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Profiles of animal consciousness: A species-sensitive, two-tier account to quality and distribution

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ABSTRACT

The science of animal consciousness investigates (i) which animal species are conscious (the distribution question) and (ii) how conscious experience differs in detail between species (the quality question). We propose a framework which clearly distinguishes both questions and tackles both of them. This two-tier account distinguishes consciousness along ten dimensions and suggests cognitive capacities which serve as distinct operationalizations for each dimension. The two-tier account achieves three valuable aims: First, it separates strong and weak indicators of the presence of consciousness. Second, these indicators include not only different specific contents but also differences in the way particular contents are processed (by processes of learning, reasoning or abstraction). Third, evidence of consciousness from each dimension can be combined to derive the distinctive multi-dimensional consciousness profile of various species. Thus, the two-tier account shows how the kind of conscious experience of different species can be systematically compared.

1. Introduction

Conscious experience seems to be the salt in the soup of human life. As humans, we have conscious experiences every day and we insist that others respect them e.g. by sharing events of pleasure, by not producing unnecessary pain to others, etc. Although it is meanwhile accepted that some nonhuman animals also enjoy some conscious experiences it is still a matter of intense debate which species enjoys conscious experiences and to which degree (Key, 2016; Klein & Barron, 2016). How can we make progress in answering these questions? Even in the case of humans we are faced with the hard problem of consciousness (Chalmers, 1995, 1996) because we do not yet have a widely accepted theory of human consciousness. We observe a tendency to either attribute consciousness in an inflationary manner by defending panpsychism (Goff, 2017; in this direction also: Tononi & Koch, 2015), or to limit it to cases of clear evidence for human consciousness due to linguistic reports or analogous cases involving meta-representation (Carruthers, 1998, 2020). How can we do justice to the variety of nonhuman animals without either just adopting the romantic view that all species enjoy consciousness just like humans do, or the killjoy view that human conscious experiences are unique?

Since the brains, typical behaviors and cognitive capacities of species like macaques, rats, chickens and octopodes differ markedly, it is to be expected that their conscious experience is quite heterogeneous as well. Thus, we are faced with two types of questions: First, the *distribution question* is about which kinds of animals (or beings generally) have conscious experiences. Second, the *quality question* concerns the differences between the conscious experiences of various species. It asks not which animals have conscious experiences, but *what* they experience and *how* it is experienced, i.e., the content and quality of experience.

As we understand them, both questions address *phenomenal consciousness* in the sense of Block (1995), not another sense of consciousness like access consciousness. The latter notion is too demanding to allow informative comparisons of many non-human animal species. A being is phenomenally conscious if and only if it has some phenomenally conscious states. A state is phenomenally conscious if and only if there is something it is like to be in that state (Nagel, 1974). In other words, phenomenally conscious states are felt from a first-person point of view which is to say that they are experienced subjectively.

Our central aim is to develop a new framework for investigating consciousness in nonhuman animals that tackles both the distribution and the quality question. Our first methodological presupposition is that consciousness is a rich phenomenon which is best captured using a multidimensional space where each dimension describes an aspect

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which is individually susceptible to testing via relevant operationalizations (this idea is based on the work of Birch, Schnell, & Clayton, 2020). Thus, these dimensions can be characterized as bridge concepts connecting the rich phenomenon of consciousness with detailed operationalizations.

The second methodological presupposition is the use of human consciousness as a starting point since it is the best understood case of consciousness. However, we are sensitive to the danger of anthropomorphizing: New insights of nonhuman animal research on consciousness may be worked out with our starting framework and then lead to systematic adjustments of the framework by modifying or exchanging dimensions such that the updated framework can be employed for future research in general or for specific purposes, e.g., particular interspecies comparisons. Thus, our framework is supposed to be the most adequate given the status quo of animal consciousness research with the aim to work out the core dimensions for a comparative perspective for multiple species.

Since we are lacking undisputed indicators of conscious experience in nonhuman animals (we neither can communicate linguistically with nonhuman animals nor do we have a generally accepted neural correlate across species), we have to focus on dimensions of animal consciousness accessible to concrete *behavioral investigations*.[2]

This includes all systematic observational studies: either field observation or laboratory cognitive tests. The latter are sometimes combining behavioral observations with neuroscientific measurements. An additional methodological step is that – for each dimension – we evaluate how good the operationalizations indicate that conscious experience is in place by distinguishing strong and weak indicators. Finally, on this basis, the operationalizations can play a dual role. On the one hand, they provide evidence of the presence of consciousness. On the other, they track different dimensions along which conscious experience may vary and thereby enable us to attribute profiles of consciousness. These methodological presuppositions express and constrain our general *epistemic-pragmatic perspective* on investigating consciousness: given the state of the science of consciousness, we can only make progress concerning questions about animal consciousness if we set aside metaphysical debates about consciousness (like the Zombie argument) and unfold an epistemic-pragmatic account on the basis of empirically testable criteria indicating the involvement of consciousness in a cognitive ability. In light of this, our dichotomous distinction between strong and weak indicators and our numerical scoring system for the strength of evidence of consciousness are pragmatically motivated idealizations.

We proceed as follows: In section 2, we start by distinguishing two different approaches for validating empirical indicators of animal consciousness: strongly anthropocentric validation and species-sensitive validation. We argue that the species-sensitive approach, which we pursue, enriches the standard strongly anthropocentric approach in an important way. Thus, it constitutes an indispensable and neglected route to increasing our understanding of animal consciousness. Subsequently, we describe the best available dimensions framework of animal consciousness by Birch et al. (2020) in more detail and highlight crucial points where we depart from it. After this stage setting, section 4 unfolds details of our own theoretical framework. Finally, in section 5, we illustrate the framework's fruitful application to the quality question via case studies of primates and rodents. Section 6 concludes.

2. The need for a multi-dimensional framework

Methodological constraints: How can we best investigate the involvement of conscious experiences? In the case of humans, we can rely on introspective access to one's own case and linguistic reports in the case of other people. But such access is lacking in the case of other animal species. In respect to neural correlates of consciousness (where we are still lacking a generally accepted realization basis), our framework allows for some systematic direct neural interventions in nonhuman animals which for ethical reasons are only available in the case of unavoidable brain operations in humans, namely the local stimulation or deactivation of specific brain areas by neural intervention. Redinbaugh et al. (2020) stimulated central lateral thalamus in anesthetized macaques and effectively restored conscious experience.[3] This illustrates that neural intervention studies could be an important complement to observing behavior. That being said, in humans we have access to experience via linguistic reports and consequently are less dependent on neural studies while in the case of animals we face the dilemma that the more we are inclined to attribute conscious experiences to them, the more ethical challenges arise (Mazor et al., 2021). Thus, the central means to investigate animal cognition remain *behavioral observations* ideally complemented with *noninvasive* neural investigations while the latter are still rare.

Motivating the new approach: This is the background for developing a multi-dimensional framework of consciousness. This framework suggests that different features of experience can in principle vary independently of each other. There is no reason to believe – or at least no a priori guarantee – that differences in conscious experience by diverse species all neatly align in one uni-dimensional hierarchy; given recent perspectives on evolution, which leave a unidirectional and teleological perspective behind (Mashour & Alkire, 2013), we expect a diverse variety of types of consciousness in different species.

