



Review article

In search for consciousness in animals: Using working memory and voluntary attention as behavioral indicators

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ABSTRACT

Whether animals have subjective experiences about the content of their sensory input, i.e., whether they are aware of stimuli, is a notoriously difficult question to answer. If consciousness is present in animals, it must share fundamental characteristics with human awareness. Working memory and voluntary/endogenous attention are suggested as diagnostic features of conscious awareness. Behavioral evidence shows clear signatures of both working memory and voluntary attention as minimal criterium for sensory consciousness in mammals and birds. In contrast, reptiles and amphibians show no sign of either working memory or volitional attention. Surprisingly, some species of teleost fishes exhibit elementary working memory and voluntary attention effects suggestive of possibly rudimentary forms of subjective experience. With the potential exception of honeybees, evidence for conscious processing is lacking in invertebrates. These findings suggest that consciousness is not ubiquitous in the animal kingdom but also not exclusive to humans. The phylogenetic gap between animal taxa argues that evolution does not rely on specific neural substrates to endow distantly related species with basic forms of consciousness.

1. Introduction

The evolution of consciousness is one of the greatest riddles in biology. Consciousness in its basic form (sensory consciousness) refers to the awareness of, and ability to report (to access) the content of subjective experiences. We are certain that we humans are consciously aware of our experiences. However, whether animals may also have conscious experiences is a matter of debate. Because subjective awareness is a private experience by definition, trying to determine its presence in animals from the outside based on third-person observations is non-trivial and error-prone.

In the past, different types of indicators—from behavioral and cognitive to neuroanatomical and neurophysiological indicators—have been suggested (Weiskrantz, 1995; Griffin and Speck, 2004; Seth et al., 2005; Butler and Cotterill, 2006; Edelman and Seth, 2009; Pennartz et al., 2019). For example, in neurobiology, corollary discharge (i.e., efference copy signals; Vallortigara, 2021; Jékely et al., 2021) and certain brain waves (Ehret and Romand, 2022) have been suggested as markers of sensory awareness. While these different types of indicators can be most valuable, behavioral/cognitive indicators still have a privileged role because consciousness expresses itself in the way an organism interacts with its world. Without denying the value of criteria from

other biological disciplines, this article therefore focuses on behavioral/cognitive features as particularly promising indicators of consciousness in animals.

2. The relationship between behavior and awareness

Many complex behaviors superficially may look as though they invoke subjective experience, but upon closer inspection operate without conscious awareness. Our human experience tells us that only a small fraction of the stimuli, thoughts, and actions we deal with day in, day out reaches conscious awareness. For instance, when driving to work, we process an almost infinite amount of information to navigate, to shift gears, to avoid crashes, to follow traffic signs, and so on; only momentarily, we may briefly be aware of the lyrics of the song played from the radio before they, too, vanish into unconsciousness. Through much of our life, consciousness is not necessary for sensing, learning, or responding, irrespective of how complex certain behaviors may be (Bargh and Morsella, 2008; Hassin, 2013; Lumer, 2019). There is no reason to believe that the significance of unconscious processing would be any less important in animals. On the contrary, due to their simpler nervous systems, unconscious operations are likely more dominant, or even all determining, in animals. Even more, complex behaviors that

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may intuitively be associated with awareness can be accomplished without a central nervous system in animals. For example, hindlimb scratching behavior in sea turtles can be controlled by the spine alone (Stein et al., 1995), and an excised octopus leg responds to noxious stimuli (Alupay et al., 2014). In principle, it is conceivable that an organism exhibits complex behavior and cognition and successfully lives its life without ever becoming aware of the content of information. The scope of unconscious processes as sufficient explanation of behavior is relevant for a scientific investigation of subjective experiences in animals. The default mode is that consciousness is not required for complex behaviors (Epstein, 1984; Sober, 2015). The question therefore is: are there still good reasons to assign subjective experiences to animals?

In search for such consciousness indicators, contemporary multi-component approaches tend to include (batteries of) complex behaviors and capabilities that, when considered in isolation, are known to function without consciousness. For example, vivid sensory abilities are taken as a proxy for the richness of perceptual experiences (Birch et al., 2020b), even though sensory processing even in humans can work without ever reaching consciousness (Axelrod et al., 2015; Prinz, 2017). Similarly, organization of behavior across time is interpreted as suggestive evidence for a “stream of consciousness” or “mental time travel” (Birch et al., 2020b), although associative learning is known to provide “for myriad unconscious ways of responding to the world” (Squire and Dede, 2015). In a similar vein, contextual learning (Birch et al., 2020a), goal-directed behavior (Pennartz, 2018), behavioral flexibility (Droege et al., 2021), susceptibility to illusions (Pennartz et al., 2019), and other behaviors have been suggested as consciousness indicators. It is questionable whether summarizing processes that do not necessarily require consciousness in isolation may in sum give rise to consciousness. Furthermore, multi-component approaches suggest “distinctive consciousness profiles” for different animal species (Birch et al., 2020b); suddenly, we seem not only to be dealing with one type of subjective experience that needs explanation, but potentially with as many forms of consciousness as there are animal species on this planet. For the quest of a scientific explanation of animal consciousness, this level of complexity could be detrimental.

3. A reductionist behavioral approach to identify animal consciousness

The approach in this article is in some sense inverse to multi-component approaches to explain animal consciousness described above. Rather than picturing consciousness as a multi-faceted and species-specific phenomenon, this article posits that consciousness in all species shares fundamental characteristics (Shelton et al., 2008). The goal therefore is to find behavioral/cognitive mechanisms or resources that are:

- a) diagnostic in the sense that they are necessary (but maybe not sufficient);
- b) foundational in the sense that they can also be part of more complex forms of consciousness;
- c) concrete in the sense that they are specific enough to allow a rigorous scientific exploration;
- d) accessible in the sense that they can be studied with standardized behavioral tests across the animal tree of life.

