the construction of complex past experiences and imagined future scenarios which can be used to play through alternative action options and to calculate their possible consequences. It is also reasonable to assume that mental time travels into the future are much more complicated to realize as compared to mental time travels into the past. Compared to mental time travel into the past, mentally travelling into the future is certainly associated with much more uncertainties, possibilities, options for action, interactions between different protagonists, events and contextual factors and thus an higher requirement to fill these gaps with information stored in episodic and semantic memory. Therefore, it is reasonable to assume that a species that is potentially able to perform mental time travels into the future has a higher level of consciousness than a species that is only able to mentally travel into the past. Generally, it can be said that the higher the working memory capacity (that is the more mental representations can be maintained and actively manipulated) and the higher the level of complexity and computation requirements of the conscious cognitive operations performed, the higher the level of consciousness of the species.

The sophistication of cognitive abilities and consciousness levels is likely to depend on the utility of this capacity for the survival and fertility of the species. Other important factors that can explain the large qualitative variation in consciousness among species are the different habitats or ecological niches occupied, social structures developed, hunting-, nutrition-, and mating peculiarities, as well as the relative stability of the environmental conditions. Altogether, these factors were probably the driving forces that have led to the evolution of a consciousness continuum, with great variation in consciousness levels among different species (Darwin, 1871). This inter-species variation is complemented by a probably smaller inter-individual variation of levels of consciousness within a species (e.g., humans).

Integrating findings from human and animal research, Fabbro et al., (2015) have proposed that a more rudimentary anoetic level of "consciousness" (lacking the awareness of the own self and existence) depends on a basal subcortical system that includes the brainstem, hypothalamus, central thalamic nuclei, optic tectum, and periacqueductal gray. These subcortical structures have been implicated in the monitoring of homeostatic physiological functions, regulation of emotional states, emotion-induced and goal-directed behavior, integration of multimodal sensory stimuli, and awareness of the external world (Fabbro et al., 2015). This form of basic "consciousness", or primary self- and world representation, is thought to be present in all vertebrates. In contrast, a more sophisticated form of noetic or autonoetic "consciousness" (Tulving, 2002), present in humans, is thought to involve a forebrain system, including the medial and lateral structures of the cerebral hemispheres (Fabbro et al., 2015).

4. Animal models of consciousness

The most widely used behavioral test for animal "consciousness" is the mark or Gallup test (Gallup, 1970; Gallup et al., 2013). In this test, the reaction of an animals to their reflection in a mirror is observed and evidence for self-recognition is inspected. Behavior indicative for self-recognition, which some animals show spontaneously, is usually triggered by secretly blotting a spot on the animals body or face, before presenting the mirror image. An animal that perceives the spot and makes an attempt

to touch that particular part of its own body (e.g. to remove the spot) obviously has a concept of how a mirror functions, and is able to recognize itself in the mirror. This, in turn, suggests the presence of a self-concept or -awareness. However, it is also important to consider whether the animal locates the spot on its own body right away, or whether it first examines or touches the spot image on the mirror surface.

Non-human primates including chimpanzees, macaques, and orangutans pass the Gallup test without great difficulty. Evidence for self-exploration or recognition in front of a mirror has been also reported for dolphins, elephants, corvid birds, and even fish (reviewed in Anderson and Gallup, 2015; Gallup and Anderson, 2020). However, it is possible that the Gallup test might not work with all animal species, and that a failure in this test does not prove the absence of self-recognition. For example, dogs and cats might simply ignore their reflected image, or show agonistic, respectively territorial, behavior (Devue and Brédart, 2011; Mashour and Alkire, 2013). It should also be noted that an important step in this test is the understanding of how a mirror functions (i.e., as a device that reflects images of individuals and things in front of it). Animals that are unable to understand the concept of a mirror will also fail to recognize themselves in the mirror image. Furthermore, the Gallup test will obviously only work with species that have an excellent visual acuity within a short distance range and that primarily utilize the visual system to interact with the environment such as primates and birds. Some animals do not rely on vision to perceive, explore and recognize objects, conspecifics (using whiskers, sense of touch, or olfaction) or to navigate through space (using the earth's magnetic field, echolocation, chemical concentration gradients) (Muheim et al., 2014).

Researchers in the field of comparative cognition have emphasized the necessity to develop more ecologically valid tests to evaluate cognitive abilities in animals (Genzel, 2021; Gomez-Marin and Ghazanfar, 2019). In this sense, a fully automatized behavioral test battery for mice has been developed which measures different forms of learning and memory in a social setting that does not requires extensive handling by the experimenter (Dere et al., 2018b). However, it is important to avoid the "congenital trap": The misinterpretation of innate behavior as a manifestation of higher cognitive processes. Birds that recover food from a cache location to hide it in another place, because they have been observed by a conspecific (Dally et al., 2004), might

be a genetically fixed behavior that is initiated and performed (without reasoning) upon the perception of certain stimulus configuration (the presence of another bird) rather than e.g., proof for theory of mind or deception (Dere et al., 2006; Dere et al., 2008). Although the Gallup- or mark test might be useful in some species to investigate self-recognition, it falls short as a routine test for neurobiological "consciousness" research.

In what follows, we will use the platform theory of consciousness (Dere et al., 2021), as a framework and evaluation standard to categorize behavioral paradigms (that have been used with laboratory rats and mice) regarding the level of consciousness involved in task performance. We aim to present a behavioral test battery composed of single tasks that probably require higher levels of consciousness, as compared to other tasks that can be used for preclinical consciousness research.

5. The platform theory of consciousness

The platform theory holds that consciousness is a process that emerges when mental representations of internal and external stimuli are maintained in a central executive/online platform in order to execute conscious cognitive operations on these representations. These conscious cognitive operations can be performed to solve a problem, to develop a strategy, to plan for the future, or to generate a creative or novel solution or outcome. Consciousness is, therefore, a transient mental state present when mental representations are maintained and effortfully manipulated.

Conscious cognitive operations are associated with a relocation of processing resources and the redirection of attentional focus. In this context the term effortful indicates that the conscious cognitive operation occupies or binds large attention and processing resources that are no longer available to perform other tasks in parallel and will generally slow down other cognitive processes and reaction times. Based on this core definition of consciousness, we have developed a psychological and neurophysiological framework (Dere et al., 2021) that can be used to determine the level of consciousness that was required for distinct responses or behavioral outcomes.