This rejection of a uni-dimensional, hierarchical model of consciousness motivates the general idea of distinguishing between dimensions of consciousness which can enrich the study of both, the quality question (in line with recent work by Birch et al. (2020)) and the distribution question. From a bird's eye view, we can distinguish two main strategies to deal with empirical evidence of animal consciousness, namely either via *strongly anthropocentric* or via *species-sensitive validation* of indicators of animal consciousness.[4] Strongly anthropocentric validation proceeds in two steps.[5] First, identify a specific type of behavior which seems to be caused by conscious experience in humans. Second, test whether the animal in question exhibits behavior which resembles the type of human behavior as closely as possible. In the paradigmatic case, an experimental paradigm which suggests that a certain type of behavior requires consciousness in humans can be transferred quite closely to other animals. Experiments conforming to this approach can provide quite strong evidence of animal consciousness. For instance, Birch et al. (2020) argue persuasively that different forms of learning, like trace conditioning and reversal learning, should

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[2] There is a line of skepticism according to which conscious experiences can in principle not be captured by investigating behavioral abilities; the only access would be direct experience of qualia. Such a skepticism would not even allow us to attribute consciousness to other humans and would make it hopeless to make progress in investigating animals. Thus, we pragmatically set aside this skepticism.

[3] A closer look at this example shows that the stimulation does not restore normal conscious wakefulness but only a basic form of conscious awareness which we call basic arousal: this is indicated by the fact that the macaques react to perceptual stimuli but were not alert enough to be able to do any more complex cognitive tasks that they could do in normal wakefulness. Thus, further investigations of consciousness may have to distinguish at least two types of phenomenal consciousness, namely basic arousal and general alertness (this is developed in Newen and Montemajor, n.d.). We ignore this distinction for the time being.

[4] We do not claim that this distinction is exhaustive, i.e., there is at least one other approach for investigating animal consciousness. This alternative approach presupposes a theory of consciousness which is then interrogated for its implications for animal consciousness.

[5] For an illuminatingly explicit example, see the description and use of 'Newton's Principle' by Tye (2017).

be used as behavioral markers of animal consciousness since empirical data ties them to consciousness in humans. To add another example: in a recent experiment, Ben Haim et al. (2021) show that macaques exhibit double dissociations of consciousness which are analogous to the ones found in humans in the same conditions.[6]

However, while the approach based on strongly anthropocentric validation is essential, it should not be the sole means to study animal consciousness empirically. We suggest that this approach is limited in important ways such that it needs to be complemented by a different strategy. For it commits to a form of *methodological anthropocentrism* by assuming that the best way to detect animal consciousness is to look for manifestations of consciousness as it is present in humans. This opens up three challenges. *First,* the challenge of finding an adequate cluster of behavioral tests: it is difficult to identify human behavior which is not just correlated with but caused by conscious experience (Carruthers, 2020; Morales, Chiang, & Lau, 2015). While we do not doubt that this is possible, it limits what we can achieve by strongly anthropocentric validation in practice.

Second, the challenge of limited access: the approach is blind to manifestations of consciousness in animals which are not shared with humans. An animal species might lack most manifestations of consciousness present in humans – either because their form of consciousness differs or because the behavior depends on other cognitive capacities the animal lacks – while nevertheless being conscious. To some extent, consciousness should be expected to support different behaviors in different species.

Third, the challenge of correct interpretation: even if we detect indicators of human consciousness in another species, this does not entail that their form of consciousness, i.e., what contents they experience and how they experience them, is similar to human consciousness. To presuppose otherwise, would be to fall prey to *form anthropocentrism* regarding consciousness. If our goal is to find differences between the form of consciousness possessed by humans and some animal species, then we cannot solely rely on strongly anthropocentric validation as our guide.

For these reasons, we suggest a species-sensitive validation of indicators as a crucial additional strategy. It goes beyond the strongly anthropocentric approach by not only closely emulating experimental conditions which clearly demonstrate consciousness in humans, but by searching 1. for new criteria indicating consciousness for some nonhuman species only, and 2. integrating weaker cognitive features which only plausibly indicate the presence of (a particular form of) consciousness. To be clear: our assessment of which features indicate properties of consciousness is provided by our understanding of consciousness which is mostly informed by the study of human consciousness, i.e. the case of human consciousness remains our starting point. Thus, species-sensitive validation maintains a residual anthropocentrism which may be unavoidable. Nevertheless, the species-sensitive approach is in the long run much less constrained by human evidence and develops a species-adequacy in investigating consciousness.

Let us shortly elaborate the distinctive aspects of the species-sensitive approach: Evidence of the function of human consciousness can suggest that certain cognitive features may be causally related to consciousness. Finding similar cognitive features in animals provides evidence of consciousness, even if there is no specific experimental paradigm which has been applied both to humans and animals. In these cases, more general evidence and theoretical considerations support the validity of putative indicators of animal consciousness, not a specific type of experiment.

For instance, we posit that episodic-like memory, i.e. the capacity to remember the type of object one encountered where, and when, is evidence of consciousness, despite that there is no specific human experiment, transferrable to animals, demonstrating that consciousness is necessary for this capacity (as strongly anthropocentric validation would demand). Our rationale is first that episodic-like memory is a sophisticated cognitive skill characteristic for human conscious experience and that consciousness in general seems to facilitate learning and memory (Baars, 1988; Birch, 2020; Ginsburg & Jablonka, 2019). Second, we can rely on neural and functional evidence concerning episodic memory that makes it probable that episodic-like memory involves consciousness.[7]

Species-sensitive validation is in general less strict. While strongly anthropocentric validation presupposes clear experimental evidence that a specific indicator is caused by consciousness in humans, the species-sensitive approach also allows for weaker indicators. If folk psychological intuition and scientific psychology both implicitly presuppose that a particular cognitive feature is linked to consciousness, we can possess reasonable grounds for believing that the presence of this feature, e.g. episodic memory or certain forms of bodily awareness, favors attributions of consciousness at least when this feature is realized to high degree. In this context, evidence that an animal displays the feature in question to a high degree is evidence of consciousness.[8]

Our account implements a species-sensitive approach. We collect different operationalizations which are plausibly tied to particular aspects of consciousness, even if there is no clear human evidence corroborating this link. In this way, we pave the way to make informed estimates of the consciousness profile of different species. At the same time, we aim to encourage empirical researchers to design tests for the features we propose which provide strongly anthropocentric validation. Consequently, we want to suggest the most plausible dimensions to characterize consciousness from a comparative perspective starting with operationalizations mainly motivated by the species-sensitive approach but expect them to be developed further into two ways: Sometimes, there will arise clear experimental evidence, satisfying strongly anthropocentric validation, that an operationalization indicates consciousness in humans. In other cases, by learning more about the cognitive organization of particular species, we can revise our framework to account for species-specific forms of consciousness. This may include modifying dimensions of consciousness or adding new dimensions.

In the next section, we characterize the framework for addressing the quality question developed by Birch et al. (2020). Our framework, which

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[6] A double dissociation of consciousness involves processing stimuli in two different, opposing ways, where two types of behavioral response correspond to behavior which is caused by human conscious and unconscious processing, respectively. In the experiment of Ben Haim et al., after a learning period, a spatial cue presented supraliminally increased the detection speed of the subsequent stimulus while a spatial cue presented subliminally slowed down detection. This mirrors the effect found in human conscious vs. unconscious processing.

[7] This is justified due to the following observations (Allen & Fortin, 2013; Schacter & Addis, 2007): 1. Episodic memory in humans is realized by a neural system involving hippocampus, parahippocampal regions, and prefrontal cortex; and this neural basis is not unique to humans, 2. These neural correlates underlying episodic memory are intensely overlapping with those of imagining future actions. 3. A central function of episodic memory seems to be to provide memory-based predictions which are used to plan future action. Such an anticipation needs some conscious simulation of future action. Thus, it is plausible that the ability of episodic-like memory indicates the ability of conscious memory or conscious simulation. Episodic-like memory is an important ability and is also described as an indicator of attributing beliefs to nonhuman animals (Newen & Starzak, 2020).

[8] Although species-sensitive validation exploits our knowledge about consciousness, it is no instance of a 'theory-heavy' approach to animal consciousness in the sense of Birch (2020): Like the strongly anthropocentric approach, the species-sensitive approach strives to be neutral between as many different theories of consciousness as feasible. Thus, investigations based on species-sensitive validation should look for an overlapping consensus between multiple theories of and views on consciousness.

we will motivate and describe later on, builds upon the foundation laid out in this article.