Two cognitive mechanisms/resources that support consciousness in humans (and are intimately linked among themselves) are working memory and endogenous attention (Shelton et al., 2008; Oberauer, 2019). This attempt to probe the presence of consciousness in animals in terms of smaller cognitive entities subscribes to methodological reductionism. Just as the presence of cells in organisms is diagnostic of life, the presence of working memory and endogenous attention is viewed as being diagnostic for awareness. Not that this does not imply that the phenomenon of consciousness should be reduced to working memory of

endogenous attention. Rather, this approach posits that the presence of working memory and/or endogenous attention is minimally indicative of awareness about stimuli. The present paper therefore explores empirical signatures of working memory and voluntary attention in different animal taxa as diagnostic features and as a prerequisite to assign a basic type of conscious awareness.

Working memory and endogenous attention are of course already difficult enough concepts in their own right (Oberauer, 2019). Therefore, before linking working memory and voluntary attention to consciousness, it is worth defining them as separate cognitive mechanisms/resources. In addition, commonly accepted and well-controlled behavioral testing protocols need to be identified that probe either working memory or voluntary attention while avoiding alternative explanations for successful task performance, such as implicit association learning (Enquist et al., 2016). This sets the stage for the following exploration for working memory and voluntary attention as indicators of the presence of sensory consciousness in different animal taxa. The advantage of this approach is that statements on consciousness in different animal taxa can be extended, corrected, or refined with increasingly more data being collected.

4. Conscious and unconscious memory systems

As the name betrays, “working memory” is one of the brain’s many memory systems. Some of these memory systems (such as working memory) are defined as “conscious”, while others operate as “unconscious”. For the arguments laid out in this article, the distinction of these memory systems and their involvement in memory-guided tasks performed by animals is therefore important. The goal is to clarify why some cross-temporal behaviors in delayed response tasks can be linked to consciousness, whereas others are best explained as unconscious.

Memory systems can be discriminated according to the duration of the memory storage: short-term memory and long-term memory. It is well established that these two memory systems are not part of a temporal memory continuum but are clearly dissociable based on psychological, neuroanatomical and neurophysiological criteria (Squire, 2004; Squire and Dede, 2015; Camina and Güell, 2017).

In the realm of short-term memory, the engagement of different cognitive systems is generally accepted (despite disagreement about the number of such systems). At the very least, a distinction between working memory and other forms of short-term memory (such as sensory memory, e.g., iconic and echoic memory) needs to be made (Shevlin, 2020). While sensory short-term memory does not require consciousness (Dehaene et al., 2006), the contents of working memory are attention-dependent and can be held in an active, conscious state for as long as attention is directed at them (Carruthers, 2013). Working memory is our “mental sketchpad”; it allows us to actively retain and manipulate information in mind towards a goal, and thus constitutes the fundamental basis of cognition. Logie and Cowan (2015) defined working memory as “the holding mechanism in the mind for a small amount of information that is kept in a temporarily heightened state of availability.” A long-standing view, and one adopted in the current paper, posits that working memory is a conscious type of memory. Working memory—with its severe capacity limitation and vulnerability to interference—therefore, “should contain what we think of as the conscious mind” (Logie and Cowan, 2015; but see Soto et al., 2011; Trübtschek et al., 2017; Persuh et al., 2018; Gambarota et al., 2022, for discussions of a contrasting viewpoints). Therefore, the importance of working memory has long been acknowledged in conceptions of consciousness (Baars, 2002; Baddeley, 2007; Dehaene and Changeux, 2011; Dere et al., 2020; Zlomuzica and Dere, 2022). Whether the concept of working memory relates to a single capacity-limited mechanism shared across sensory modalities (Cowan, 2010) or specialized subsystems (Fougnie et al., 2015) is one of the unresolved issues; for the current treatise on animals, a single central working memory mechanism is assumed.

In terms of long-term memory, two types are accepted in humans:

non-declarative and declarative memory. Non-declarative memory is a type of implicit/unconscious long-term storage; imprinting, skill learning, classical conditioning, or priming are all part of non-declarative long-term memory (Squire, 2004; Squire and Dede, 2015; Camina and Güell, 2017). These memory contents are inaccessible to conscious recollection. With the exception of the simplest learning forms (habituation and sensitization), non-declarative learning and memory relies on stimulus–response associations that can also operate across time. Non-declarative memory is regarded a phylogenetically early form of behavioral plasticity and is thus widespread across the animal kingdom; its power as a unconscious source of behavioral flexibility, usually called “association learning”, cannot be overestimated (Squire and Dede, 2015; Enquist, 2016).

The second type of long-term memory is declarative memory as a form of explicit/conscious memory. As expressed by Squire and Dede (2015) “*declarative knowledge is knowledge available as conscious recollection*”. There are two types of declarative memory: semantic memory (facts about the world that are symbolic in nature and thus unique to humans) and episodic memory (the ability to re-experience a time-and-place-specific event as the foundation of autobiographical memory; Tulving, 1983). Whether nonhuman animals have the capacity for true episodic memory including the capacity for mental time travel that can return an animal to the scene of an earlier event is controversial. While some comparative psychologists claim “episodic-like” capabilities in animals (Clayton et al., 2003; Jozet-Alves et al., 2013; Breeden et al., 2016; Dere et al., 2018, 2019), others maintain that only human being possess episodic memory and the ability to mentally travel into the past and into the future (Tulving, 2005; Suddendorf and Corballis, 2007; Penn et al., 2008). Note that time travel not only requires sensory consciousness, the topic of the current article, but a higher, self-reflective form of consciousness that could be called self-consciousness (Tulving, 1983). Despite the obvious relevance of episodic-like memory for the question of consciousness in animals, a detailed discussion of this issue is beyond the topic of this article. Here, as in many other types of complex animal behaviors, a reductionist approach would be beneficial by first trying to clarify whether conscious cognitive components required for the encoding, storage and retrieval of episodic memories, such as working memory and endogenous attention, can be found in animals.