389   The level of consciousness that can be attributed to an animal species is a function of the
390   sophistication of conscious cognitive operations, which, in turn, is determined by evolutionary
391   pressure and various aspects of species ecology. Ecological factors such as social structure,
392   food search and hunting behavior, position in the food chain, climate stability and other
393   environmental particularities can be used as proxies for the likely complexity of conscious
394   cognitive operations to be revealed in the species. In conclusion, we assume that
395   consciousness is involved in cognitively complex / effortful processes and that differences in
396   consciousness are based on differences such cognitive effort and complexity. Furthermore, it
397   should be noted that according to the platform theory phenomenal "consciousness" (Allen and
398   Williams, 2011; Mylopoulos et al., 2020; Wagemann, 2018), including "raw feels" are not
399   considered as being conscious cognitive operations.

400

401   In the following, we will categorize different behavioral paradigms according to the level
402   of consciousness required. For example, the execution of a learned operant response
403   in a Skinner-box (e.g., pressing a lever to obtain food, drug-infusion, rewarding brain
404   stimulation etc.; Huston and Borbély, 1973) probably occurs without consciousness
405   and consequently without the activation of neural correlates of consciousness, which
406   are assumed to be located in the frontoparietal cortex. In contrast, the appropriate
407   response to the detour-problem (Glosser and Resnick, 1965; Tolman, 1948) (rats can
408   spontaneously take an alternative, longer path, when the direct path to the goal has
409   been blocked) probably requires a higher level of consciousness, together with
410   neocortical activation.

411

412   According to the platform theory a behavioral paradigm involves conscious cognitive
413   operations, when the problem posed is unexpected (f. e., detour task), novel (f. e.,
414   initial acquisition stage of incremental spatial learning in the Morris water maze) or
415   requires the maintenance and manipulation of a large amount of information to perform
416   cognitive operations on them (retrospective or prospective memory in the 16-arm radial
417   maze, see below). The simple application of one or more learned rules (f. e., pressing
418   a lever for food) as it is the case in the test phases of behavioral paradigms that are
419   based on incremental learning do not require conscious cognitive operations, but if the
420   rules suddenly change a conscious operation mode is switched on. Likewise, the early
421   stages of acquisition of an incremental learning task are equally associated with
422   conscious cognitive operations until the task is mastered and can be performed

automatically and without consciousness it is as defined by the platform theory (Dere et al., 2021).

In line with these assumptions, lesion studies have shown that even a complete decortication, in the so called "thalamic rat", does not block the learning of an operant response (Huston and Borbély, 1974). In contrast, lesions to the prefrontal cortex in marmosets impair performance in the detour task (Wallis et al., 2001; Wilkinson et al., 1997). In the following, the functions of and interactions between different components of the platform theory will be presented. We will also present behavioral evidence from human and animal research that is in line with the activity of different components of the platform theory (Dere et al., 2021).

5.1. The central executive/online platform
The central executive/online platform is responsible for the generation of short- (in the rage of minutes), intermediate- (hours), and long-term (weeks) daily schedules, and larger behavioral agendas. To accomplish daily schedules or agendas, the central executive/online platform orchestrates different subordinated platforms, which either perform cognitive operations (e.g., reconstructing past events or constructing novel scenarios by the mental time travel platform), keep semantic and episodic information ready in the background to execute behavioral habits and scripts (steady-state platform), maintain information about intended actions and the spatiotemporal context in which these planned actions should be executed (stand-by platform), or more generally provide a store of semantic, episodic, and procedural information (off-line memory platform) that can be selected by the central executive/ online platform to be actively manipulated or distributed to the subordinate platforms (Figure 1) (Dere et al., 2021).

The mental representations and cognitive operations executed in the central executive/online platform are extensive and include basic perceptions, emotions, motivations, thoughts, contents of memories, problem solving, comparisons, categorization, concept forming, hypothesis testing, reality checks, plausibility assessments, development of strategies, forming of short daily schedules and long-term agendas, intentions, and planning of actions. The central executive/online platform controls attentional filters and receives information from all extero- and

interoceptive systems, as well as from motivation, emotion, vegetative, and motor systems. Intense stimuli could invade the central executive/online platform at any moment and ensure orienting responses to sudden changes in the environment. The central executive/online platform can also search the off-line memory platform to activate stored contents, extract information, knowledge, or memories, after being prompted by external or internal stimuli or cues, such as thoughts, ideas, emotions, and perceptions.

Neuropsychological and neuroimaging studies suggest that the prefrontal and orbitofrontal cortices of human and nonhuman primates (reviewed in Barbey et al., 2011; Desrochers et al., 2016; Funahashi et al., 2017) are implicated in the planning, organization, attentional execution and monitoring of task-related performance.

Evidence for impaired executive function and cognitive flexibility after frontal cortex dysfunction has been also reported in studies using laboratory rats and mice (Dalley et al., 2004; Johnson and Wilbrecht, 2011; Kesner and Churchwell, 2011; Young et al., 2010).

These studies suggest that the cognitive operations of the central executive/online platform can be traced back to neuronal activation in the frontal- and orbitofrontal cortices and that this functional specialization might be conserved in primates.

5.1.1. Conceptual delimitation from Baddeley's scientific concept of the central executive

The central executive subsystem in the working memory model of Alan Baddeley and Graham J. Hitch (Baddeley and Hitch, 1974) is conceptualized as an attentional filter that controls attentional processes, selects task-relevant sensory information, focusses and divides attention, provides access to the content of long-term memory and monitors the activity of the other subsystems of working memory, namely the visuospatial scratchpad, phonological loop and episodic buffer (Baddely, 1983; Baddeley, 2001; Baddeley, 2003). Baddeley's central executive has no intrinsic capacity for information storage, nor can it perform complex cognitive operations. The central executive in Baddeleys working-attention model (Shah and Miyake, 1999) seems to be limited to the processing of acoustic and visuospatial stimuli. Although Baddeley emphasized that "the central executive is not an organ that might or might

not exist, but a scientific concept" (Baddeley, 1998), it is thought to be localized in the prefrontal cortex and its multi-modal association cortices. In contrast to Alan Baddeley's working-attention model the central executive/online platform does not only serves as an attention allocation or control center. The central executive/online platform adjusts and utilizes attention filters it also maintains mental representations to perform complex cognitive operations on them. There is evidence that in humans conscious cognitive and executive functions including mental time travel require the participation of the prefrontal cortex (Corballis, 2019; Del Cul et al., 2009; Knight et al., 1995; Nyberg et al., 2010). Comparative anatomical studies of the medial prefrontal cortex between rodents and non-human primates revealed a similar intrinsic functional organization, but a different whole-brain functional connectivity (Schaeffer et al., 2020). These differences between rodents and non-human primates suggest that non-primate animals might have a more limited level of central executive/online platform function and consciousness (Breeden et al., 2016; Dere et al., 2019; Dere et al., 2021).

