Do animals dream?

J.E. Malinowski [a,*], D. Scheel [b], M. McCloskey [b]

[a] *School of Psychology, University of East London, Stratford, UK*
[b] *Institute of Culture & Environment, Alaska Pacific University, Anchorage, AK, USA*

A B S T R A C T

The understanding of biological functions of sleep has improved recently, including an understanding of the deep evolutionary roots of sleep among animals. However, dreaming as an element of sleep may be particularly difficult to address in non-human animals because in humans dreaming involves a non-wakeful form of awareness typically identified through verbal report. Here, we argue that parallels that exist between the phenomenology, physiology, and sleep behaviors during human dreaming provide an avenue to investigate dreaming in non-human animals. We review three alternative measurements of human dreaming – neural correlates of dreaming, 'replay' of newly-acquired memories, and dream-enacting behaviors – and consider how these may be applied to non-human animal models. We suggest that while animals close in brain structure to humans (such as mammals and birds) may be optimal models for the first two of these measurements, cephalopods, especially octopuses, may be particularly good candidates for the third.

1. Introduction: Is the study of non-human animal dreaming possible with current dream science methods?

Human dream science is heavily reliant on verbal reports of dream experiences. A question therefore arises as to whether dreaming in non-human animals is inaccessible to science because animals cannot provide verbal report of dream experiencing (e.g. Moorcroft, 2013). Even in humans, the study of dreaming and consciousness during sleep poses both empirical and metaphysical questions (e.g. Dennett, 1976; Windt, 2020). We do not accept the view of the "hard problem" of consciousness (e.g. Chalmers, 1996; Nagel, 1974) as such perspectives on consciousness have been thoroughly considered and rebutted by others, particularly Daniel Dennet (e.g. Dennett, 1993, Dennett, 2008).

Instead, we adopt an understanding of consciousness rooted in evolutionary theory and accessible to science (e.g. Denton, 2005; Godfrey-Smith, 2016, 2020), albeit with challenges. We begin by asking what we know about human sleep and dreaming, and whether that knowledge depends strictly on human verbal reports expressing dream content. We argue that it does not, and that offers hope to investigate dreaming in non-human animals. We consider three alternative methods of measuring human dreaming – neural correlates, 'replay' of newly-acquired waking memories during sleep for memory consolidation/assimilation, and dream-enacting behaviors – and illustrate how these may be applied to various animal models. While non-human animal models that most closely match humans (i.e. mammals and potentially also birds) are optimal for some of these measurements (namely, neural correlates and replay), a less obvious animal model is offered that may be particularly suited to dream-enacting behaviors – the octopus. Octopuses may offer a promising

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* Corresponding author.
E-mail addresses: josie.malinowski@kcl.ac.uk (J.E. Malinowski), dscheel@alaskapacific.edu (D. Scheel), mmccloskey@alaskapacific.edu (M. McCloskey).

model for studying not simply animal dream experiencing, but particularly animal dream content.

2. Human sleep and dreaming

2.1. REM and non-REM sleep

Human sleep occurs in stages, among which aspects of dreaming differ. Adult human sleep is well-delineated (Carskadon & Dement, 2017) by polysomnography, which minimally comprises recordings of eye (EOG recordings), muscle (EMG) and brain (EEG) activity. Sleep is divided into two main stages: rapid-eye-movement, or REM, sleep; and non-REM sleep. Each stage of sleep is accompanied by its own physiological, behavioral, and psychological characteristics. REM sleep is characterised by asynchronous EEG patterns, skeletal muscle atonia, and eponymous rapid eye movements. Dreaming is very common in this stage of sleep: approximately 80% of REM sleep awakenings elicit verbal dream reports (Nielsen, 2000). Although REM is not subdivided into further stages, tonic and phasic REM are sometimes described, the later comprising sudden clusters of activity involving eye movements and muscle twitching.