3. The dimension framework and a two-tier account of quality and distribution

The first multi-dimensional framework to investigate animal consciousness was offered by Birch et al. (2020). They aim for fine-grained characterizations of the different features of conscious experience characteristic of particular animal species. We will summarize their work, since our investigation of the different facets of non-human consciousness rests on it but we aim to make an important step forward. After a short characterization of their approach, we outline how we enrich it to a two-tier account of consciousness with the methodology of a species-sensitive approach.

The core claim of Birch et al. (2020) is that variations in the degree of consciousness of different species can be captured along five different dimensions: (1) *Perceptual richness* refers to the level of detail with which animals consciously perceive the world. Perceptual richness consists in the bandwidth (the amount of content experienced at any given time), acuity (the sensitivity to fine perceptual differences) and categorization power (the capacity to group perceived properties into more abstract categories) of perceptual experience.

(2) Evaluative richness concerns the richness of features involved in the experience of valence specifically. It captures differences between animals in how many features can be part of a valenced content they can experience at any given time (bandwidth) and how fine-grained their evaluative appraisals of the world are (acuity), i.e. how sensitive those are to minimal changes. In addition, there are probably kinds of evaluative experience, e.g. regret or shame, which not all species can experience. While (3) *integration at a time* (synchronic unity) concerns the degree to which experience is unified at any single point in time, (4) *integration across time* (diachronic unity) is about the degree of temporal unity, i.e., whether the world is experienced as a continuous stream rather than through temporally fragmented experiences. Human split-brain patients, for instance, have a low degree of synchronic unity.

Lastly, an organism possesses (5) *self-consciousness* to the extent that it is consciously aware of itself as distinct from the external world. According to Birch et al., distinguishing between experiences that represent external states and that represent internal bodily states in the service of movement may involve a minimal form of self-consciousness. Having an awareness of one's body as persisting object may be a more demanding form of self-consciousness, while an even more sophisticated capacity consists in attributing mental states to oneself, as distinguished from other subjects.

All five dimensions of consciousness admit of degrees. Moreover, the framework tentatively presupposes that those five dimensions vary to some extent independently from each other while properties belonging to the same dimension, like the different properties comprising evaluative richness, correlate. Furthermore, the framework assumes that the nature of an animal's conscious experience can be sufficiently captured by situating it with respect to those five dimensions. Thus, no dimension is missing.

Birch et al. suggest multiple empirical operationalizations for each dimension. Let's look at two of them. To ascertain perceptual richness, one has to test for the ability to discriminate between slightly different consciously perceived features. This requires means to detect when a stimulus is perceived consciously. One potential candidate is trace conditioning. Trace conditioning differs from standard classical conditioning only in that the unconditioned and the conditioned stimuli are separated by a temporal interval. It seems that trace conditioning in humans relies on conscious awareness of the stimuli and the time gap separating them (Clark & Squire, 1998, 1999). If so, when a non-human animal is able to perform trace conditioning on some stimulus, this is a hint that the stimulus is perceived consciously (Dung, 2022a).[9] If an animal can do trace conditioning on a wide range of stimuli in different modalities, that may be claimed to reveal a significant degree of perceptual richness.

A famous operationalization of self-consciousness, mentioned by Birch et al., tests whether an animal is able to recognize a mark seen in a mirror as belonging to its own body. If an animal can recognize itself as itself in the mirror, then it might need to possess the mid-level form of self-consciousness which involves awareness of one's own body as an object persisting in time.[10] Notably, this test of self-consciousness is already quite demanding in that only relatively few animal species pass it while even many mammals and birds, including some primate species, seem to fail.[11] While the two preceding operationalizations belong to the ones especially emphasized by Birch et al., they present a more encompassing overview of promising empirical tests which we cannot summarize here.[12]

We are very sympathetic to the approach of Birch et al. which is why the framework we propose retains several elements of their framework. However, we aim to make four key advances. First, in our view, their framework conflates two distinct questions which need to be separated:

1. The distribution question: In what conditions are we justified in ascribing (*some* form of) consciousness to some animal species?
2. The quality question: In which conditions are we justified in ascribing a *particular* form of consciousness to some animal species?

Their conflation is manifest through the operationalizations of the conscious dimensions proposed by Birch et al. Some, like trace

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[9] For a more detailed examination of the relation between trace conditioning and animal consciousness, see Droege, Weiss, Schwob, and Braithwaite (2021) and Mason and Lavery (2022). In a nutshell, the evidence seems to imply that associative connections between stimuli separated by a temporal interval can be learned without conscious experience of the stimuli. However, learning the exact temporal relationship, i.e. how long it takes for the second stimulus to appear after the first disappeared, seems to require consciousness.

[10] Despite some debate on the merits of the mirror self-recognition task, we maintain that it, at a minimum, shows that an agent is able to recognize himself or herself on the basis of expectations about how one looks like (Nielsen, Suddendorf, & Slaughter, 2006) This also plausibly transfers to nonhuman animals. Recent developments highlight that mirror self-recognition is a gradually evolving phenomenon (Clary & Kelly, 2016) with species-specific forms (Brandl, 2018). Thus, the mirror self-recognition task is an interesting instrument to indicate self-awareness. One worry may be that mirror self-recognition is not only demonstrated in great apes, monkeys, dolphins and elephants which are known for having quite some complex cognitive abilities but also for magpies and cleaner fish. We believe that mirror self-recognition indicates basic self-awareness, also in cleaner fish. However, our concept of profiles of consciousness enables us to do justice to the intuition that the basic self-awareness may be experientially different for different species, namely due to the varying profiles of consciousness.

[11] Meanwhile, there are tests which are less demanding than standard mirror recognition. One can test for a behavioral difference between observing one's mirror image and observing a conspecific. Such a sensitivity can be characterized as a simple form of self-sensitivity which is prior to mirror self-recognition (Wittek et al., 2021).

[12] Another experimental paradigm stressed by Birch et al. is motivational trade-off which has been detected in fish (Millsopp & Laming, 2008), hermit crabs (Appel & Elwood, 2009) and bees (Gibbons, Versace, Crump, Baran, & Chittka, 2022).

Category	Dimension	Operationalization
External Representation	P(erceptual)-Richness	Perceptual categorization, nonconceptual multisensory integration, cross-modal learning and discrimination learning
	E(valuative)-Richness	Motivational trade-off, play, judgement biases and preference testing
	E(valuative)-Intensity	Direct behavioral expressions of conscious experiences like pain or pleasure behavior together with further processing evidence[12]
	Ext(ernal)-Syn(chronic)-Unity & Ext-Dia-Unity	Interocular transfer, meta-control and conceptual multisensory integration & apparent motion, flicker-fusion threshold and (on longer time scales) memory of objects and events
Self-Representation	**Self-Syn-Unity & Self-Dia-Unity**	Bodily awareness, mirror self-recognition & episodic-like and autobiographical memory as well as future planning
	Experience of Agency	Response inhibition and delay of gratification
	Experience of Ownership	Body-world discrimination and rubber-hand illusion (and similar illusions)
Cognitive Processing Strategies	Reasoning	Transitive inference, mindreading (e.g. deception), metacognition (e.g. uncertainty monitoring) and tool-use
	Learning	Trace conditioning, imitation learning, one-trial learning and reversal learning
	Abstraction	Conceptual categorization and perspective-taking

Fig. 1. This table shows the ten dimensions of consciousness, the three categories in which the dimensions subdivide and respective operationalizations for each dimension. Dimensions comprising strong indicators of consciousness are bold (see below for the distinction between strong and weak indicators).