5.2. Mental time travel platform

The mental time travel platform is responsible for the reconstruction of past events and imagination or anticipation of future events, as well as for future scenario construction. This information is transferred to the central executive/online platform for the planning of daily schedules or behavioral agendas, to increase the probability of positive outcomes, and to minimize the probability of negative outcomes of current and future actions. The semantic, episodic, and procedural information from the off-line memory platform that is required for the reconstruction of past events, the imagination of future events, and the construction of novel scenarios in the mental time travel platform is selected by the central/executive online platform (Dere et al., 2021).

In humans, mental time travel to the past and future can be measured with paradigms based on the induction and measurement of one-trial space-time-content (or what-where-when) associations (Pause et al., 2010; Pause et al., 2013; Kinugawa et al., 2013; Zlomuzica et al., 2018a; Zlomuzica et al., 2018b) and the utilization of established space-time-content memories to plan for future actions, or to prepare oneself for problems that are announced to be posed in the near future (Zlomuzica et al., 2016).

Mental time travel into the past and into the future was proposed to be mediated by the same neurobiological substrates. Mental time travel has been attributed to an extensive neural network that includes the posterior cingulate cortex, precuneus, prefrontal cortex, left parietal cortex, thalamus, hippocampus, and cerebellum (Nyberg et al., 2010; Viard et al, 2011). Furthermore, it has been shown that aging-related changes in mental time travel into the past are correlated with working memory capacity (Kinugawa et al., 2013). These results are in line with the major assumptions of the platform theory of consciousness (Dere et al., 2021).

Mental time travel into the past or future is impaired in amnesic patients (Kwan et al., 2012; Tedder et al., 2016) and several mental diseases including major depression, anxiety disorders (Miloyan et al., 2014; Moustafa et al., 2018), post-traumatic stress disorder (Zlomuzica et al., 2018), and schizophrenia (Fornara et al., 2017). Impaired prospective cognition, as well as the inability to imagine or anticipate positive events in the future might be a major obstacle for psychotherapeutic success and social and professional inclusion (Dere et al., 2010; Kellogg et al., 2020; Roepke and Seligman, 2016; Zlomuzica et al., 2014).

In animals, evidence for mental time travel into the past is deduced from behavior that indicates that the animal remembers the space-time-content triad of a personal experience. On the other hand, proof for mental time travel into the future presupposes behavior that is exerted to ensure the satisfaction of a future need without any evident utility in the present context (Correia et al., 2007; Raby et al., 2007; Suddendorf and Corballis, 2007). Behavioral paradigms for mental time travel into the past in rodents are generally based on the spontaneous non-rewarded acquisition of a one-trial what-where-when association (Binder et al., 2015; Dere et al., 2003; Dere et al., 2004; Dere et al., 2005; Dere et al., 2018b for a fully automated version of this test).

Evidence for mental time travel into the past, based on the acquisition of space-time-content associations in one-trial or multiple learning trials (see Dere et al., 2006 for a critique of multiple-learning trials), has been found in several different species. Great apes (Martin-Ordas et al., 2010), dogs (Fugazza et al., 2016), cats (Takagi et al., 2017), mice (Dere et al., 2005), rats (Kart-Teke et al., 2006), birds (Clayton and Dickinson, 1998; Zentall et al., 2008), zebrafish (Hamilton et al., 2016), cuttlefish (Jozet-Alves et

al., 2013), and insects (Pahl et al., 2007) were all reported to have the ability to mentally travel though time.

It is obvious that the development of paradigms measuring mental time travel into the future in animals is much more complicated than tests that indicate mental time travel into the past (Osvath and Martin-Ordas, 2014). Paradigms used to measure mental time travel into the future are sometimes difficult to interpret and certainly require some refinement or modification. Among these tests, one finds tests that are based on prospective memory (forming an intention or memory to perform an action at a certain time point in the future), food-caching and retrieval, and tool acquisition or preparation for future use. Only a few reports are available that demonstrate mental time travel into the future by animals. The list of species which have passed the future thinking test is relatively short and includes: Scrub jays (Raby et al., 2007), monkeys (Beran et al., 2012a; Beran et al., 2012b; Evans and Beran, 2012; Kabadayi and Osvath, 2017; McKenzie et al., 2004; Naqshbandi and Roberts, 2006; Osvath and Martin-Ordas, 2014), rats (Cook et al., 1985; Flaherty and Rowan, 1986; Flaherty et al., 1994; Kametani and Kesner, 1989; Kesner, 1989; Wilson and Crystal, 2012), and dolphins (Arranz et al., 2018). Until more valid and reliable tests for mental time travel into the future are available to disprove the following conclusion, we must assume that most animal species are likely to be "stuck" either in the past or present (Redshaw et al., 2017).

The continuum of intellectual capacities and levels of consciousness in the animal kingdom holds also true for the ability to mentally time travel into the future (Breeden et al., 2016; Dere et al., 2019). Potential reasons for the relatively short list of animals that are capable of mentally travelling into the future might be the consequence of the specific ecological niche occupied by the species, the complexity and stability of the social structure, individual or group hunting, prey availability, mobility and seasonality, and the range of climatic conditions. Here, the simple rule might be that the more complex, unstable, and unpredictable these factors are, the more foresight or planning and thus mental time travel into the future will be required to survive and transfer its genes to the next generation. Species that are perfectly adapted to an ecological nice, having no strong competition for food resources, living either as loners or in stable social structures, with little concurrence for mating partners, that do not hunt together

with others, having invariable access to food or prey, and that are living in a climate zone without gross weather extremes, certainly do not require sophisticated future thinking and time travel abilities.

Lesion studies that attempt to identify the neurobiological substrate of mental time travel in animals are scarce and almost exclusively focused on mental time travel into the past. Retrosplenial cortex lesions in rats blocked the processing of temporal information and their integration with object and spatial information in a space-time-content task (Hayashi et al., 2020). Mice with lesions to the medial prefrontal cortex or the hippocampus showed impaired integration of space-time-content information (DeVito and Eichenbaum, 2010). The disconnection of the projections from the medial prefrontal cortex to the lateral entorhinal cortex (an input structure of the hippocampal formation) or hippocampal subregions CA1 or CA3, impaired the integration of space-time-content information in rats (Chao et al., 2016; Chao et al., 2017; De Souza Silva et al., 2016). These results suggests that mental time travel critically depends on the integrity of the medial frontal cortex in both humans and rodents. The specific role of the hippocampus in this context seems to be related to the integration of space-time-content information during acquisition (Li and Chao, 2008). The hippocampus might unimportant for the conscious recollection of experiences during mental time travel into the past.