Non-REM sleep is characterised by synchronous EEG patterns and low muscle tone. Dreaming is common in this stage of sleep also, but is less frequent than in REM sleep: approximately 50% of non-REM sleep awakenings elicit verbal dream reports (Nielsen, 2000). Non-REM sleep is subdivided into three numbered stages, respectively (N1, N2, and N3). The three stages of non-REM sleep have their own characteristics. N1 is the liminal state between relaxed wakefulness and light sleep, lasting only one to seven minutes (Carskadon & Dement, 2017). Muscle tone gradually decreases, slow, rolling eye movements may occur, and EEG patterns transition from rhythmic alpha (relaxed wakefulness) to low-voltage, mixed frequency. N2 follows N1, is longer in duration (10–25 min), and is characterised by sudden increases in electrical activity wave frequency (sleep spindles) and sudden increases in wave amplitude (K-complexes). Via increasingly slow, high-voltage EEG patterns, N2 gradually transitions into N3, also known as Slow-Wave Sleep.

Sleep onset (N1) is experienced first, followed by N2 and then N3, and finally REM. This cycle lasts approximately 90 min and is repeated (minus N1) throughout the night. Non-REM periods dominate the first half of the night but decrease in duration with time spent asleep. REM sleep periods operate in the inverse, gradually increasing in duration with time spent asleep. During sleep the body is typically at rest, but may be active in certain parasomnias such as somnambulism (sleepwalking) and REM Sleep Behavior Disorder.

2.2. Defining "dreaming"

A broadly accepted defintion of dreaming is subjective mental experiences or cognitions occurring during sleep (e.g. McNamara, 2019; Sikka, 2019). Human dreaming, however, is not as clearly delineated as human sleep, and there is no unanimously agreed-upon defintion for "a dream". For example, Pagel, Blagrove, and Levin (2001) found 20 different definitions of "dream" in a dreaming journal over a nine-year period. Some researchers have argued for more nuanced defintions of dreaming, such as only those mental experiences during sleep in which an immersive simulated world is imagined (Windt, 2010), or only those mental experiences during sleep that occur in fully matured, healthy brains, when a specific neural network is activated (Domhoff, 2003). Dreaming has also been postulated to exist on a spectrum of mental functioning, whereby focused waking thought is at one end and dreaming at the other, with dream-like states such as daydreaming and mindwandering between them (Hartmann, 2010). Dreaming also overlaps with several waking experiences including psychedelic experiences and psychosis (Carhart-Harris, 2007; Kraehenmann, 2017; Malinowski, Tagliazucchi, Timmerman, & Carhart-Harris, 2019). For the purposes of this article, we conform to the broad and widely-used defi-niton of "subjective mental experiences or cognitions occurring during sleep".

2.3. Measuring dreaming

2.3.1. Verbal report
Human dreaming has been researched, until very recently, almost exclusively via verbal dream report. If we only allow dreaming to be confirmed by verbal report then we cannot know whether or not animals dream. However, in the following sections we will offer three alternative possibilities of measurement for human dreaming: dream-enacting behaviors, neural correlates of dreaming, and memory reactivation during sleep (or "replay").

2.3.2. Dream-enacting behaviors
Just as human dreaming occurs in both REM and non-REM sleep, so too have dream-enacting behaviors been reported from both REM and non-REM sleep. These behaviors occur when the sleeper physically enacts some of a dreamt-of behavior (dream-action isomorphism). Although dream enactment has been observed mostly in REM and non-REM sleep parasomnias (see below), it also occurs in typical sleep. Dream-enacting behaviors were reported by the vast majority of undergraduate students across three studies, and these behaviors were relatively independent of other parasomnias (Nielsen, Svob, & Kuiken, 2009). Similarly, violent sleep be-haviors were reported in a random stratified sample (Ohayon & Schenck, 2010), the majority of which were accompanied by violent dreams (these participants mostly self-reported parasomnias, but were not diagnosed).