5. Working memory as indicator of consciousness

As outlined above, behaviors of animals can typically be explained in terms of non-declarative (association) learning and memory, and as such do not require any conscious processes. Only when the content of a stimulus needs to be kept in an active state for later task processes will working memory be required. This is a crucial aspect when evaluating cognitive components in different types of “delayed response tasks”, an umbrella term for a variety of different tasks that are all characterized by a temporal gap between a stimulus and a response. Importantly, an animal’s success in a delayed response task does not yet indicate awareness. This is because a temporal delay between stimulus and response does not automatically qualify for an engagement of working memory; unconscious short-term memory and/or non-declarative memory processes (such as imprinting; see Vallortigara et al., 1998) typically suffice to explain performance. This is the case for static stimulus–response associations, such as “hit the break on red”. Moreover, some variants of delayed response tasks may not capitalize on the active maintenance of stimulus content in working memory during at temporal gap but only require the early preparation of a contingent response. This scenario exists when, for instance, the goal of a motor response is known throughout the delay. For example, an animal may be able to prepare a movement right at the appearance of a cue stimulus, without the need to memorize any information of the stimulus during a delay (Curtis et al., 2004; Messinger et al., 2021). Movement preparation without working memory is also the most parsimonious explanation when the cue presentation is sufficient for the focal animal to determine

the appropriate response that is only delayed in its execution. For instance, when male zebrafish chose to approach a group of more females over a group of fewer females, no working memory is required even if the actual response (i.e., swimming towards the larger quantity of females) is postponed or the quantity of female fishes has been equalized between the two choice groups during the waiting period (Potrich et al., 2015). A similar explanation holds for approach behavior to conspecifics that are no longer visible at the time of the response (Lee et al., 2013, 2015). It is therefore relevant to determine when and under what circumstances in the transformation from perception to action the response can be selected. If this selection process coincides with the cue stimulus, no working memory is needed. If the selection process relies on the cue stimulus in conjunction with other types of information (e.g., rule information or comparison stimuli presented after the delay), working memory needs to be engaged.

A classic task to probe working memory capacities in animals is the delayed match-to-sample task (DMS task; Hunter, 1913). In the DMS task, a subject is first presented with a variable sample stimulus that is subsequently removed. After a delay period (of variable duration) without any stimulus, two or more choice stimuli are presented, and the subject receives a reward for choosing the one that matches the sample (Fig. 1a). To succeed, the subject needs to actively maintain relevant information that changes after each trial and to compare it against alternative choice stimuli to guide subsequent responses; in other words, the subject uses working memory (Baddeley, 1991). Working memory processes become even more explicit when the DMS task is combined with distractor stimuli that actively needs to be suppressed (Jacob and Nieder, 2014; Jacob et al., 2018) or variable rule information the animal needs to integrate to successfully solve a task (Wallis et al., 2001; Bongard and Nieder, 2010; Eiselt and Nieder, 2013; Veit and Nieder, 2013). The DMS task has been used in many animal species from different taxa (Lind et al., 2015) and will be used here to identify the presence of working memory capabilities.

6. Voluntary attention as indicator of consciousness

Attention captures the selective processing of one aspect of the environment at the expense of others. Attention can either be defined as a (limited) resource or as a selection mechanism (Oberauer, 2019). Importantly, attention comes in two different flavors (James, 1890; Weichselgartner and Sperling, 1987). The first type is exogenous (reflexive) attention, which operates in a passive, fast, transient, involuntary, stimulus-driven, and bottom-up manner. Exogenous attention allows an automatic orienting response to sudden stimulation. It is thought to be a phylogenetically older capability because it works in an automatic fashion that can be implemented with reflex-like circuits to react quickly to stimuli, such as food or predators (Carrasco, 2011; Krauzlis et al., 2018). Exogenous attention is certainly widespread in the animal kingdom as it allows for life-saving orienting responses.

The second type is endogenous (voluntary) attention. It operates in an active, slow, sustained, volitional, goal-driven, and top-down manner. Endogenous attention pertaining to perceptual input is also termed “selective attention” (Oberauer, 2019). Although voluntary attention is usually necessary to provide the contents for conscious experience, endogenous attention and consciousness are not identical processes (Haladjian and Montemayor, 2015). Endogenous attention is under conscious control and allows us to willfully monitor currently relevant information at the expense of irrelevant distractors (Goldstein et al., 2001; Carrasco, 2011). Therefore, only endogenous attention can be used as an indicator of subjective, conscious experience. The key question addressed in this review is not which animals possess attention in general, but more specifically which animals are endowed with endogenous attention.