5.3. Steady-state platform

The contents of the steady-state platform are pre-selected by the central executive/online platform to accomplish a daily schedule or behavioral agenda that must be realized within minutes or hours. The information deposed in the steady-state platform includes autobiographical information, habits and scripts, rules and concepts, general-, specific-, personal-, as well as normative information that is important for the current agenda. These mental representations and contents are thus maintained in the background and do not block working memory resources in the central executive/online platform, however, they become active periodically to guide ongoing behavior. Thus, mental representations and contents placed in the steady-state platform become conscious periodically and influence cognition and behavior controlled by the central executive/online platform (see Dere et al., 2021 for details).

This phenomenon has been observed in operant conditioning tasks with concurrent reinforcement schedules where humans, rats, or pigeons are rewarded for the first response after a number of responses (variable Ratio) or a variable time interval has elapsed. The switch in the contents of consciousness and the corresponding change or adjustment of ongoing behavior, can be modeled in operant conditioning experiments with *concurrent variable-interval x variable-ratio schedules* generating a dynamic choice environment (Aparicio and Baum, 2006; Bell and Baum, 2017; Davison, 1982). Specifically, rats can be tested in an operant conditioning task (usually a Skinner-box) with two active levers that provide a food reward according to variable interval and variable ratio reinforcement schedules. In a typical experiment, the first response to lever A (e.g., after a variable interval with a mean of 30 s has elapsed), will result in the delivery of a food pellet. (In a variation of the experiment, premature responses before the interval have elapsed could lead to a time-out punishment to examine impulsivity, respectively behavioral inhibition). Concurrently, the first lever press to lever B after a variable number of responses had been performed (e.g., with a mean of 30 responses), will also lead to the delivery of a food pellet. Successful performance on lever A would normally lead to a cessation of responding immediately after a rewarded response, followed by slowly increasing rates of responding (if premature responses are not punished), until the moment when the variable time interval has elapsed. In contrast, responding in the variable ratio schedule will evoke regular and constant response rates. In this situation, maximizing rewards would require continuous shifts between the consciousness of the two reward schedules and the corresponding change in response behavior. Some animals including pigeons however adopt a matching strategy (staying with one reward schedule) rather than using a flexible maximizing strategy. Adaptation of this paradigm to human subjects demonstrated that humans generally adopt a maximizing over a matching strategy (Silberberg et al., 1991). These findings point to the existence of inter-species differences in the function and effectiveness of the steady-state platform.

The concurrent variable-interval x variable-ratio schedule requires a switch between two operant levers and reinforcement schedules. The platform theory assumes that the contents of the steady-state platform will be activated periodically and will influence contents and cognitive operations in the central executive/online platform (Dere et al., 2021). In the case of the concurrent variable-interval x variable-ratio schedule, the

central executive places the mental representation that contains the information of the reinforcement schedule that will provide a reinforcement later than the other reinforcement schedule onto the steady-state platform, from where it will invade the central executive/online platform according to a pre-defined excitation protocol. The platform theory further assumes that the contents of the steady-state platform are represented by reverberating neuronal circuits, coupled via gap junctions, in which the neurons fire with relative synchronization. The neural circuits in the steady-state platform are activated periodically and exponentially by pacemaker cells within the neuronal circuits. These cells are controlled and pre-set by the central executive/online platform (Dere et al., 2021). Recently, it has been shown that human pluripotent stem cell-derived neural networks show synchronous neural activity that can be modulated by the gap junction blockers. Carbenoxolone a gap junction blocker decreased or gradually abolished the occurrence of synchronous peaks of activity in the network. Interestingly, the authors have identified a subpopulation of neurons that exhibited an inter-peak interval change that was similar to that observed in the whole network (Mäkinen et al., 2018), but proceeded the later change in the whole network. It is conceivable that this subpopulation of neurons plays the role of pacemaker cells or "neural circuit pulsars" as Dere and colleagues (Dere et al., 2021) have put it, to maintain synchronized activity within the neural network.

In conclusion, the steady-state platform includes autobiographical information, habits and scripts, rules and concepts, general-, specific-, personal-, as well as normative information that is important for the current agenda. The steady-state platform maintains a default bias, complied by the central executive/online platform, that is composed of routines, habits, rules and concepts etc. This default bias is maintained in the background and required to accomplish a current agenda. In humans, task performance based on default bias seems to be mediated by the insula, subgenual cortex and ventral striatum (Liljeholm et al., 2015; Yu et al., 2010). In rodents, task performance controlled by habits seems to be mediated by the infralimbic cortex (Smith et al., 2012; Smith and Graybiel et al., 2013).

5.4. Stand-by platform

The central executive/online platform places mental representations or contents in the stand-by platform to be preserved until they become relevant at a certain time or after

a specific stimulus, or a constellation of stimuli is perceived/detected. The mental representations and contents in the stand-by platform then invade the central executive/online platform in order to execute planned or scheduled actions. One particularity of the stand-by platform is that it does not remain "silent" until the right moment comes, but rather generates sporadically intrusive reminders with decreasing intervals as the execution time approaches, thereby interrupting ongoing activity in the central executive/online platform. The stand-by platform is used for forming intentions and initiating their execution under pre-specified conditions at a certain time, place, or when cue stimuli or specific constellations of stimuli are perceived (Dere et al., 2021; Kliegel et al., 2016; O'Rear and Radvansky, 2019).

The stand-by platform ensures a function that is known as prospective memory, that is a memory for intentions (Einstein and McDaniel, 1990), that has to be distinguished from episodic future thinking (Atance and O'Neil, 2001). According to most of the researchers in the filed episodic future thinking denotes the ability to imagine or simulate experiences that might occur in the future (Schacter et al., 2017), while a prospective memory refers to the creation of an intention to do something in the future at a certain time or after a predefined stimulus constellation is perceived. However, a prospective memory can be the behavioral consequence respectively outcome of episodic future thinking.

Foraging experiments with rats suggests that they can form time- or event-based response or action intentions, specifically prospective memories (Crystal and Wilson, 2015). It has been proposed that the mental representation of an intention is temporarily put in an inactive state (while the subject is engaging in other activities), until it is activated at a certain time, place or in response to a perceived stimulus or stimulus constellation. The activation of a response intention that has been placed in an inactive state (into the stand-by platform), has been shown to perturb ongoing performance of rats in a temporal bisection task (Wilson and Crystal, 2012). Likewise, rats which were performing a temporal discrimination task to obtain a small quantity of food displayed a significant drop in performance accuracy after it was announced that a large quantity reward would be available after the presentation of an acoustic cue (Wilson et al., 2013). It is possible that the announcement of the large quantity disturbed the current performance via the generation of intrusive reminders of the

expected large quantity reward. The phenomenon of intrusive reminders that interfere with performance in an ongoing task has also been observed in human studies. The perturbation of ongoing behavior is more pronounced, when the context in which the planned action must be executed, approaches (Smith et al., 2017).