Apparent dream enactments have also been observed in pregnant and postpartum women (Nielsen & Paquette, 2007) – specifically, dreams enacting behaviors pertaining to anxiety about motherhood. For example, several postpartum women dreamt of looking for their baby, and felt around the bed while dreaming this; several pregnant women woke up crying following unpleasant dream sce-narios about the baby. Dream-associated motor activity was twice as likely in postpartum women than pregnant women, which may

reflect the intense sleep interruption experienced by the former group. Sleep fragmentation/interruption may result in the blurring of wake/sleep borders, as also occurs for severe obstructive sleep apnea/hypopnea patients (discussed below).

Other normal overt motor activity during sleep may also correlate with dream experiences. The rapid eye movements observed during REM sleep, for example, appear to reflect visual scene scanning in dreams (Arnulf, 2011; Leclair-Visonneau, Oudiette, Gaymard, Leu-Semenescu, & Arnulf, 2010; Sprenger et al., 2010) and dream visual imagery changes (Andrillon, Nir, Cirelli, Tononi, & Fried, 2015). Hypnic jerks, the sudden start a sleeper may experience as they are transitioning from wakefulenss to N1, are often accompanied by dream imagery such as falling (Nielsen & Zadra, 2010). These are very common and are experienced "by almost everyone at one time or another" (Walters, 2007, p.1265).

Sleeptalking (or somniloquy) also offers a behavioral window into dream processes. Although classified as a parasomnia, sleeptalking is a common experience: Bjorvatn, Grønli, and Pallesen (2010) report a lifetime prevalence of 67%. Concordance between sleeptalking speech and sleep mentation elicited immediately after the sleeptalking episode is high for REM sleep (79%) and lower but still common in non-REM sleep (46%) (Arkin, Toth, Baker, & Hastey, 1970). Sleep speech may comprise nonverbal utterances such as mumbles or moans, or understandable words and sentences (Arnulf et al., 2017). Alfonsi, D'Atri, Scarpelli, Mangiaruga, and De Gennaro (2019) argue that sleeptalking may offer an alternative method for studying mental activity during sleep to verbal reports produced upon awakening.

Facial expression during sleep may also provide an observable behavior linked to oneiric expeirence. Clé et al. (2019) found that healthy participants exhibited smiling expressions during sleep, and Maranci, Aussel, Vidailhet, and Arnulf (2021) found that healthy participants exhibited frowning experiences during sleep. However, it is not yet clear whether these facial expressions reflect oneiric experiencing.

Lucid dream research further supports the connection between mental activity during sleep and concomitant body physiology during sleep. Lucid dreaming primarily occurs during REM sleep; as such, skeletal muscle atonia occurs during lucid dreaming. However, various studies illustrate that the sleeping body experiences the dreams as if they were being enacted: the sleeper's heart rate increases when the dream self exercises (Erlacher & Schredl, 2008); there is a direct relationship between gaze shift in a dream and the sleeper's eye movements (LaBerge, Nagel, Dement, & Zarcone, 1981); smooth eye movements during sleep accompany figure tracing in a dream (LaBerge, 1985); sleeper left and right forearm twitches match dreamt-of left and right fist clenches (LaBerge et al., 1981); dreamt-of sexual activity ending in orgasm correlates with sleeping body increases in respiration, skin conductance level, vaginal EMG, and vaginal pulse amplitude (LaBerge, Greenleaf, & Kedzierski, 1983)[1]; and dreamt-of respiratory activity corresponds with observable respiratory behaviour (Oudiette, Dodet, & Ledard, 2018). Dreamt-of hand movements also correlate with neurophysiological activity in the sensorimotor cortex in lucid dreams (Dresler, 2011). All of these findings support the notion that subjective dream experience is correlated with appropriate physiological response to the extent possible under the condition of skeletal muscle atonia.

2.3.2.1. Dream-enactment in disordered REM sleep. Increased muscle activity (that might permit dream enactment) during REM sleep is a diagnostic criteria of sleep dysfunction. Thus, in REM Sleep Behavior Disorder (RBD) parasomnia, dream-enacting behaviors are common. RBD patients display typically violent and aggressive behaviors in bed during REM periods (Schenck, Bundlie, Ettinger, & Mahowald, 2002), such as punching or kicking (Comella, Nardine, Diederich, & Stebbins, 1998). Non-violent behaviors are also occassionally seen, such as dancing or applauding (Oudiette et al., 2009). Movements are thought to occur as a result of neurodegeneration in the pontomedullary brain stem, which leads to loss of the skeletal muscle atonia that would otherwise accompany REM sleep (Arnulf, 2012).