Although pain or pleasure behavior alone is not a clear indicator of conscious experience it remains a strong indicator, especially when we can combine pain behavior with relevant evidence from a pain processing system and the relevant neural correlates. The idea that some behavioral criteria need additional neural processing evidence in biological systems to be telling is highlighted at the end of our proposal.

conditioning, are good tests of consciousness simpliciter but not particularly illuminating with respect to the kind of conscious experiences animals have. Others, for instance discrimination learning, do not qualify as credible evidence of consciousness. However, they can be valid indicators that a particular form of consciousness is present (in this case a high degree of perceptual richness), if one antecedently assumes that (perceptual) consciousness is present at all. We clearly distinguish these two questions and therefore call our alternative view a *two-tier account of consciousness*. Second, our taxonomy possesses more structure than the framework proposed by Birch et al. The crucial difference in this regard (pertaining to the distribution question) is that we distinguish strong and weak indicators of consciousness. The presence of a strong indicator of consciousness provides solid evidence that the animal displaying the indicator is conscious. By contrast, the evidential strength of weak indicators depends on the extent to which they are present since all indicators come in degrees. Only if a weak indicator is present to a high degree, e.g. a flexible and demanding form of learning, it can be taken as an interesting piece of evidence of consciousness. However, the mere presence of one weak indicator is inconclusive while the presence of a bunch of weak indicators interestingly points in the direction of the presence of consciousness.

Third, the framework of Birch et al. distinguishes dimensions only in terms of differences concerning features of the contents which are consciously experienced (e.g., whether they are evaluative, unified or represent oneself). By contrast, we hold that differences in consciousness profiles also include differences in the way particular contents are processed, e.g. by processes of learning, reasoning or abstraction (see below). Fourth, while their framework contains only five different dimensions, our account distinguishes consciousness along ten dimensions. This is mainly due to two changes: First, as just described, we add three dimensions of cognitive processing strategies, and second, we include the experience of body ownership and of agency, including mental agency (Metzinger, 2015), as further dimensions in respect to which the conscious experience of various animals can differ mutually.

Finally, with this two-tier account we propose a tractable research program for comparing and relating the various consciousness profiles characterized in terms of our framework. Eventually, this research path is intended to reveal when consciousness profiles of two different species belong to the same family because they manifest the same type of profile to different extents and when consciousness profiles differ in kind, not just in degree.

The next section will detail the structure and components of the taxonomy of consciousness we propose. More precisely, it states which dimensions our taxonomy posits, how they are organized, how they can be operationalized and how our framework licenses inferences on the distribution of consciousness and the kind of consciousness profile species possess. Thereby we elaborate on the four advantages we just outlined.

4. The two-tier account of consciousness

In this section, we are unfolding the structure of our taxonomy in more detail. Positing multiple dimensions of consciousness enables us to fruitfully address both, the questions about distribution and quality of conscious experiences. We first present the ten dimensions and then describe their application to both questions.

4.1. Ten dimensions of consciousness and their operationalization

We propose that one needs to specify how an animal scores on 10 conceptually independent dimensions of consciousness to fully capture the relevant aspect of its *consciousness profile* for a comparative perspective and we will illustrate how these dimensions are used to clarify the distribution question. They group into 3 categories, namely: capacities for the representation of the external world, capacities for the representation of oneself and general cognitive abilities to process information in sophisticated ways.[13] Here is the overview which will be described in the text below (Fig. 1).

The first two world-related dimensions concern the perceptual and evaluative richness of experiences. *Perceptual richness* is the level of detail with which animals consciously perceive the world. Like Birch et al., we take it to include not just pure unconceptualized experience, but an animal's capacity to perceptually categorize the surrounding world. *Evaluative richness* concerns the richness of features involved in the experience of valence specifically. We understand it way more inclusively than Birch and colleagues. Their characterization provide for evaluative richness limits it to the complexity and diversity of evaluative content that can be integrated for the purposes of decision making. This is unnecessarily constraining since animals can differ in the complexity, fineness of grain and diversity of their evaluative representations of the world, independently of their capacity to combine this information for decision making.

Apart from the two richness dimensions, conscious experiences differ in their evaluative intensity, i.e., how strongly the positive or negative valence is felt. Different pain experiences, for instance, can possess the same degree of richness but differ in their strength. Analogously, an unpleasant taste experience A (negative valence) can be more unpleasant than an unpleasant taste experience B, although B is richer than A, i.e., the number of features constituting the negative valence is higher. This *evaluative intensity* of conscious experience constitutes the third dimension. It is of special significance from an ethical point of view because – in many contexts – the value or disvalue of an evaluative experience does not depend on its richness (how many features are involved in an evaluative experience), but on its intensity. For instance, while the complexity of an animal's emotional life may have relevance for how to treat it, it seems that especially strong prohibitions against hurting an animal derive from the intensity of its pain experience.

Our taxonomy comprises the synchronic and diachronic unity of conscious experience. However, in contrast to Birch et al., we distinguish a world-related and a self-related unity dimension. With respect to the category targeting capacities for the representation of the external world, the unity dimension captures whether an animal experiences the world as unified at a certain point in time (synchronically) as well as across time (diachronically). That is, is the animal confronted by many isolated sensory impressions or do its experiences form a connected whole and does it experience the world as one continuous stream rather than a series of disjointed sensations?

The next dimension is the self-related unity dimension which involves the unity of (immediately) self-representational information in form of conscious self-awareness or self-consciousness. Synchronically, this dimension refers to the capacity for self-consciousness of being a unit, a self at a certain time point. Diachronically, it refers to the experience of oneself as persisting in time. This is intimately linked to episodic and autobiographical memory. Moreover, the category of self-experience comprises two other dimensions central to human experience of themselves: *Experience of agency* concerns whether an animals' actions feel like something it voluntarily initiates or controls rather than like events that passively happen to it. Also, the flow of experience itself might either be experienced as something under one's voluntary control or not involve such a sense of initiation or control (for example, the latter is the case in daydreaming). Finally, depending on the *experience of ownership*, an animal experiences its body parts as something that intimately belongs to it or as just another object in the external world.

As already revealed, the last category, containing three dimensions, comprises cognitive capacities which depend on types of processing strategies which are characteristic for consciousness in the sense that complex forms of these three dimensions are typically realized on the basis of conscious experiences. That is, conscious experience makes complex forms of these types of processing possible. However, this does not entail that the processes are themselves experienced consciously. The first of these dimensions concerns *complex forms of reasoning*, including the capacity to form complex trains of thought (like transitive inferences) and to reason on multiple domains (like mental states of others and oneself as well as causality). Second, consciousness is related to *complex forms of learning*. However, not all learning requires being conscious. For instance, simple classical and instrumental conditioning can occur in spinally transected rats (Grau, 2002; 2014). Due to the transection, the stimuli which are associated can't reach the brain, so we can be reasonably certain that the rats are not conscious of them. Further evidence of classical (Lipp et al., 2014) and instrumental conditioning (Pessiglione et al., 2008; Atas et al., 2014) on stimuli which were not consciously perceived exists. Hence, one needs to look for more sophisticated forms of learning which involve cognitive processes which are plausibly sufficient for or at least contribute to consciousness. For this reason, capacities like learning from a single or very few trials, learning associations between stimuli whose occurrences do not overlap in time or learning to successfully imitate goal-directed behavior are better candidates for being indicators of consciousness. They indicate a way of processing stimuli which is tied to consciousness.

The final dimension captures an animal's ability to build and use *high-level abstract forms categorizing specific sensory stimuli and single events*. According to our hypothesis, consciousness is associated with the capacity to behave sensitively to distinctions within general and abstract, as opposed to specific and concrete, categories.