As with working memory, the precise relationship between selective attention and consciousness is an area of ongoing investigations. Under certain laboratory conditions, selective spatial attention can occur

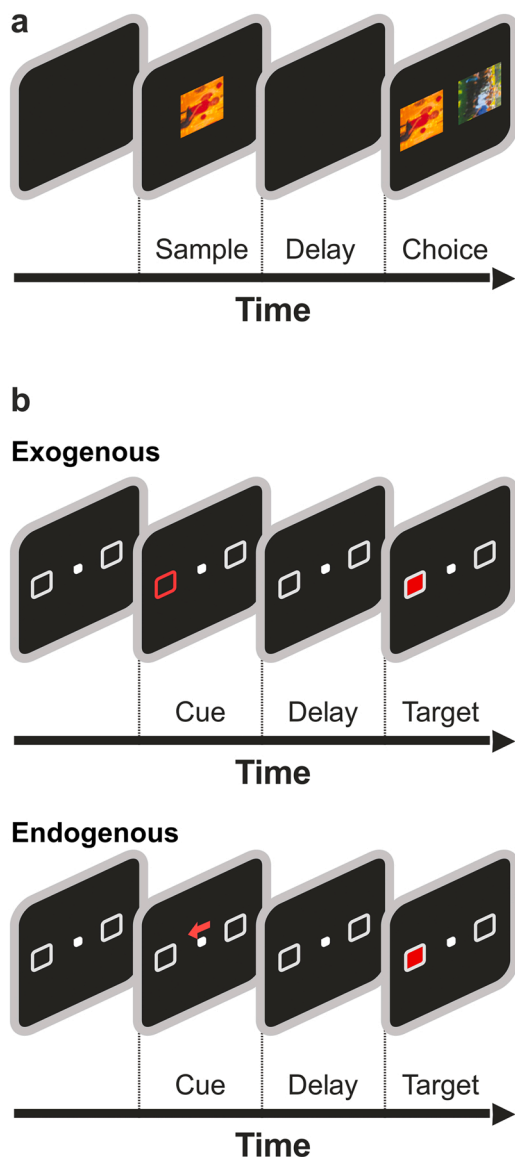


Fig. 1. Layout of behavioral protocols. (a) Delayed match-to-sample task as a classic protocol to test working memory capacities. The subject needs to remember the variable sample image during a working memory period and chose it again in the choice period. The sample image randomly changes from trial-to-trial. (b) Posner's spatial cueing task as a classic protocol to test attention capacities. Subjects have to fixate at the central fixation spot and are required to detect as quickly as possible a peripheral target stimulus that was preceded by a cue stimulus and a brief delay. Only valid cue-conditions (not invalid or neutral conditions) are shown. *Top:* Task layout to test exogenous attention. The valid cue (red square) is presented at the same location as the upcoming target. *Bottom:* Task layout to test endogenous attention. The "symbolic" valid cue (arrow) is presented in a neutral location (centrally). The pointing of the arrowhead has been associated with a particular location of an upcoming stimulus.

without awareness of stimuli, whereas in displays containing distractors, selection appears to be a prerequisite of conscious access (for reviews and discussions, see Koch and Tsuchiya, 2007; Dehaene and Changeux, 2011; Mashour et al., 2020). These findings emphasize that selective attention and conscious access are related but dissociable concepts.

The most common approach for studying both exogenous and endogenous (spatial) attention effects is Posner's spatial cueing task (Posner, 1980). In this task, subjects are required to detect as quickly as possible a peripheral target stimulus that was preceded by a cue stimulus (Fig. 1b). The task design allows the comparison of performance (as

measured by correct detections and reaction times) in trials in which attention is either directed to a given location (attended condition), away from that location (unattended condition), or to random locations (neutral or control condition; Carrasco, 2011). In the attended condition, performance is typically better (i.e., more accurate, faster, or both). Importantly, the nature of the cue determines whether exogenous or endogenous attention is being addressed. Exogenous attention is addressed if the cue is uninformative (i.e., could not previously been associated with the location of the upcoming target) and is presented at the same location as the upcoming target (thus activating the sensory input channel in a bottom-up way). However, if the cue (presented in a neutral location) is informative because the subjects had learned that it predicts a particular location of an upcoming stimulus, endogenous attention is engaged.

7. Intertwining of working memory, attention, and consciousness

Working memory, attention, and consciousness do not operate in isolation but are intertwined. Because of this, working memory and voluntary attention can serve as tools to understand consciousness (Shelton et al., 2008). In other words, voluntary attention and consciousness are cognitive processes that are inherent to explanations of how working memory operates (Baars, 1983, 2002; Baddeley, 2000, 2007; Cowan, 1995; Oberauer, 2002). Within working memory, information is actively maintained and manipulated in a highly accessible state to ensure its availability for conscious awareness. Attention is then used to select information from working memory to become available to conscious awareness. Put differently, the selection of individual items for conscious processing in the working memory system is achieved via attention (Shelton et al., 2008). The flexible nature of the focus of attention enables a subject to make instantaneous behaviorally relevant adjustments, which may constitute an adaptive function as a result from the process of biological evolution (Baddeley, 2007). Models of working memory therefore can "serve as a general framework for the conscious mind. Within that model, like many others, the focus of attention is assumed to be the same as the contents of conscious awareness." (Cowan, 1995, p. 200).

Working memory as a storage unit, and voluntary attention as a selection mechanism of consciously accessible information, render these two cognitive functions ideal agents for an empirical inquiry into the prerequisites of conscious awareness in animals. The rationale of this article is that animals that possess both working memory and voluntary attention also possess consciousness. The following paragraphs provide a detailed scientific evaluation of working memory and voluntary attention capacities in different animal taxa, starting with the five classical (but taxonomically simplified) vertebrate classes (mammals, birds, reptiles, amphibians, and fishes), and closing with the two protostome groups that have been studied in this realm (insects and cephalopods). The phylogenetic relationships between these animal taxa are shown in Fig. 2.