It is commonly agreed that these behaviors are (at least on some occasions) dream-enactments (e.g. Arnulf, 2012; Boeve, 2010; Högl & Stefani, 2017; Schenck et al., 2002) or attempted dream-enactments (Arnulf, 2018). Many are violent or aggressive, such as a man who choked his wife during sleep while he dreamt of breaking the neck of a deer (Schenck & Mahowald, 2002). Occasionally, entire dream scenarios are enacted (Arnulf, 2018). Valli et al. (2012) found that blind judges were able to match RBD patients' movements with their dream reports more often than would be predicted by chance. These studies illustrate that subjective mental content may be expressed behaviorially during REM sleep in the absence of normal REM sleep muscle atonia.

Two main counterarguments exist to the concept that RBD patients' movements constitute dream-enacting behaviors. Firstly, it has been noted that central pattern generators in the spinal chord and brainstem may generate movements, such as muscle twitches in newborn babies in REM sleep (Blumberg & Plumeau, 2016). However, while this may account for automatically-generated movement that may occur without conscious experience, it does not account for RBD patients' reports of dreaming in the cases where this is evident. Dream-action isomorphism can include complex sequences of movements that align with dream content, such that generation within the brainstem or from central-pattern generators and absent a dream-narrative is implausible. Any such complex sequence instead must evidence the content of a dream experience.

Secondly, it has been argued that apparent dream-action isomorphism in RBD may result from dreaming around an external action, such as a patient who dreamt of an earthquake while sleeping in a car during a bumpy ride (Boeve et al., 2007). Indeed, incorporations of external stimuli into dream mentation is well-documented (e.g. Nielsen, 1993). Blumberg and Plumeau (2016) suggest that apparent RBD dream-enactments may be a result of dream-incorporation of violent limb movements; hence the apparent preponderance of

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[1] Note, however, that penile erection, which is common among male sleepers, was not associated with erotic dreaming in an RBD patient (Oudiette, Leclair-Visonneau, & Arnulf, 2010).

violent dreams in RBD patients. Arnulf (2018) suggests that both ascending and descending processes may be at play, whereby motor cortex activity generates movements, and these movements feedback into sensorimortor cortex and further influence dream content generation. However, some examples of dream-behavior isomorphism cannot convincingly be ascribed to ascending processes, such as a deliberately performed action in a lucid dream (e.g. exercise) being accompanied by concomitant physiological changes (e.g. increase in heart rate).

2.3.2.2. Dream-enactment in disordered non-REM sleep. Human non-REM sleep also is characterised by decreases in muscle tone, especially during Slow-Wave Sleep (Purves et al., 2018), so complex behaviors such as dream enacting behaviors also do not occur during normal non-REM sleep. However, parasomnias may lead to complex behaviors during disordered non-REM sleep. The parasomnias sleep-walking (or somnambulism) and sleep terrors occur during Slow Wave Sleep (SWS). Sleepwalking may entail simple (e. g. sitting up in bed) or complex (e.g. driving a car) behaviors, and are initiated following incomplete arousal from SWS. Sleep terrors are sudden arousals from SWS coupled with expressions of intense fear, such as screaming or crying. The same abnormal SWS physiology underlies both conditions, including higher sleep fragmentation (Espa, Ondze, Deglise, Billiard, & Besset, 2000). Sleepwalking and sleep terrors occur due to many SWS arousals which do not lead to full wakefulness; thus they may be a hybrid state between SWS and wakefulness.