Rats with parietal cortex lesions exhibited difficulties when they had to change their performance based on retrospective memory into a performance based on prospective memory in a complex 12-arm radial maze. It was hypothesized that the parietal cortex might mediate expectancy-based memory processing in line with prospective memory formation (Kametani and Kesner, 1989).

In humans, functional neuroimaging studies indicated an involvement of the rostral prefrontal cortex, parietal cortex, precuneus, and the anterior cingulate cortex in prospective memory performance (reviewed in Burgess et al., 2011). These brain structures and regions are regularly listed among the candidates for the neural correlates of "consciousness" (Engel et al., 2001; Koch et al., 2016a; Koch et al., 2016b; Sormaz et al., 2018; Von der Malsburg, 1995; Mashour and Alkire, 2013).

5.5. Off-line memory platform

The mental representations and contents stored in the off-line memory system are either activated by the central executive/online platform or become conscious after the perception of intense external and/or internal cues. Ongoing activity in the central executive/online platform is then interrupted and the activated content is used to provide an appropriate response. The mental representations and contents of the off-line memory platform are extremely heterogenous and include reflexes, conditioned and physiological responses, episodic-, semantic-, emotional-, and motor memories. For a detailed presentation of the platform theory, see Dere et al. (2021). The off-line memory platform covers both declarative and non-declarative memory systems with distinct neuroanatomical substrates (reviewed in Squire, 2004; White and McDonald, 2002).

5.6. Interaction of the central executive/online platform with the subordinate platforms

The mental time travel platform is recruited by the central executive/online platform to reconstruct events or construct future scenarios which serve as virtual spaces in which

conscious cognitive operations, including the simulation of actions and alternative events and their consequences, can take place. The steady-state and stand-by platforms on the other hand do not execute conscious cognitive operations, but rather serve as stores for information and content that has been previously selected by the central executive/online platform in order to be at hand when needed to accomplish tasks or solve problems. The steady-state and stand-by platforms can also bear the results of conscious cognitive operations performed in the central executive/online platform (such as a behavioral sequence that must be initiated at a certain time, place or when a certain stimulus constellation has been perceived). The information and material placed in the steady-state and stand-by platforms is also fitted with an "activation protocol" that specifies with what frequency, or under which circumstances the stored information should enter the central executive/online platform (Dere et al., 2021). The neuroanatomical and neurophysiological basis of the different components of the platform theory remain to be identified in future experiments. However, the expectation to be able to identify a specific brain structure as a "residence" for the central executive/online platform would be probably too optimistic, it is more likely that the central executive/online platform will involve various brain structures and that the exact composition of this consciousness consortium will change in dependence of the type of conscious cognitive operation to be performed. A simple example for such a "diffusionist neurocognitive hypothesis" is the ability of every neuron to show synaptic plasticity or learning at a cellular level. Learning and memory processes are therefore not the exclusive characteristic of a particular brain structure. Similarly, there are different ultra-short term memory stores for each sensory modality and not a shared store that includes the totality of sensory information.

5.7. Conceptual delimitation of the platform theory from the global workspace theory
The global workspace theory attempts to explain conscious and unconscious processes (Baars, 1988; Baars 2002). It postulates a system of specialized unconscious vaguely defined "receiving processes" that are working in parallel. The most peripheral "receiving processes" transmit information from the sensory systems to downstream "receiving processes" that further process and interpret these information's. The most significant or essential information is allowed to enter the global workspace that consists of a fleeting memory area with a duration of a few seconds (<30s) in which only extremely limited amounts of information can be

passively preserved. The global workspace is therefore not suited to maintain a larger number of information's to solve complex problems or to perform mental time travels. The content entering the global workspace is then projected to wide parts of the brain in order to hit those brain structures that are able to respond to the sensory information. In essence, the global workspace theory describes a sensory gripping reflex without specifying the neuronal or molecular mechanisms that underlie this function. The global workspace theory postulates that only information that is passively stored (for a few seconds only) within the global workspace is conscious. "Consciousness" is regarded as a passive response (the information in the global workspace is not subject to cognitive operations) to a significant and intense sensorial stimulation. It is therefore not clear how this model can explain conscious cognitive operations, including problem solving or mental time travel into the past and the future. The level of consciousness that is provided by the global workspace might serve the requirements of a goldfish in a spherical aquarium, but not the richer conscious experiences of humans and non-human primates. The global workspace theory that has been criticized by Dalton (1997) as an "unfinished theatre". He complains that the origin of the global workspace as well as its mechanism of operation are not defined. As compared to the platform theory (Dere et al., 2021), no neurophysiological or molecular mechanisms that supports the global workspace theory has been delineated. Furthermore, the global workspace theory holds that conscious cognitive content is globally available for diverse cognitive processes. However, according to Dalton (1997) it falls short in explaining the nature of consciousness. In conclusion as influential the global workspace theory might have been in the past decades, the insight provided by this theory is rather limited.

6. Towards an animal model of consciousness

Behavioral test batteries for the behavioral phenotyping of animal models of human disease become more and more important in preclinical research (Dere et la., 2014). Currently, there is no animal model of consciousness available that could be used for research to determine the neuroanatomical substrates, electrophysiological, cellular, and molecular mechanisms of consciousness. A major obstacle in developing behavioral paradigms to investigate human and animal consciousness was the lack of an operational definition of consciousness that could be translated into novel

behavioral paradigms. The recently developed platform theory of consciousness provides such an operational definition (Dere et al., 2021) that can serve as the basis for novel paradigms, and additionally provides a conceptual framework to determine the level of consciousness required for successful performance in existing behavioral paradigms and tasks. In the following, we will evaluate routinely used behavioral tasks that assess different types of cognitive functions in order to identify tests that could be incorporated into a consciousness test battery (see Dere et al., 2018a), which could be used to reliably evaluate the effects of experimental manipulations on consciousness. In order to facilitate within- and between group comparisons, as well as to compare the effects of experimental manipulations across different studies, we also provide a guideline to compute a composite score (Dere et al., 2014; El-Kordi et al. 2013), which is based on the individual performance in different tests of the consciousness test battery proposed below. Here, each animal that ran through a behavioral test battery to assess consciousness will end up with a single value or score that can be directly compared with other individual scores within that group, between experimental and control groups, and even across different studies. The composite scores determined in different studies could then be used for meta-analysis, which normally struggle with huge methodological, level of measurement and statistical differences between the studies compared.

Generally, it should be noted that performance in a cognitive task, similar to motor task acquisition (Bebko et al., 2005; Boisgontier et al., 2013), probably requires a high level of consciousness in its initial acquisition stage (that also comprises procedural learning of the general rules of the task, e.g., procedural use of platform learning in the Morris water-maze prior to spatial learning). However, with increasing proficiency in the task, the performance requires less monitoring and consciousness. When the routine or automatic stage of task performance is reached, the level of consciousness involved is expected to be minimal or even absent. However, the exact switch point from conscious/controlled to automatic task performance is difficult to determine. It is only safe to say that after performance has reached a stable asymptotic plateau, without further improvement, the automatic stage has been reached with little consciousness involved in task performance.