8. Evaluation of working memory and voluntary attention in animal taxa

8.1. Mammals

Early research in nonhuman primates (such as rhesus monkeys, *Macaca mulatta*) has shown primates are able to successfully perform the DMS task with delay lengths of 5, 10, and 15 s (Weinstein, 1941). Since then, the same task has been used in many different primate species (Etkin, D'Amato, 1969; Baron and Wenger, 2001; Vonk, 2003; Merten and Nieder, 2009; Dahl et al., 2013). Monkeys have also mastered more complex versions of the task in which the subject is required to flexibly manipulate abstract sample information in working memory in accordance with changing rules (Wallis et al., 2001; Bongard and Nieder,

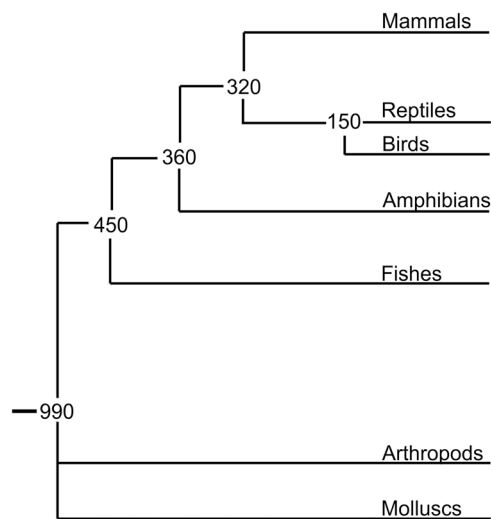


Fig. 2. Phylogenetic relationship and divergence times (millions of years ago) of animal taxa treated in this review. Branch lengths are not proportional to time. Based on Hedges (2002) and Striedter and Northcutt (2020).

2010). In combination with electrophysiological recordings, work with primates trained to perform the DMS task has also been used to explore the neurophysiological mechanisms of different aspects of working memory (Fuster and Alexander, 1971; Miller et al., 1996; Nieder et al., 2006; Viswanathan and Nieder, 2015; Ramirez-Cardenas et al., 2016; Mansouri et al., 2020). A variety of other mammalian species, such as rats (*Rattus norvegicus domestica*; Mumby et al., 1990; Prusky et al., 2004), bottlenose dolphins (*Tursiops truncatus*; Herman and Thompson, 1982), dogs (*Canis lupus familiaris*; Kuśmierk and Kowalska, 2002), and sea lions (*Zalophus californianus*; Pack et al., 1991), have also mastered the DMS task. It is therefore safe to conclude that mammals as a class possess working memory.

Endogenous attention in nonhuman primates has been demonstrated in a range of studies. In these studies, an informative cue presented in a neutral spatial location allowed monkeys to shift their spatial focus of attention. One of the earliest studies testing rhesus macaques in an endogenous spatial cueing task was performed by Bowman and colleagues (Bowman et al., 1993). In this Posner-like task, an arrow was presented at the center of the screen that cued the side on which the target would most probably appear. The monkey exhibited strong endogenous attention effects, meaning that target detection speed was significantly enhanced and long-lasting. Both the overall reaction time advantage and the duration of the attention effect were larger compared to purely exogenous attention effects in the same animal (Bowman et al., 1993).

Besides reaction time advantages, detection precision enhances with attention. In an electrophysiological study, monkeys were trained to fixate and to release a lever as soon as one of three moving dot patterns at a peripheral location (the cued target dot pattern), changed its direction of motion, while ignoring other distractor dot patterns (Busse et al., 2008). In one condition, a second cue appeared during the trials after a first cue had been presented, forcing the monkey to shift its location on-line to the newly cued location. This shifting attention to the new location was accompanied by gradually increasing hit rates of the monkeys; within the first 400 ms after the onset of the second cue, hit rate rose from 50% until it plateaued at 90% (Busse et al., 2008). This relatively slow shift in subsequently long-lasting attention is characteristic for volitional top-down processes. Moreover, endogenous attention enhances target visibility in monkeys; with attention allocated to goal locations, monkeys detect targets at lower contrasts (Bisley and Goldberg, 2003). Such endogenous attention effects have been described in several neurobiological studies with behaving monkeys (Roberts

et al., 2007; Yoshida et al., 2017; Messinger et al., 2021). Recent research in mice (*Mus musculus*; Wang and Krauzlis, 2018; You and Mysore, 2020; Goldstein et al., 2022) and rats (*Rattus norvegicus domestica*; Marote and Xavier, 2011) also shows robust endogenous attention effects in spatial cueing protocols in rodents, complementing voluntary attention findings in primates. Despite the limited number of tested orders (primates and rodents), voluntary attention seems to be present across mammals.

The clear evidence for conscious processes in mammals (Table 1), particularly in primates (Ben-Haim et al., 2021), allows one to directly investigate the neuronal correlates of consciousness in trained animals. These studies exploit the so-called “contrasting method”, i.e., the alternating subjective perception of physically identical stimuli (Logothetis and Schall, 1989; de Lafuente and Romo, 2005; van Vugt et al., 2018). As an objective marker of sensory consciousness, a proportion of neurons modulate their activity in relation to the subject’s alternating conscious percept for physically identical stimuli. This neuronal pattern signifies a neural correlate of consciousness. Neuronal correlates of consciousness have been detected in various neocortical regions of monkeys, such as visual areas (Logothetis and Schall, 1989) and associative regions of the prefrontal cortex (de Lafuente and Romo, 2005; van Vugt et al., 2018). The neuronal correlates of consciousness in nonhuman primates concur with those found during single-cell recordings in human participants (Kreiman et al., 2002; Quiroga et al., 2008; Reber et al., 2017). These direct findings indicating that the cerebral cortex plays a key role in conscious processing in mammals.