We have arrived at this list of ten dimensions by taking human consciousness as a starting point. Every dimension corresponds to one feature of human phenomenology or human consciousness-related processing which can conceivably vary independently of changes in the other dimensions. Furthermore, all dimensions are supposed to be important to an animal's experiential access to the world or itself and to be fundamental, i.e., not reducible to other dimensions or other important phenomenal (for the first seven dimensions) or cognitive (for the last three) properties. These 10 dimensions remain our anchoring framework for any general investigation of consciousness from a comparative perspective. That is, a general comparison of animal consciousness profiles should make use of all ten dimensions. That being said, the framework can be enriched and modified for the purposes of other kinds of comparisons: If only two particular species are compared or even just individuals within one species, the most telling profile characterization may require to add, differentiate or remove certain dimensions. Thus, the exact shape of the framework should adjust to its context of application.

To transform our framework into a useful research tool, we suggest operationalizations for each of the ten dimensions.[14] To be clear, it is perfectly *possible* for animals to display many of these indicators without being conscious. Given the current stage of consciousness research, there are no foolproof indicators of animal consciousness. Unavoidably, the indicators we choose are fallible. However, they are justified by an

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[13] We are not presupposing that these capacities are clearly distinct and independent but only that most capacities typically have a dominant role either in enabling the representation of the external world or the representation of oneself, like visual perception predominantly serves to represent the external world while proprioception or the experience of agency are mainly informing us about ourselves. In principle, all capacities process both information about the external world and information about oneself. When seeing a car, I receive a lot of information about the car but also the information how I am spatially located in relation to the car. Some capacities are intermediate ones like the capacity to experience pain: in many situations, we receive with pain mainly information about bad influences of the environment on our body, e.g. when I stepped on a sharp object. In other situations, like visceral pain, by pain we mainly receive information about our bodily situation. Actually, it seems that, to understand the phenomenon pain, we need to account for both, internal and external information, as equally relevant.

[14] Many of our suggestions overlap with empirical tests proposed by Birch et al. (2020).

inference to the best explanation, in line with the species-sensitive validation we described earlier. Thus, exhibiting many of these indicators increases the chance that an animal is conscious, and scores high on the relevant dimension, without guaranteeing it.

Perceptual categorization, non-conceptual multisensory integration, cross-modal learning and discrimination learning (with a focus on learning to discriminate stimuli which only differ slightly) function as tests of *perceptual richness. Evaluative richness* is operationalized through motivational trade-off behavior, play, judgement biases ("optimism" and "pessimism" bias) and preference testing (where the fineness of grain of those preferences is ascertained).

Means to compare the *intensity* of particular *evaluative experiences* of *different species* in detail are not available at the moment. Since we focus on a comparative perspective in this paper, this dimension is only of limited help here while it is fruitful for intraspecies comparisons.[15] However, studying pain behavior in conjunction with evidence on the neural processing of pain may get us some grip on the intensity of evaluative experience.[16] While the dimensions proposed aim to be pragmatically useful, the function of our framework is not exhausted by encouraging attributions of consciousness profiles in the light of presently available methods. The framework is also supposed to guide future research and encourage the adoption of new methods. Since a better understanding of e-intensity seems especially important from an ethical point of view, the inclusion of this dimension serves to point researchers to this important gap in our understanding of animal consciousness.

Evidence of *external synchronic unity* is provided by capacities for interocular transfer, thorough (conceptual) multisensory integration and meta-control, i.e., the ability to make coherent actions when the two visual hemifields are presented with conflicting information (Adam & Güntürkün, 2009; Birch et al., 2020).[17] *External diachronic unity* can be ascertained via apparent motion, an animals' flicker-fusion threshold[18] and (on longer time scales) memory of objects and events sufficient for recognizing the identity of individual objects or types of events.

Self-related synchronic unity manifests in bodily awareness and the ability to pass the mirror-mark test (or other tests of self-recognition). *Self-related diachronic unity* is operationalized via tests of episodic and autobiographical memory as well as future planning. *Experience of agency* is operationalized through response inhibition and delay of gratification[19] and *experience of ownership* through the ability to discriminate between one's own body and the world as well as the rubber-hand illusion (and similar illusions).

Reasoning is operationalized as the capacity for transitive inference, mindreading (e.g. deception), metacognition (e.g. uncertainty monitoring) and tool-use. *Learning* is tested as trace conditioning, imitation learning, one-trial learning and reversal learning. Finally, *abstraction* is expressed in abilities for conceptual categorization and perspective-taking.

4.2. Addressing the distribution question

In respect to the distribution question, i.e. which animals have conscious experiences at all, the ten dimensions and their associated operationalizations differ in relevance, i.e. we need to distinguish strong and weak indicators mainly depending on how informative the operationalizations are for the presence of conscious experiences. We submit that – when following the cognitive approach – the operationalizations of evaluative intensity, external and internal diachronic and synchronic unity, feeling of agency and feeling of ownership should be considered as *strong indicators of consciousness* since clear forms of them seem to be enabled or enhanced by consciousness. For instance, the sense of ownership of body parts is important for caring about the integrity of one's own body which is especially obvious if, e.g., conscious pain experience is lacking: infants with inborn lack of pain sensitivity do not live long as they destroy their own body carelessly. Finding those strong indicators clearly realized, as manifested through the operationalizations, in an animal to a large extent provides significant evidence of consciousness.

By contrast, the operationalizations of the other dimensions are rather weak indicators, i.e., they only provide some evidence of consciousness if they are realized to a rather high degree in a large cluster of indicators. Without any strong indicator being involved, a single weak indicator does not warrant any attribution of conscious experience but invites for further investigations. A cluster of weak indicators should be taken as provisionally indicating conscious experiences which still needs further evidence for a final clarification. But a provisional attribution of conscious experience may be sufficient to justify the ascription of certain (pro tanto) ethical rights, e.g. not to be harmed with unnecessary (potential) pain (Birch, 2017; Dung, 2022b).

Thus, the distinction of weak and strong evidence of consciousness enables us to express the degree to which attributions of consciousness to a species are supported by empirical evidence, namely no support (if there is no evidence for any dimension), weak support (if there are only a few weak indicators or only very few realized to a high degree), intermediate evidence of consciousness (many weak indicators are realized to a high degree), strong evidence (if there is clear evidence for at least one strong indicator) and compelling evidence of consciousness (if there is clear evidence for several strong indicators). Notably, our framework is not designed to provide strong evidence for the absence of consciousness because it does not preclude that alternative approaches, for instance based on analogy or particular theories of consciousness, can find additional evidence of consciousness.

4.3. Describing the quality of conscious experiences with a dimensional profile

In addition, we can paint a multi-facetted, nuanced picture of what having conscious experiences is like for different kinds of animals given that they are conscious. For our two-tier account allows that the experiential life of different animals can diverge in some respects but converge in others. For the same reason, it equips us with the tools to express that some types of experience are richer or more complex in one kind of animal while other types of experience are simpler or less rich. In short, our framework aspires to supply adequate, fine-grained descriptions of conscious experience.

As will be illustrated in the next section via case studies, these operationalizations can be used to empirically justify ascriptions of a score for each consciousness dimension to an animal. The totality of 10 scores – one for every dimension – constitutes the *total consciousness profile* of the species for a multi-species comparative perspective. By investigating the consciousness scores and consciousness profiles of many animals, a new research avenue opens up. Having numerical scores for different consciousness dimensions allows to search for (positive or negative) correlations between scores in different dimensions. Moreover, one can group consciousness profiles into families.

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[15] If we answered the distribution question positively, i.e. the species is conscious, then behavior indicating different evaluative intensities is quite informative for the profile of consciousness, e.g. in rat studies (Khan, Benavent, Korczeniewska, Benoliel, & Eliav, 2014).

[16] For a review of pain processing in the human brain, see Coghill, Sang, Maisog, and Iadarola (1999).

[17] Some abilities have analogs for other sense modalities.

[18] The flicker-fusion-threshold is the frequency at which an intermittent light stimulus appears to be completely steady to an observer. Arguably, it captures the temporal acuity of vision.