7. Tasks requiring higher levels of consciousness

7.1. Working memory in the radial arm maze

Consciousness requires the maintenance of mental representations or contents in the central executive/online platform to perform cognitive operations on them (Dere et al., 2021). Therefore, a prerequisite for consciousness is a functional working memory. Working memory capacity is thought to be an invariant characteristic of the species-specific central nervous system, which, in theory, cannot be expanded by training (Dere et al., 2001; Zlomuzica et al., 2009). Both the 8- and 16- radial arm maze can be used for mice and rats to measure working memory capacity (Olton, 1987). In this test, food-deprived mice or rats are allowed to search the arms of a radial arm maze for food rewards. In this situation, the food deprived animals are highly motivated to avoid re-entries into arms already visited in order to collect the food more efficiently. In consequence, the working memory load (the number of arms that should be avoided) increases with each arm entry. The capacity or functionality of the working memory system is assessed by the mean number of working memory errors (the number of re-entries into empty arms) after the performance has reached an asymptotic plateau and without further improvement due to procedural learning of the general rules of the task. It has been shown that lesions to the medial prefrontal cortex that include prelimbic area impair working memory performance in rats (Fritts et al., 1998).

7.2. Episodic-like memory

One-trial space-time-content (or what-where-when) learning tasks, also known as episodic-like memory tasks, can be used to model the function of the mental time travel platform in animals (Dere et al., 2006; Dere et al., 2007; Pause et al., 2013). In order to test one-trial space-time-content memories, the animal is placed in a situation that has familiar and novel components, however which differ from a stored experience (Dere et al., 2005). It has been proposed that the behavior of rats and mice during the recall of such integrated space-time-content information is indicative of a mental comparison operation between the space-time-content information recalled and the current stimulus configuration perceived. During this comparison process to determine whether there is a difference between the stored memory and the current perception, the animal generates and tests hypotheses about similarities and differences between the space-time-content association recalled and the current stimulus configuration

perceived (Binder et al., 2015). The animal's behavior during the space-time-content memory test can thus be used to model the function of the central executive/online platform after reconstruction of past experiences by the mental time travel platform. The verification and plausibility of memories and their comparison with present stimulus configurations is thought to be dependent on the integrity of the frontal cortex (Hwang et al., 2007; Johnson and Raye, 1998). The formation of episodic-like memories in tasks that are based on object exploration in rodents seem to be dependent on the integrity of the hippocampus and its substructures CA1 and CA3, as well as on the function of entorhinal and perirhinal cortices (Binder et al., 2015; Chao et al., 2020; Dere et al., 2006; Dere et al., 2008). In this regard it has been proposed that the entorhinal cortex is essential for the integration of spatial and contextual object information (Chao et al., 2016). The hippocampal CA1 region is important for the processing of spatial information (Chao et al., 2017), while the perirhinal cortex seems to be essential for the processing of object information (reviewed in Dere et al., 2007). Finally, the CA3 region has been shown to mediate the integration or binding of multimodal what, where and when information in episodic-like memory tasks (Li and Chao, 2008).

7.3. Prospective memory

Prospective memory requires the creation of a mental representation of a future action, which must be performed either at a certain time, in a particular place, when a certain stimulus is perceived, or after the perception of a specific time-place-stimulus combination. That mental representation of the intention is temporarily stored, creates intrusive reminders, and will be retrieved at the right time point in the future. Prospective memories thus require the participation of the central executive/online platform for planning the action and forming the action intention. The action intention is then stored in the stand-by platform. The scenario in which the action should take place as well as possible outcomes of this action have been previously simulated in the mental time travel platform using information from the off-line memory platform. The most promising action scenario is then selected by the central executive/online platform to be transferred to the stand-by platform.

Prospective memory has been measured with food-rewarded radial arm maze tasks with all arms baited. In this test, a mouse is allowed to make a fixed number of arm

entries in an 8-arm radial maze (to more than half of the baited arms) and to consume the food reward. After the last entry, the animal is either removed from the maze or trapped in the central platform of the maze for a delay period, until it has the opportunity to enter the remaining baited arms. The idea is that the mouse will form a prospective memory with the intention to visit the baited arms not already visited after the delay period. In order to initiate prospective memory formation, it is important that the retention delay is introduced after more than half of the arms have been visited. This is because the decision of whether a prospective or retrospective memory strategy will be used by the animal, has been shown to be dependent on a complex working memory load cost-benefit analysis. The animal will use a retrospective memory strategy if unvisited arms > visited arms, while it will prefer a prospective memory if unvisited arms < visited arms (Kametani and Kesner, 1989; Kesner, 1989).

A typical experiment to measure prospective memory in rats would require a 16-arm maze with all arms baited to provide sufficient working memory load. In the prospective memory test trial, the animal is allowed to make 12 free choices (arm visits) and then suddenly and unexpectedly is enclosed in the central platform. In this situation the animal enters a conscious cognition operation mode recalls the arms visited and forms the intention to enter the 4 arms not visited when the access to the entire maze is provided. Before the intention is formed the animal must decide whether it should keep information about visited arms or about not visited arms in working memory. It will certainly choses the option that puts less load on working memory. In the present example the rat will choose to remember the 4 arms left instead of the 12 arms visited. Classical experiments by Ray Kesner colleagues (Kametani and Kesner, 1989; Kesner, 1989) revealed that the number of errors is equally low when the animal is allowed to make few (4 choices) or many choices (12 choices) but made a high number of errors after 6 choices. These results demonstrate that performance the prospective memory test developed by Ray Kesner and colleagues clearly depends on working memory capacity and that the rat chooses a prospective or retrospective memory strategy in dependence of the working memory load that is associated with the strategy. In any case behavior in this task qualifies as a simple form of planning ahead that requires conscious cognitive operations.

7.4. Detour test

The problem-solving abilities of the central executive/online platform can be measured with the detour task. In this task the animals use incidentally learned spatial information to navigate through a maze, when, suddenly the most direct path to the goal box is blocked. This test can be performed with mazes of varying complexity, adapted for the use with either mice or rats (Grosser and Resnick, 1965; Juszczak and Miller, 2016; Wallis et al., 2001).