8.2. Birds

Birds, together with mammals, belong to the most cognitively flexible classes of vertebrates. This is remarkable because birds evolved independently from a last common stem-amniote with mammals 320 million years ago (Hedges, 2002). The parallel evolution between mammals and birds had major consequences for the avian brain’s intelligence centers. While mammals transformed the dorsal part of the telencephalic pallium into a unique six-layered neocortex, the ventral part of the pallium (called the dorsal ventricular ridge) became the dominating associative structure in birds (Striedter and Northcutt, 2020). Despite these and other major differences in the endbrains, birds show complex cognition on par with mammals (Nieder, 2017).

Different species of birds have been shown to master the DMS task with variable delay durations. Among these are pigeons (*Columba livia*; Blough, 1959; Roberts, 1980; Johnston et al., 2019), chickens (*Gallus gallus domesticus*; Nakagawa et al., 2004), and different species of songbirds, such as black-capped chickadees (*Parus atricapillus*), dark-eyed juncos (*Junco hyemalis*; Brodbeck and Shettleworth, 1995), jays (nutcrackers (*Nucifraga columbiana*), pinyon jays (*Gymnorhinus cyanocephalus*), scrub jays (*Aphelocoma coerulescens*), and Mexican jays (*A. ultramarine*; Olson et al., 1995), and carrion crows (*Corvus corone*; Veit et al., 2014; 2018; Ditz and Nieder, 2020). Crows not only show working memory for visual items, but also for auditory categories (Wagener and Nieder, 2020), and they exhibit a working memory capacity comparable to monkeys (Balakhonov and Rose, 2017). Under-scoring their capacity to manipulate complex information in working memory, crows have also been shown to process sample information in accordance with changing abstract rules in a similar manner to monkeys (Veit and Nieder, 2013). Neurons in the pallial association areas of birds show persistent (or sustained) neuronal activity throughout the memory phase of a delay period (Moll and Nieder, 2015; Ditz and Nieder, 2016; Rinnert et al., 2019; Hartmann et al., 2018); such persistent activity is widely believed to reflect active maintenance and goal-directed transformation of stimulus information in working memory.

Endogenous attention has been rarely studied in birds, but the few existing studies indicate that birds can volitionally direct attention to specific locations. Using a cross-modal spatial cuing paradigm, Johnen et al. (2001) demonstrated attentional influence on sound-localization

Table 1
Evidence for working memory, endogenous attention, and consciousness in different animal taxa.

Taxon	Working Memory	Endogenous Attention	Cognitive Indicators of Consciousness	Neuronal Correlate of Consciousness
Vertebrates (Deuterostomes)				
Mammals	+	+	++	+
Birds	+	+	++	+
Reptiles	-	-	-	-
Amphibians	-	-	-	-
Fishes	+/-	+/-	+/-	-
Protostomes				
Insects (Phylum Arthropods)	+	-	+/-	-
Cephalopods (Phylum Molluscs)	-	-	-	-

Symbol meaning:

+ strong evidence;

+/- suggestive/partial evidence;

- no evidence;

behavior in barn owls (*Tyto alba*). In this experiment, owls were surrounded by speakers and cued to the probable side of an impending target sound by a central but slightly left- or rightward aligned visual cue stimulus in front of them. Based on this cue, the owls localized subsequent auditory target stimuli with a head turn toward the position of the sound source. In valid cueing conditions, in which the visual cues pointed toward the side of the upcoming auditory target stimulus, the owls turned their heads significantly faster, arguing for spatial-selective attention mechanisms. Although exogenous and endogenous attention effects are difficult to dissociate in this protocol, top-down attention might have been responsible for parts of the behavioral effects. This notion is supported by the finding that the effect of cue validity was not influenced by the detailed appearance of the central cueing stimulus; whether target side was indicated by switching on a visual cue or by using the switching off of a long-lasting stimulus as a cue, the owls exploited the cueing stimulus to better estimate the most probable position of the next upcoming auditory stimulus (Johnen et al., 2001). In addition, the central cueing stimuli were well outside of the auditory target locations, thus preventing a cue-based bottom-up activation of the channel encoding spatial location. In another study with owls trained to search for visual Gabor patterns on a computer screen, attention was automatically captured by task-irrelevant distractors (Lev-Ari and Gutfreund, 2018). These findings argue for the presence of top-down attention mechanisms in addition to bottom-up effects in owls (Lev-Ari et al., 2020).

Detailed selective attention effects in a Posner-like spatial cueing task were studied in only a few bird species. In their study with pigeons, Shimp and Friedrich (1993) concluded that cue validity did not drastically influence the effectiveness of the cue. However, clear validity effects were shown in chickens (Sridharan et al., 2014). Sitting in front of a touch-sensitive screen, the chickens had to peck their way through different trial phases. After starting a trial, the chickens were first shown a spatial cue that indicated the side of the future target in some trials, or no cue in other trials. Crucially, the cue only indicated the side of the upcoming target (left or right), not the precise location of the target. After a black delay screen, the target stimulus and a distractor stimulus on opposite sides of the screen were displayed. After another delay, the chickens were required to peck at the target location indicated by one of two horizontally shifted response boxes on the cued side. In doing so, the chicken needed to suppress information about the vertical position of the distractor that was shown on the other side of the screen. As signatures of selective attention, the chickens localized the targets more often and more rapidly on trials with a cue but could be misled into reporting the vertical position of the distractor, particularly in no-cue trials, if the distractor was physically brighter (i.e., more salient) than the target (Sridharan et al., 2014). Because cue and target locations were not identical, the behavioral effects can be attributed to endogenous attention. These examples in phylogenetically disparate avian species illustrates that endogenous attention together with working memory is

present and probably widespread among birds as a sign of consciousness (Table 1).