Sleepwalking/sleep terrors may be accompanied by dream experiences that correspond to the waking behavior. Recorded cases include running into walls/furniture or jumping out of windows during dreams situations that require escape (Schenck et al., 2002), violent behavior in response to a dreamt-of attack (Pressman, 2007), hiding a child when dreaming of social services threatening to take the child away (Pillmann, 2009), and attempting to hold up the bedroom ceiling when dreaming of a collapsing roof (Bhat, Chokroverty, Kabak, Yang, & Rosen, 2012). The majority of sleepwalkers (71%) can recall at least one incident in which an episode was accompanied by a related dream (Oudiette et al., 2009). Oudiette et al. conclude that the evidence suggests "mind-behavior isomorphism" (p.1624).

2.3.2.3. Dream-enactment in other sleep-related disorders. Dream-enacting behaviors are also occasionally seen in patients with severe obstructive sleep apnea/hypopnea (Iranzo & Santamaria, 2005). Abnormal sleep motor behaviors were seen in 16 sleep apnea/ hypopnea patients. As with disordered REM sleep, both dreams and behaviors typically involved violence and aggression. When successfully treated, dream-enactments no longer appeared. While the cause of dream enactments in sleep apnea/hypopnea is not known, it may occur due to repeated confusional arousal arising from severe drop in oxygen levels, perhaps producing a "hybrid" state between waking and sleep similar to that seen in sleepwalking/sleep terrors. However, it should be noted that these cases were very rare.

Conversely, when Brion et al. (2012) examined the sleep-eating episodes of individuals diagnosed with sleep-related eating disorder (SRED), a parasomnia similar to sleepwalking but with sleep actions specifically centred on eating and drinking, they found sleep-eating was not associated with related dream content for any partipicants. This may be because the disorder is first and foremost a disorder of eating rather than a disorder of sleep; SRED participants often also had abnormal daytime eating and a history of eating disorders. This may indicate that sleep-eating arises from the disordered eating in SRED sufferers, as opposed to from attempted dream-enactment.

2.3.2.4. Dream-enactment as evidence for dreaming. There is now strong evidence for dream-enactment in both healthy individuals and individuals with REM or non-REM parasomnias. Overt behavior in humans is therefore at least on some occasions accompanied by corresponding dream content in both REM and non-REM sleep.

A corollary of this is the notion that individuals who report themselves to be non-dreamers may in fact be dreamers without recall, since RBD patients who self-report as non-dreamers do also perform the complex actions indicative of dreaming (Herlin, Leu-Semenescu, Chaumereuil, & Arnulf, 2015). This calls into question the validity of restricting the measurement of dream experiencing to dream reports, since non-dreamers cannot recall any dreams to report, but perform what appear to be dream-enactments. While it could be argued that they are performing complex, and occasionally apparently scenic, movements completely without subjective mental content, the evidence for dream-action isomorphism in RBD patients who do recall dreams makes it more likely that the non-recallers are simply non-recallers rather than non-dreamers.

The argument that we cannot ever know if an animal dreams because it cannot tell us, then, may be questioned following these lessons from RBD patients. Following this line of thought, RBD non-recallers would be classified as non-dreamers because they cannot tell us about any dreams they have. Yet behavioral evidence indicates that they do dream. Defining dream experiences as only those that we can verbally report would result in the conclusion, countered by the behavioral parallels between RBD dream-reporters and non-recallers, that RBD non-recallers are non-dreamers; likewise it would force the conclusion that animals do not dream, or that we cannot know whether or not they dream. But animal dream-enactment behaviors potentially could reveal otherwise.

2.3.3. Neural correlates of dreaming

While the discovery of REM sleep in 1953 initially led to a belief in REM-dream isomorphism, this was subsequently found to be erroneous as REM sleep and dreaming are doubly dissociable (Solms, 2000), and this left a limited understanding of the neural underpinnings of dreaming. However, later work has begun to unravel the neural correlates of dreaming.