7.5. Concurrent variable-interval variable-ratio schedules

As outlined above, the activity of the steady-state platform, which feeds the central executive/online platform with mental representations to accomplish a daily schedule or agenda, can be modeled with operant conditioning tasks that involve concurrent reinforcement schedules. Given that this paradigm is based on operant conditioning (a universal form of learning), it has been adapted for a variety of different species including pigeons (Bell and Baum, 2017), mice (Sakagami et al., 1989), rats (Galizio and Allen, 1991), and monkeys (Meisch and Spiga, 1998).

8. A behavioral test battery for measuring consciousness

A minimal behavioral test battery to assess consciousness in rodents should at least involve the following tests: Working memory in the radial arm maze, episodic-like memory, prospective memory, detour test, and operant conditioning with concurrent variable-interval variable-ratio schedules. These tests are not invasive and only require mild food deprivation. The behavioral equipment requires an automated radial arm maze, operant conditioning devices, and a semi-automated tracking system to analyze behavior in the detour and episodic-like memory test. The behavior in the consciousness test battery can be contrasted with the performance in paradigms and tests that probably require lower levels of consciousness, including simple operant and classical conditioning, continuous spatial alternation in the Y-maze, and behavioral habituation to novel environments or objects.

In order to ensure that the phenotypes observed in the consciousness test battery are not the consequence of secondary effects of the experimental manipulation, a second more general behavioral test battery should be performed with a separate animal

1001 cohort (Ambrozkiewicz et al., 2020; Dere et al., 2014; Dere et al., 2015; Netrakanti et
1002 al., 2015). Such a general behavioral phenotyping battery should include assessments
1003 of motor functions (rotarod, running wheel, pole-test, grip strength, automated home
1004 cage activity observation, including stereotypic behaviors), sensory functions (visual
1005 cliff test, acoustic startle response, cookie finding test, hot plate test), attention and
1006 vigilance function (5-choice serial reaction time task), emotionality (elevated-plus
1007 maze, graded anxiety-test, light-dark test, height-fear test), and reward-related
1008 behavior (conditioned place-preference, positive and negative contrast/Crespi-effects),
1009 neurological symptoms (clasping response, PTZ-induced seizure activity), and
1010 symptoms of mental disorders (major depression: sucrose preference/anhedonia-
1011 tests, tail-suspension and forced swim-tests; schizophrenia: sensory-motor gating/pre-
1012 pulse-inhibition; autism spectrum disorder: social interaction in pairs, social preference,
1013 discrimination and memory; bipolar disorder: marble burying/impulsivity). Ideally,
1014 different cohorts would be tested in the behavioral test batteries for consciousness-
1015 related behavior, general phenotyping, and disease-related symptoms to avoid carry-
1016 over, or order effects.

1017

1018 **9. Composite scores**

1019

1020 In order to directly compare the performance of different individuals, experimental
1021 groups, and to reduce the complexity and variation that goes along with several
1022 different readouts of a behavioral test battery, a composite score can be calculated as
1023 a single value representation of the severity of the affectation of experimental animals
1024 by the experimental manipulation across different tests (or different readouts within
1025 one test). Composite scores have been proven to be extremely useful in research with
1026 animal models of human disease (Dere et al., 2014; El-Kordi et al., 2013). A detailed
1027 manual to calculate composite scores from test batteries can be found in Dere et al.
1028 (2014).

1029

1030 Some of the tests in the consciousness test battery proposed above are performed
1031 with a single test trial and cannot be repeated multiple times with the same animal.
1032 This "one-shot" limitation inevitably goes along with a higher variability than one would
1033 find in behavioral tests that are based on multiple trials, such as the Morris water-maze
1034 test (Morris, 1984); the Morris water maze test is utilized to measure spatial learning

1035 and memory, in which single trial variability has a minor impact on the final outcome

1036 and the conclusions derived from the test.

1037

1038 The variability generated by single tests could cause problems in the interpretation of

1039 the behavioral test battery. This problem can be circumvented by the calculation of a

1040 composite score, which represents the overall performance of the animal in the test

1041 battery. Furthermore, since the composite score is calculated from z-standardized

1042 readouts (having no physical value/unit, see the section on the calculation of the

1043 composite score) (see Dere et al., 2014), it can be directly compared to reference

1044 values from other studies (e.g., to the severity of the syndrome of other mouse/rat

1045 models of the same disease or other experimental manipulations).

1046

1047 In conclusion, composite scores provide a potent tool to assess the overall severity of

1048 disease-specific changes in consciousness between genotypes (e.g., mutants vs. wild-

1049 types), treatment groups (drug vs. vehicle), as well as between single individuals

1050 covering all construct or disease-relevant behavioral domains. It also allows the direct

1051 comparison of the severity of a syndrome across different mouse/rat models of the

1052 disease or even across different animal model species (e.g., by comparing the severity

1053 of the consciousness alteration in a mouse model of schizophrenia (Pletnikov, 2009)

1054 with a transgenic rat model of schizophrenia (Klein et al., 2013)).

1055

1056 The standard operating procedure for calculating the behavioral composite score have

1057 been described previously (see Dere et al. 2014, for a standard operating procedure

1058 using the statistics software SPSS®v.17).

1059

1060 The first step in generating the composite score is the selection of the relevant readouts

1061 or tests that would cover the consciousness syndrome induced by the experimental

1062 manipulation. It is mandatory to include readouts from tests that reflect the functioning

1063 of the different platforms. The raw data that has been collected with these tests of the

1064 consciousness test battery have to be recoded in a way that higher values always

1065 correspond to higher levels of symptom severity in a specific test. If mice or rats are

1066 tested over weeks or even months in a large disease-specific behavioral test battery,

1067 it can happen that not every readout is available for each animal. Either due to

1068 unpredictable confounding factors that require the exclusion of an animal from the data

set or it happens that individual mice are statistically confirmed outliers (e.g., using the Grubb's test) and, therefore, have to be removed from a particular data set. However, in order to avoid the extensive use of laboratory animals and the necessity of complete data sets to work with, one can impute the missing values. Of course, it is important that the percentage of missing values per dataset or readout does not exceed 30%. Otherwise, the generation of complete datasets via imputation is probably not valid, because the imputed missing values are calculated from the available values in the dataset. Similarly, every animal must have performance values for at least 70% of the readouts in order to be maintained in the composite score calculation (otherwise it must be excluded from all datasets/readouts).

Data from different behavioral tests come with different physical units such as cm, cm/s, s, frequency, or as percentages. In order to generate datasets that are directly comparable, one must perform a z-transformation of the data. For z-transformation, the deviation of the raw values of a dataset from the mean of all values are divided by the variance of the dataset. The resulting z-transformed dataset or readout then has a mean of 0 and a variance of 1 and then corresponds to a variable with a standard normal distribution.