[19] Future research on experience of agency should investigate affective responses to self-efficacy in animals. If animals display different affects in response to changes in the environment they caused themselves versus changes that happened independently, this provides clues that those animals sense themselves as agents.

Some consciousness profile A may be a sub- or superset of B in the sense that A scores lower or higher than B on every consciousness dimension. If this is the case, A and B may belong to the same family, even if their consciousness profiles differ, because A may just be a stronger or weaker manifestation of the same underlying consciousness structure. By contrast, if A scores higher than B on some dimensions and lower than it on others, they don't belong to the same family. It may turn out that some form of *monism*, in which all consciousness profiles belong to roughly the same family, is true. On the other hand, the reverse – a *pluralism* of different consciousness families – is possible as well. Now, we display the virtues of our framework by applying it to some selected animal species. In this way, we can illustrate how the consciousness profile of a species is measured and how the relations between the profiles of different species can be analyzed fruitfully.

5. Applying the species-sensitive, two-tier account of consciousness

The *total* consciousness profile of an animal is the conjunction of the consciousness scores pertaining to every individual dimension. How do we assign consciousness scores to different dimensions? We stipulate that every dimension can either not be present or be present to a weak, moderate or strong degree. These qualitative assessments correspond to pragmatically chosen assignments of numerical scores of 0 (absent), 1 (weak), 2 (moderate) or 3 (strong) to the different dimensions. The assignment of the score is determined by the extent to which different operationalizations suggest that animals possess features relevant to consciousness. How the operationalizations we suggested flow into a particular consciousness score cannot be fully captured by an algorithmic procedure. For it depends on how the different operationalizations should be weighted which in turn depends on context factors, in particular the specific species that is examined, interdependencies between different operationalizations and the reliability of the particular set of studies under scrutiny. Thus, such judgements should eventually be left to subject matter experts.

Crucially, the consciousness scores of different dimensions are *minimal* in the sense that they likely underestimate the consciousness scores of different species. This is the case because 0 is used as the default score which is increased proportionally to the evidence of consciousness suggested by the operationalizations which is contained within the scientific literature. Thus, a species gets a score of 0 if the literature contains neither evidence for nor against the possession of the relevant feature. Further research will likely find evidence of consciousness-relevant animal capacities that we don't know of yet, such that consciousness scores will tend to increase over time. This is an adequate strategy since we want to prevent a too quick ascription of consciousness due to anthropomorphizing.

In this section, we illustrate our framework by assigning consciousness scores to two kinds of well-studied animals: primates and rodents. This selection exemplifies another feature of our framework: It can be applied to different taxonomic groups. In addition, one may assign consciousness scores to the set of members of a species which belong to certain age groups, e.g., mice younger than three months. In principle, one can even attribute consciousness scores to specific individuals. In general, the selection of units of analysis is subject to competing demands. On the one hand, the category of animal evaluated should be sufficiently narrow and homogenous that all its members can be expected to share the same total consciousness profile and to exhibit the same indicators of consciousness. On the other, the class should be sufficiently large that, among some members of the category, there is credible evidence regarding the presence or absence of many of the proposed indicators.

This trade-off poses the risk that pooling information from indicators found in different species can mislead. Suppose we aim to estimate the score of the taxonomical group T on dimension d_1. Suppose further that I_1 and I_2 jointly serve as sufficient indicators of a high degree of d_1. It might be that species s_1 and s_2 both belong to T and that s_1 possesses I_1 and lacks I_2 while s_2 possesses I_2 and lacks I_1. If we applied the method we espouse blindly, we would conclude that T possesses a high degree of d_1 since there is evidence of I_1 as well as I_2. But this would be a mistake. In this scenario, there is no animal species belonging to T which possesses all requisite indicators, i.e., I_1 and I_2. Hence, we should not be confident that d_1 is high. Thus, when applying our two-tier account, it is important to guard against overestimating evidence of consciousness due to combining data from many different species.

5.1. Consciousness in primates and rodents

Let's begin with primates. Primates are able to group their surroundings into categories (Haun & Call, 2009; Mendez, Prado, Mendoza, & Merchant, 2011). Also, they are used as model organisms in research on human multisensory integration (Juan et al., 2017; Lanz, Moret, Rouiller, & Loquet, 2013) and cross-modal learning (see also: Ettlinger & Jarvis, 1976). Their use as model-organism in the study of perception also suggests that they can learn to make visual discriminations whose fineness of grain is similar to human perception. For this reason, primates get a p-richness score of 3, i.e., the highest that is possible. Their e-richness score is 3 as well since they perform motivational trade-offs, play, have judgement biases (Bethell, Holmes, MacLarnon, & Semple., 2012), and show fine-grained preferences when tested (Mason, Saxon, & Sharpe, 1963). Since we currently do not have the requisite means to compare e-intensity between species, primates get a score of 0 on this dimension (like every other species).[20] With respect to external synchronic unity (ext-*syn*-unity), primates get the full score of 3, since they possess capacities for meta-control (Redford, 2010), inter-ocular transfer (Chow & Nissen, 1955; Noble, 1973) and conceptual multisensory integration. Primates are subject to motion illusions, they have impressive long-term memory (Lewis, Berntsen, & Call, 2019) and their flicker-fusion threshold is within the normal range which is why they get 3 points on the external diachronic unity (ext-dia-unity) dimension.

In respect to self-related diachronic and synchronic unity (self-syn-unity and self-dia-unity), primates receive the maximum score as well. They earn three points for bodily awareness, e.g. shown by their sensitivity for peripersonal space (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009), and the fact that some species passed the mirror-mark test (self-syn-unity).[21] While the extent of mental time travel in primates is contested, their capacities of episodic memory and future planning seem to be at least as pronounced as in any other non-human animal (self-dia-unity), leading to a score of 3 (Martin-Ordas, Berntsen, & Call, 2013; Osvath & Martin-Ordas, 2014; Suddendorf & Corballis, 2007; van Schaik, Damerius, & Isler, 2013).

Since primates show response-inhibition (Barth & Call, 2006; Vlamings, Hare, & Call, 2010) and delay of gratification (Anderson, Kuroshima, & Fujita, 2010; Beran, 2002) (feeling of agency) as well as body-world discrimination (Lriki, Tanaka, & Iwamura, 1996) (feeling of ownership), they earn three more points on the feeling of agency dimension. However, they do only get a score of 2 for feeling of ownership, signifying that the capacity is present to a moderate degree. They do not receive the full score because – as far as we know – there is only weak confirmation of the rubber-hand illusion in primates in the literature (Shokur et al., 2013). Finally, primates receive the full score in all three processing dimensions. For they excel in transitive inference (Gillan, 1981; Gillan, 1982; MacLean, Merritt, & Brannon, 2008), social

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[20] This score of 0 does not entail that primates do not have evaluative consciousness, as the e-richness dimension indicates.

[21] The species that pass the mirror self-recognition test in addition to humans include at least chimpanzees, orangutans, Asian elephants, bottlenose dolphins and magpies. For monkeys a recent observation is reported in Chang, Zhang, Poo, and Gong (2017). However, the ability to pass the mirror test might extend more widely in the animal kingdom (see footnote 8 and footnote 9).