The neuronal correlates of consciousness have recently been explored directly in crows confronted with identical visual stimuli at the perceptual threshold that elicited alternating visual precepts in these birds (Nieder et al., 2020). Despite independent and anatomically distinct evolution, the neuronal signals recorded from the associative pallium of the crow endbrain mirrored the neuronal correlates of consciousness that had previously been reported in primates (de Lafuente and Romo, 2005; van Vugt et al., 2018). This finding suggests that consciousness in birds (and potentially other animals) can in principle arise even in the absence of a cerebral cortex that endows mammals with consciousness (Nieder, 2021).

8.3. Reptiles

Birds as “non-reptilian dinosaurs” are closely related to the original group of reptiles with which they form the sauropsids. However, in contrast to birds, modern reptiles (crocodiles, turtles, lizards, and snakes) are relatively confined in terms of cognition. Reptiles have not been trained (or cannot be trained?) on tasks requiring working memory or endogenous attention in a strict sense. Reptiles show basic forms of learning, including operant conditioning, and memory, but so far have only succeeded on relatively simple discrimination tasks (Szabo et al., 2021). As an exception from this rule, bearded dragons have been shown to imitate contextual actions from conspecific demonstrators and thus show a surprising level of social learning (Kis et al., 2015). The underlying mechanisms of true imitation learning are debated (Zentall and Akins, 2001). Some have described it as a purposive, goal-directed copying behavior (Galef, 1988), whereas others see it as an extension of simple associative learning (Gewirtz, 1969; Heyes and Ray, 2000). Whether reptiles possess cognitive control required to learn and pass Posner’s spatial informative-cueing task requiring endogenous attention and the DMS task relying on working memory remains to be seen. Currently, there is no evidence for conscious processing in reptiles (Table 1).

8.4. Amphibians

Amphibians (newts and frogs) constitute the earliest land tetrapods. Compared to reptiles, amphibians seem to rely even more on stereotyped behavior. Compared to all other vertebrate classes, amphibians seem to be the most limited in terms of learning, memory, and executive functions; like many other bilaterian animals, amphibians exhibit exogenous attention and orient towards salient stimuli (Ingle, 1975; Ewert, 1987). In addition, poison frogs (*Dendrobates auratus*) show serial reversal learning as an indication of behavioral flexibility (Liu et al., 2016). However, currently there is no sign that they could voluntarily guide their attention or manipulate explicit memory contents as a

requirement for conscious processing (Table 1).

8.5. Fishes

Fishes (cartilaginous fishes such as sharks and rays; and bony fishes such as coelacanths, lungfishes, and ray-finned fishes), together with the jawless cyclostomes (hagfish and lampreys), constitute the most basal but also extremely diverse group of vertebrates (Hedges, 2002). The most species-rich teleost fishes (of the group of ray-finned fishes) experienced several whole genome duplications and thus exhibit many evolutionary innovations that are reflected in surprisingly elaborate cognition (Pasquier et al., 2016). Even though rarely investigated, recent studies discussed in the following suggest that some species of teleost fishes may have rudimentary working memory and endogenous attention.

The archerfish (*Toxotes chatareus*) is a popular teleost subject for visual discrimination studies due their specialized hunting technique of spitting water at insects in overhanging foliage (Potrich et al., 2022). However, this fish species has failed to show evidence of working memory. When archerfish were tested in a DMS task by hitting matching stimuli with a jet of water, none of the four tested archerfish were able to reach statistical significance (Newport et al., 2014). Only a recent study using zebrafish (*Danio rerio*) reported some working memory success. Using a DMS protocol with color stimuli, zebrafish were tested for working memory competence with delay periods of 3–4 s (Bloch et al., 2019). The fish were considered to have learned the task only if they performed at a level of $\geq 70\%$ correct for three consecutive sessions. The fish could obtain this meagre behavioral performance level only in a certain set-up, and they could maintain this performance for only a limited number of sessions (Bloch et al., 2019). Given that this investigation with zebrafish is the only study in which fishes barely mastered a DMS task at low accuracy, it is tempting to conclude that working memory in fishes—if it can be attributed at all—is qualitatively different (i.e., worse) compared to birds and mammals.

Despite the failure to perform a controlled working memory task, archerfish so far are the only fish species that have succeeded in an endogenous Posner-like spatial cueing task. In this task, centrally presented, spatially informative cues (i.e., color squares associated with the left or right side, respectively) were followed by a target, and the fishes detected the target by shooting a stream of water at it (Saban et al., 2017). As expected for attention effects, their reaction times to targets on the cued side were faster compared to reaction times to un-cued targets. However, the fish showed a behavioral signature unexpected for endogenous attention but predictive for exogenous attention, namely an early facilitation of responses to targets at the cued location followed by a later inhibitory effect (an effect termed “inhibition of return”; Gabay et al., 2013). The authors of the study offer two alternative interpretations for this finding (Saban et al., 2017). One explanation is that archerfish, unlike primates, may possess a shorter attention time constant and are only capable of short-lasting (a few hundred milliseconds) volitional control over the spotlight of attention. The alternative, less cognitive explanation would be that archerfish may not show volitional control at all, but an implicit (unconscious) associative learning of cue-target contingencies. The latter explanation would not invoke attention at all. Similar to working memory, endogenous attention (if present) is also qualitatively different and worse in this fish species. At present, the existing data provide at best suggestive evidence for working memory and voluntary attention in fish as an indicator of consciousness (Table 1).

8.6. Insects

Insects belong to the phylum arthropods, the most species-rich and diverse animal phylum exhibiting a central nervous system (a ventral nerve cord with an anterior brain) quite different from vertebrates. Despite the evolutionary distance of insects as protostomes to the

deuterostome vertebrates (the last common ancestor lived at least 600 million years ago; Hedges, 2002), insect cognition offers some surprises.