Dreams ceased following lesions in or near the parieto-temporo-occipital (PTO) junction of the cerebral cortex, while dreaming was not disrupted by lesions to the brainstem, despite the fact that the latter led to the loss of REM sleep (Solms, 2000), indicating a role for

the PTO junction in dream generation. Dream experiencing (in both REM and non-REM sleep) is also highly predictable from patterns of neurological activity in the "posterior hot zone", an area in the parieto-occipital region similar to the PTO junction (Siclari et al., 2017). Dream experiencing in non-REM sleep is also is immediately preceded by a decrease in slow wave activity (Siclari, Bernardi, Cataldi, & Tononi, 2018), and dream recall is associated with frontocentral high-amplitude slow-waves, followed by microarousals.

These findings clearly illustrate how dream experiencing often occurs without dream recall: experience and recall are controlled by different brain regions. Dream experience appears to occur with the relative decrease in posterior slow wave activity, while dream content recall occurs with increased frontocentral slow wave activity plus microarousals. This further bolsters the argument that we cannot reduce dreaming only to dream reports, but must consider other methods for perceiving and measuring dreams, since sampling dream experiencing via verbal reporting depends on recall.

Aspects of dream content may also be revealed when the same brain regions that are active in the experiences when awake are also active during dreaming (Siclari et al., 2017), such as high-frequency activity in a region closely related to the fusiform face area when dreaming of faces, high-frequency activity in the right posterior parietal cortex (an area associated with spatial perception) when the dream had a definite spatial setting, and high-frequency activity in a region close to the right superior temporal sulcus (an area associated with perceiving and viewing movement) when dreaming of movement. Likewise, Hong et al. (1996) observed activity in Broca's and Wernicke's area correlating with dream talking and listening, respectively. Thus EEG is a valid method for determining not only that a person is dreaming, but may also facilitate a basic understanding of what they are dreaming. Novel methods are also in development that may one day lead to dream imagery being transposed onto a computer monitor (Horikawa, Tamaki, Miyawaki, & Kamitani, 2013).

Thus we expect brain activity in dream non-recallers during an apparent dream-enactment to match that of dream experience recallers. The outcome of recall is not necessarily expected to be linked to the neurological pattern of dream experience. If this expectation is met in future research, this would provide yet more evidence that dream report is not the only verifiable evidence of dream experience and content.

2.3.4. Replay in human sleep/dreaming

Another way of measuring dream experiencing involves observing reactivation or "replay" during sleep of new memories recently formed during wakefulness.

Replay occurs when a specific pattern of neural activity fires in response to the formation of a new memory during wakefulness, and then replays during sleep. Replay has been evidenced extensively in rats (see below, Section 3.2.2), and a few times in humans. Neuronal replay is evidenced in all stages of human sleep: increased premotor cortex activity in REM occurs following motor learning (Maquet et al., 1996), replay of sequences occur across widespread cortical regions in Slow Wave Sleep (Jiang et al., 2017), and neural firing patterns corresponding to a newly-learnt motor sequence are replayed in the cortex during non-REM stages 1 and 2 (Eichenlaub et al., 2020). Replay during sleep has also been observed behaviorally: a sleepwalker trained in the serial reaction task partially re-enacted this motor behavior during sleep (Oudiette et al., 2011), and a sleeptalker uttered a sentence semantically related to a text learnt in a verbal memory task the previous evening (Uguccioni et al., 2013).

Dream reports were not elicited in any of these studies, but there is much evidence that newly-acquired memories are not only replayed neuronally and behaviorally during sleep but also consciously in dreams, and that this conscious "replay" may contribute to the strengthening of those memories (Picard-Deland, Aumont, Samson-Richer, Paquette, & Nielsen, 2021; Plailly, Villalba, Vallat, Nicolas, & Ruby, 2019; Stickgold, Malia, Maguire, Roddenberry, & O'Connor, 2000; Wamsley, Perry, Djonlagic, Reaven, & Stickgold, 2010; Wamsley & Stickgold, 2019). These provide reason to believe that the refiring of neuronal patterns first expressed during new memory formation may be accompanied by conscious subjective experience in the form of dream experience. The link between neuronal replay and conscious dream experience was clearly illustrated in a recent study by Picard-Deland and Nielsen (2021), who played a four-tone melody to subjects during wakeful virtual reality task training (navigating a virtual environment in flight). Subjects who subsequently heard the four-tone melody during REM or non-REM sleep (targeted memory reactivation, TMR) within 1–6 days after the training dreamed more about the task than those for which the melody was not replayed.