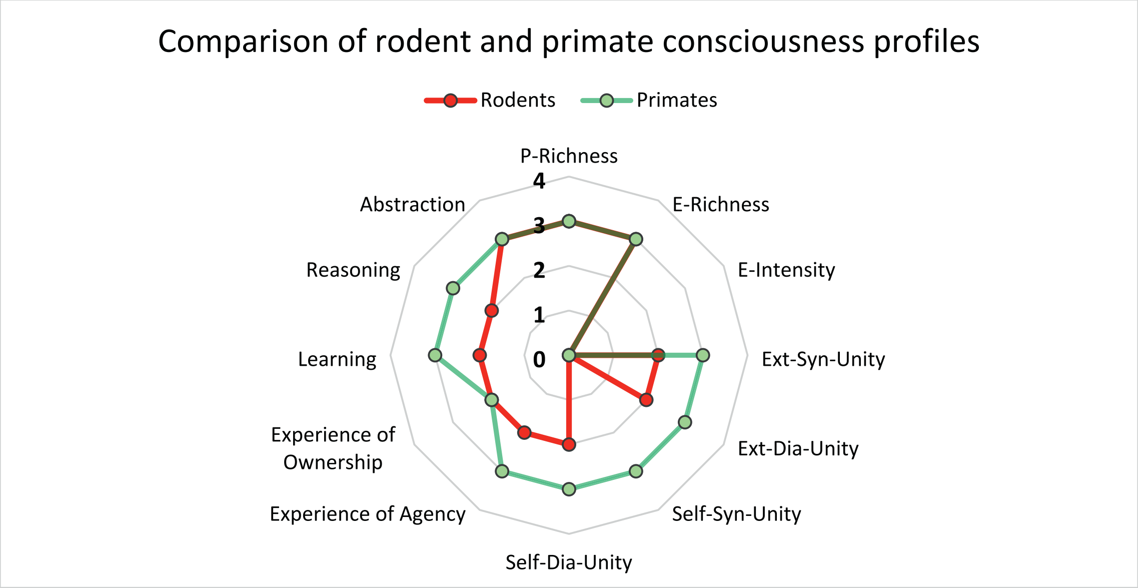

Fig. 2. Based on the literature review below, those are the consciousness profiles for rodents and primates. Brown color signifies the parts of the diagram where both consciousness profiles overlap.
Note that nothing in the framework guarantees that humans will always have the highest value in all dimensions. The framework of 10 dimensions is made for an epistemically adequate comparison of multiple species. Given this structure and purpose, humans score high on all the suggested dimensions. However, the framework can be adjusted to account for fine-grained comparisons of fewer species, e.g., humans and dogs only. In this case, for instance, the dimension of perceptual richness may be unfolded into five dimensions about all five human perceptual senses with the plausible consequence that dogs score higher with respect to olfactory richness, since their ability to smell is more pronounced. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

cognition (Andrews, 2012; Heyes, 2017; Martin, 2019; Savage-Rumbaugh & McDonald, 1988), uncertainty monitoring (Call, 2010), tool-use (Vale et al., 2016) (reasoning), trace-conditioning (Clark & Zola, 1998), one-trial learning (Achterberg et al., 2020; Ben-Haim et al., 2021), imitation learning (Buttelmann, Carpenter, Call, & Tomasello, 2007) reversal learning, conceptual categorization and visual perspective-taking (Krachun & Call, 2009; Okamoto-Barth, Call, & Tomasello, 2007). Insofar as any non-human animals possess these capacities, primates do too. In conclusion, primates receive the maximum score on every dimension except for e-intensity – due to limitations of current scientific methods – and feeling of ownership because there are no published studies similar to the rubber-hand illusion in primates. Arguably, if not for our current epistemic limitations, primates would receive the maximum score on all of our dimensions. This means that there is a high probability that primates possess consciousness and that their conscious experience is pronounced among all known facets of consciousness.

The same type of reasoning can now be applied to other types of animals. Next, we look at rodents. Starting with p-richness, current research suggests that rodents can group objects perceptually into categories according to sameness and difference as well as according to shape (Brooks et al., 2013); furthermore they can categorize conspecifics (Vinken, Vermaercke, & Op de Beeck, 2014). Rats have been shown to perform similarly to humans in tasks of multisensory decision-making (Raposo, Sheppard, Schrater, & Churchland, 2012) and there is some evidence of cross-modal learning (Lipton, Alvarez, & Eichenbaum, 1999; Winters & Reid, 2010). In addition, mice have been used as model organism for research on multisensory processing (Siemann et al., 2015). Even though there are no studies of discrimination learning which can be used to ascertain fineness of grain of perception, rodents' capacities for multisensory integration and categorization warrant a p-richness score of 3. Rodents play, have judgement biases (Burman, Parker, Paul, & Mendl, 2008; Harding, Paul, & Mendl, 2004), show fine-grained preferences when tested (e.g., Hernández, Navarro-Castilla, Planillo, Sánchez-González, & Barja, 2018) and perform motivational trade-offs (Hanmer, Riddell, & Williams, 2010). Thus, their e-richness score is 3 as well. For the same reason as primates, rodents receive an e-intensity score of 0.

Rodents do exhibit conceptual multisensory integration and inter-ocular transfer while there are no studies (that we are aware of) demonstrating meta-control. Taking all this into account, they receive an ext-*syn*-unity score of 2. The flicker-fusion threshold of different rodent species varies widely. Schukraft (2020) reports the flicker-fusion threshold of the brown rat (*rattus norvegicus*) as 39 Hz and of the golden-mantled ground squirrel (*spermophilus lateralis*) as 120 Hz (for comparison, the human threshold is 60 Hz). Rats show good long-term memory (Vnek & Rothblat, 1996) while we are not aware of any evidence of relevant motion illusions in the literature. This leads us to attribute an ext-dia-unity score of 2. Since we do not know any particular relevant evidence for bodily awareness in rodents and they have not passed the mirror-mark test, they receive 0 on the self-syn-unity dimension. Despite some limitations relative to human or primate capacities (Roberts & Feeney, 2009), rats have episodic memory and can plan for the future (Crystal, 2012; Eacott & Easton, 2007; Sato, 2021). Hence, they receive a self-dia-unity score of 2. There is some indication of response-inhibition in rats (Broersen & Uylings, 1999) and delay of gratification has been observed, albeit less reliably and over shorter intervals than in primates (Bizot, Le Bihan, Puech, Hamon, & Thiébot, 1999; Chelonis, Logue, Sheehy, & Mao, 1998; Evenden & Ryan, 1996). We assign a score of 2 to feeling of agency. Mice are subject to the rubber-tail illusion (Wada, Takano, Ora, Ide, & Kansaku, 2016). Since we do not know of other telling evidence of experience of ownership in rodents, we assign a score of 2 as well.

Rodents attain a score of 2 for learning as well. It is unclear whether they learn by imitation (Galef Jr., 2008) while there is evidence of some degree of trace conditioning (Moye & Rudy, 1987), reversal learning (McAlonan & Brown, 2003) and rapid learning (Hermer-Vazquez et al., 2005). Rats are capable of transitive inference (Dusek & Eichenbaum, 1997; Roberts & Phelps, 1994; van Elzakker, O'Reilly, & Rudy, 2003), uncertainty monitoring (Foote & Crystal, 2007), and tool-use (Nagano,