The composite score is then calculated by building the mean of the z-standardized behavioral readouts for each animal. In order to have an idea whether the selected readouts indeed capture different aspects of the psychological construct measured (e.g., consciousness) or disease syndrome assessed, the internal consistency of the composite score can be determined by calculating the Cronbach's-Alpha, which is based on an intercorrelation reliability analysis of the selected readouts. In a final validation step of the disease-severity composite score, one must test whether the composite score is able to reliably predict the individual performance, genotype or disease status of a given mouse (that is the probability of a correct performance level, genotype, or disease status assignment or diagnosis based on the composite score). This prediction analysis is done using a binary logistic regression analysis (see also Dere et al., 2014; El-Kordi et al., 2013).

10. Conclusions

It is widely accepted that the evolution of intellectual capacities has brought forth a continuum of consciousness levels subserved by neuronal networks of varying morphology, cytoarchitecture, connectivity, and complexity. However, the neurophysiological basis of consciousness is still under investigation and clearly the most challenging question in the field of neuroscience and related disciplines. It is well known that brain pathology and injury, as well as neurodegenerative and mental disorders affect conscious cognition and behavior. Although impairments in consciousness are among the most devastating consequences of neurological and mental diseases, valid and reliable animal models of consciousness that could be used for neurobehavioral research are still missing. One important factor that has contributed to this methodological scarcity is the fact that the nature of consciousness is still under debate, and that operational definitions of consciousness have only recently developed. According to the platform theory, the brain is in a conscious operation mode when mental representations of stimuli, associations, concept, memories, and experiences are effortfully maintained in working memory and actively manipulated in a central executive/online platform.

Behavioral test batteries for the behavioral phenotyping of animal models of human disease become more and more important in preclinical research. Currently, there is no behavioral test battery for the assessment of consciousness available that could be used for research to determine the neuroanatomical substrates, electrophysiological, cellular, or molecular mechanisms of consciousness. We, therefore, used the recently developed platform theory of consciousness as a framework and evaluation standard to categorize behavioral paradigms with respect to the level of consciousness involved in task performance. We here propose a minimal consciousness behavioral test battery, composed of tests that are assumed to require higher levels of consciousness as compared to other tasks and paradigms, which can be used for preclinical research on consciousness with laboratory rats and mice. The consciousness behavioral test battery includes the following tests: Working memory in the radial arm maze, episodic-like memory, prospective memory, detour test, and operant conditioning with concurrent variable-interval variable-ratio schedules.

The behavior in the consciousness test battery can be contrasted with the performance in paradigms and tests that probably require lower levels of consciousness including simple operant and classical conditioning, continuous spatial alternation in the Y-maze, and behavioral habituation to novel environments or objects. In order to ensure that the phenotypes observed in the consciousness test battery are not the consequence of secondary effects from the experimental manipulation, a more comprehensive general behavioral test battery should be performed with separate animal cohorts. Within-, between group, and cross study comparisons could be facilitated by the use of composite scores, where individual performance in different tests of the battery are condensed into a single value without a unit of measure. We hope that the novel concepts and ideas presented in this article could serve as a guidance for the decryption of the neurobiological basis of consciousness in health and disease.

Figure legend

Figure 1: The platform theory of consciousness. The central executive/online platform is a consciousness control center that organizes and monitors conscious mental operations by the orchestration of subordinated operation and storage units called "platforms". The main function of the central executive/online platform is the generation of a daily schedule or agenda with goals to archive and the allocation of different grades of consciousness to mental representations or contents that are required to accomplish these tasks. The central executive/online platform selects mental representations (internal or external stimuli, stored content from the off-line memory platform) to be maintained, used, and manipulated, or to be placed in the steady-state or stand-by platforms. The steady-state, stand-by, and off-line memory platforms do not execute conscious cognitive operations, but rather provide information and content that is important to accomplish tasks or solve problems. The contents of declarative and non-declarative memory including episodic, semantic, and procedural information are stored in the off-line memory platform and are accessible to the central executive/online and mental time travel platforms. The central executive/online platform controls and presets attentional stimuli filters and receives input from sensory systems, as well as from motivation, emotion, vegetative, and motor systems. Intense stimuli can by-pass the attentional filters and directly access the central executive/online platform. The central executive/online platform recruits the mental time travel platform to re-construct past experiences, anticipate future events, or simulate and calculate the outcomes of different actions in imagined scenarios by feeding this platform with information from external and internal perceptions, as well as stored content from the off-line memory platform. For further information see main text.

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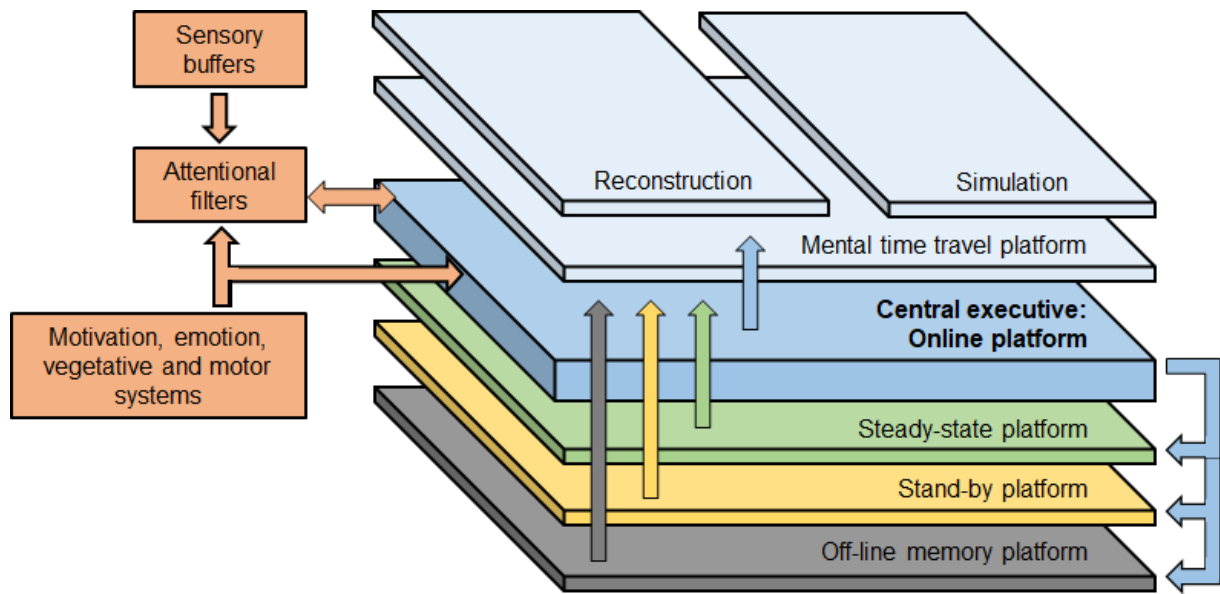
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