Among the most cognitively advanced insects are honeybees (*Apis mellifera*). Work with trained honeybees suggests that this insect species trained on a DMS task possesses working memory (Giurfa et al., 2001). In these studies, honeybees learn to forage in a so-called Y-maze. The honeybee is first presented with a sample stimulus at the entrance of a maze. Next, the honeybee enters the maze and is faced with a binary choice situation represented by the two shanks of the Y-maze. If the honeybee chooses the stimulus shown at the end of the shanks that matches the sample at the entrance, it is rewarded. The matching performance of honeybees in this DMS task is in the approximately 75% correct. Remarkably, honeybees have been successfully trained to perform the DMS task with colors, visual quantities, and odors as stimuli (Giurfa et al., 2001; Zhang et al., 2005; Gross et al., 2009). This insect even transfers this competence to novel stimuli and across sensory modalities, thus showing a conceptual grasp of “same” versus “different” (Giurfa et al., 2001). However, with a relatively low overall correct performance of around 75% in the DMS task, it stands to reason that working memory in honeybees (as in fishes) is qualitatively less potent compared to birds or mammals, which usually reach performances of 90% and more.

In contrast to working memory, endogenous attention has not been demonstrated in insects. Like virtually all tested animals, insects show attentional effects in reflexive orientation tasks (de Bivort and van Swinderen, 2016), and honeybees exhibit exogenous attention in spatial cueing tasks (Eckstein et al., 2013). However, neither bees nor other insects have been trained on endogenous Posner-like protocols, potentially because this might be too difficult a task for the honeybee (Eckstein et al., 2013). Moreover, there is currently no evidence for endogenous, volitional attention in insects or any other arthropod. Only the presence of working memory may be taken as evidence for some sort of subjective experience in insects (Table 1).

8.7. Cephalopods

Cephalopods (octopus, cuttlefish, and squid) belong to the phylum molluscs that have a similarly large phylogenetic distance to vertebrates as arthropods (Hedges, 2002). Cephalopods have the highest numbers of nerve cells and the most intense encephalization of all protostomes (Young, 1963), therefore these molluscs have a reputation of the most cognitively advanced group of invertebrates. However, behavioral evidence of complex cognition is largely based on anecdotal evidence (Schnell et al., 2021). There is ample evidence that different species of cephalopods, such as sepia (*Sepia spec.*) and octopus (*Octopus vulgaris*) learn and remember over different time scales (Sanders and Young, 1940; Schiller, 1949; Fiorito and Scotto, 1992), but this does not necessarily require subjective experience. Cephalopods have neither been trained on DMS tasks for working memory, nor on Posner-like cueing tasks with informative cues suitable to pin down endogenous attention. In the absence of such well-controlled empirical tests, flexible behavior can emerge from simpler mechanisms that work implicitly. Despite other claims (Mather, 2008), there is no behavioral evidence for consciousness in cephalopods based on working memory or endogenous attention (Table 1).

9. Conclusions

- (1) Complex behavior is not indicative of awareness of the content of stimuli. Unconscious processes, such as short-term memory or nondeclarative, associative learning and memory, are responsible for an astonishing range of elaborate behaviors. If this is true for humans, unconscious processes and resources are even more important in animals. Without a convincing argument, the default mode is that consciousness is not required for complex animal behaviors.

- (2) If sensory consciousness is present in (some) animal groups, it must share fundamental characteristics, both with human consciousness and among animals. The goal therefore is to find behavioral/cognitive mechanisms or resources that are diagnostic of awareness in humans and can therefore be used for the investigation of animal consciousness. Empirical signatures of working memory and voluntary/endogenous attention, both intimately linked to consciousness in humans, are suggested as diagnostic features to assign a basic type of conscious awareness. The DMS task is used as a classic task to probe working memory capacities in animals, and the informative-cue version of Posner's spatial cueing task is adopted as a test for endogenous attention.
- (3) The evaluation of the current literature investigating working memory and endogenous attention as necessary ingredients of consciousness in different animal taxa provide the following picture (Table 1): the clear evidence of working memory and endogenous attention in mammals and birds, together with direct neuronal correlates of subjective experience, confirms conscious processing in these two amniote classes. Interestingly, neither working memory nor volitional attention have been demonstrated in the last common ancestor amniotes between mammals and birds, the reptiles. This suggests that consciousness emerged independently in mammals and birds based on convergent evolution of different pallial structures of the telencephalon. No sign of consciousness has been found in amphibians, the tetrapod group that preceded the amniotes. Seemingly rudimentary but qualitatively worse working memory and endogenous attention effects have been reported for very few species of teleost fish, providing suggestive evidence for rudimentary consciousness in fish that evolved again independently after the phylogenetic segregation leading to the amphibians which show no sign of consciousness.
- (4) The existence of subjective experience in insects, cephalopods, or any other protostome based on cognitive indicators is more than doubtful. Honeybees would be the most serious contenders for conscious processing as they show working memory; however, in the absence of any demonstration of volitional attention it would be premature to conclude that these insects experience conscious contents. For cephalopods, the group of protostomes usually for advanced cognition, evidence for working memory or endogenous attention as indicators of consciousness is entirely lacking.
- (5) Of course, one may say that "absence of evidence (for endogenous attention or working memory) is not evidence for absence". However, in light of many decades of intensive cognitive research with animals from different taxa, cognitive skills that have not been found by now are most likely absent. In principle, the confirmatory findings in mammals and birds (and to some extent in fishes and honeybees) suggest that evolution does not rely on specific neural substrates (such as the mammalian neocortex) to endow distantly related species with forms of consciousness. Brain anatomy alone is thus not a good predictor of the presence or absence of consciousness; studying the brain at work is a much more promising approach to decipher consciousness as an emergent biological process.

Declaration of interest

The author declares that he has no competing interests.

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