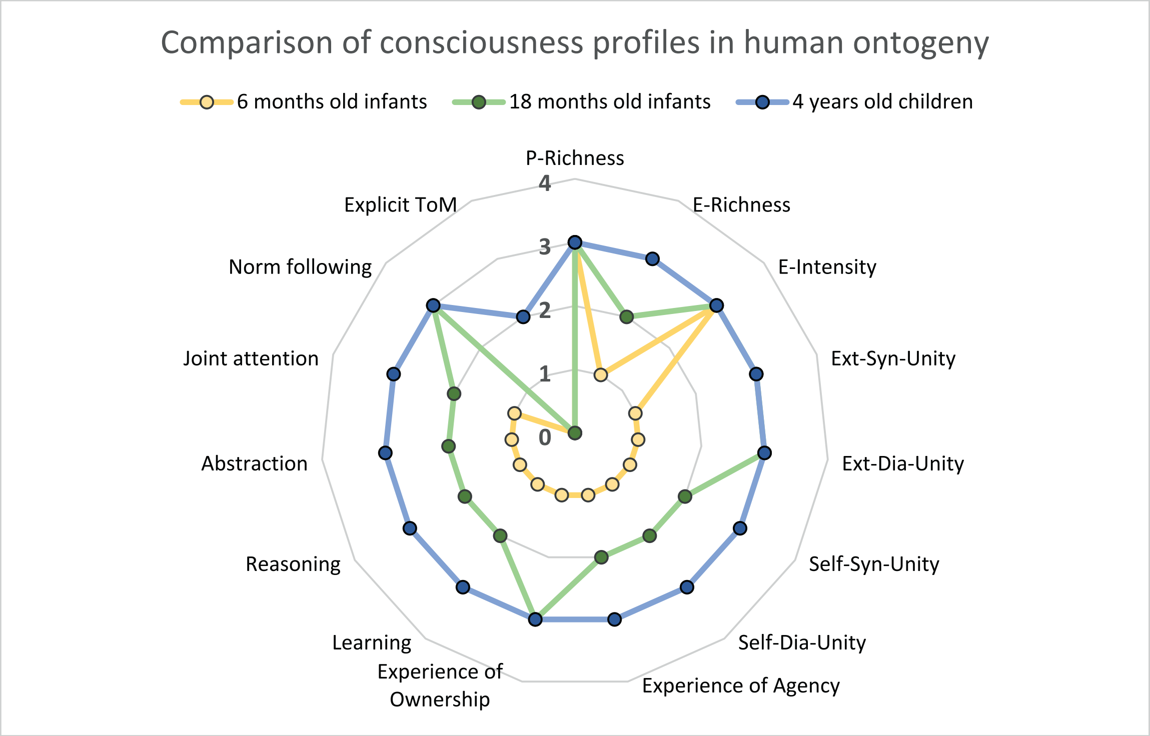

Fig. 3. This diagram illustrates how the two-tier framework can be adjusted to enable more specific types of comparisons. In this case, consciousness profiles of humans in different stages of development are contrasted. The concrete profiles are loosely based on the developmental literature but serve only an illustrative function.
Note also that the fruitful comparison of human infants requires that the numerical scale we apply (0–3) is interpreted more demandingly than in interspecies comparisons of animals. To discern interesting differences in consciousness profiles between neurotypical humans, the highest value (3) has to represent a stronger manifestation of a consciousness dimension than what can be found in all non-human animals.
For the same reason, we are not committed to the claim that there are no relevant differences in consciousness profiles between 4 years old humans and adults.

2019; Nagano & Aoyama, 2017a, 2017b). However, we know of no evidence for mindreading in rodents which is why they receive a reasoning score of 2. Finally, rodents receive a score of 3 on the abstraction dimension. We already mentioned their categorization ability and we take their performance at hide-and-seek as evidence of perspective-taking (Reinhold, Sanguinetti-Scheck, Hartmann, & Brecht, 2019).

It should be noted that there is no dimension on which rodents score higher than primates while there are of course several dimensions on which primates are superior. As shown in Fig. 2, when depicted graphically the consciousness profile of rodents is contained within the consciousness profile of primates. Hence, if this relation between the two consciousness profiles survives further research and scrutiny, there is a meaningful sense in which primates have a “higher level” of consciousness than rodents. One might say that primates and rodents belong to the same family of consciousness profiles, even if the one of primates is more pronounced.

5.2. *Advantages of the two-tier account of consciousness*

As these two case studies illustrate, our taxonomy makes it possible to integrate various sources of empirical data into empirically justified and sufficiently fine-grained attributions of the presence of consciousness and consciousness profiles to various animal species. As such, its dimensions and operationalizations are selected to optimally serve for inter-species comparisons of consciousness. Furthermore, these dimensions are understood as core dimensions for species comparison within a flexible two-tier account. Since the framework is strongly shaped by relevant empirical evidence, we allow for an enrichment of the framework in at least three ways: 1. We can combine the mainly behavioral operationalizations with new types of empirical evidence for animal cognition, e.g. neural correlates, 2. we can adjust the operationalizations, i.e. make them more fine-grained or coarse-grained, 3. we may add a dimension if we discover a new telling dimension or ignore one for a comparison if it is not applicable. This includes strong modifications to account for completely different cognitive systems, e.g. AI systems.

Concerning 1: This enables us to improve the relevance of operationalizations. For instance, binocular rivalry was for quite a while seen as a strong indicator of consciousness until binocular rivalry from invisible flicker stimuli was discovered (Zou, He, & Zhang, 2016). But interestingly due to fMRI measurement, these stimuli activated the visual areas, but not the prefrontal and parietal areas. Thus, binocular rivalry together with certain neural processing can be used as a strong indicator of conscious experiences. Future research has to enrich our framework by especially enriching the behavioral test with neuroscientific processing evidence.

Concerning 2: Adjustment is important in respect to intra-species comparisons, for instance comparisons of humans in different stages of ontogenetic development: the same basic dimensions can be employed but some need to be differentiated more finely. For instance, to capture consciousness differences central to understanding human variation, more kinds of self-consciousness may need to be distinguished. It follows that new operationalizations of these dimensions need to be introduced.[22]

Concerning 3: Our framework cannot be directly transferred to the question of machine consciousness since it does not have the tools to distinguish strong, weak and no evidence of consciousness in machines.

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[22] By adjusting the dimensions and operationalizations, our account could also be applied to humans with disorders of consciousness.

Good evidence of animal consciousness is not always good evidence of machine consciousness. This has several reasons, a central one being that the inference to the best explanation is weaker in the case of machines because they don't share biological features and evolutionary history with humans which makes it more likely that the same types of capacities are caused differently in humans and machines. Nevertheless, our taxonomy can provide a starting point for developing a framework which characterizes *different forms* of machine consciousness, if machine consciousness is possible at all. Since there are large differences between kinds of conceivable conscious machines, we may need to analyze consciousness dimensions in a more coarse-grained manner and may need to posit entirely new consciousness dimensions in addition to the core dimensions to compare types of artificial consciousness.

We consider it an open question whether, and how, the framework could be adjusted to make empirically motivated attributions of consciousness profiles to artificial systems possible. In the light of this uncertainty, we propose introducing precautionary measures to save intelligent machines from harm if they satisfy many indicators to a strong degree, just to make sure that we do not mistreat a potentially conscious system.

So, to recap the core point: Our framework is sufficiently fine-grained in that it includes all important dimensions of human experience. Simultaneously, it is sufficiently coarse-grained to be pragmatically useful, as finer distinctions are hard to confirm empirically and including more dimensions threatens the role of the framework in providing guidance on what future research efforts should focus on.

Moreover, and crucially, the ten dimensions we propose are claimed to be suitable for a general comparison of consciousness profiles in all animal species simultaneously. When we conduct different more specific comparisons, for instance between two particular species or between ontogenetic stages of the same species, the dimensions need to be adjusted. In particular, when similar species are compared, the fineness of grain needs to be increased (see Fig. 3 for an illustrative example), and when very different species are compared, it needs to be decreased. Depending on the comparison, the appropriate degree of abstraction varies.

6. Conclusion

In this paper, we adopted the assumption that animal consciousness should be described along various dimensions and developed it further. Our two-tier account of phenomenal consciousness is distinctive in multiple ways. Most crucial are the following: First, it clearly separates the distribution and the quality question and provides distinct strategies to answer them. Second, the central tool is our taxonomy of dimensions of consciousness to handle both questions where each dimension is characterized by a series of operationalizations which are justified via species-sensitive validation. Third, it structures the profiles of consciousness into three relevant categories (external representation, self-representation and cognitive processing strategies) and differentiates them into ten dimensions. Finally, we hope that – by motivating and guiding further empirical research into animal consciousness – our taxonomy will shed light on which animals are conscious and what consciousness profiles different species have.

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Credit author statement

This article is based on equal contribution from both authors.
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Declaration of Competing Interest

No competing interests.

Data availability

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