Interestingly, in this study the melody played during REM sleep evoked dreams of the task in the first 1–2 days post-training, but when played during non-REM sleep, dreaming increased 5–6 days post-training. Similarly, stage-of-sleep differences that have been observed for different aspects of memory consolidation are reflected in stage-of-sleep dream content differences. Non-REM sleep is more beneficial for consolidating declarative memories and abstracting gist information, while REM sleep is more beneficial for procedural and some emotional memories and forming novel, unexpected connections leading to creativity and insight (Ackermann & Rasch, 2014; Born & Wilhelm, 2012; Cai, Mednick, Harrison, Kanady, & Mednick, 2009; Lewis, Knoblich, & Poe, 2018). Dream content reflects this: non-REM dreams and those sampled from the early night (non-REM-rich) are more directly related to waking-life memories, while REM dreams and those sampled from the late night (REM-rich) are more emotional, bizarre, and hyperassociative (Battaglia, Cavallero, & Cicogna, 1987; Malinowski & Horton, 2020). These findings demonstrate that memories reactivated in dreams may contribute to, or at least reflect, continued processing and consolidating (strengthening and transforming) of those memories.

In this way, dream content aligns with sleep stage roles in consolidation: declarative memories and abstraction are consolidated by replay during non-REM sleep (directly-related dream content) while procedural and emotional memories and novel connections essential for creativity are strengthened by replay during REM sleep (hyperassociatively-related dream content).

Consolidation comprises two specific processes: synaptic consolidation and systems consolidation. The former, also termed late-phase long-term potentiation, occurs within the first few hours after learning on a small scale in the synaptic connections and neural circuits, while the latter occurs over a period of weeks to years on a much larger scale in the brain as hippocampus-dependent memories become independent of the hippocampus.

Together, these findings indicate that, following new memory formation, "replay" may occur during sleep in three clear ways: reactivation of specific neuronal firing patterns; reenactment of newly learnt motor behaviors; and re-experiencing of conscious memory experience in dreams. It is worth noting that "replay" is perhaps a misleading word, however, since the reactivation of previously acquired memories is not an exact replica (e.g. in human dream reports (Wamsley et al., 2010, and in rat neuronal firing patterns as below)). The extent to which these three reactivations coexist is not yet known. However, as we have seen, dream en-actments can reflect dream content, and the fact that reactivated memories in human sleep are observable both with objective measures (at the neuronal level) and subjective measures (conscious mental content) offers the possibility that dream reports are a direct, albeit altered, reflection of neuronal reactivation of memories.

So far, then, we have offered three alternative methods of observing dream experiences in humans: dream-enacting behaviors, neural correlates of dreaming, and "replay" of newly-acquired memories. We will now discuss parallels of these in non-human animals.

3. Animal sleep and dreaming

3.1. Two sleep signatures across animal taxa

It now appears that all animals sleep (Ungurean, Van Der Meij, Rattenborg, & Lesku, 2020), and that during sleep, behavior and brain activity have two major sleep signatures (i.e. phases, for example in humans REM and non-REM sleep) in all taxa for which the question has been studied (i.e. well-studied: mammals, birds; less well-studied: other vertebrates (Leung et al., 2019; Libourel & Barrillot, 2020), cinidaria (Lesku & Ly, 2017), nematodes (Moosavi & Hatam, 2017), arthropods (Beckwith & French, 2019; Mendoza et al., 2010), mollusks (Meisel, Byrne, Mather, & Kuba, 2011; Vorster, Krishnan, Cirelli, & Lyons, 2014; Medeiros, de Paiva, Lopes, Blanco, de Lima, de Oliveira, Medeiros, Sequerra, de Souza, Leite, & Ribeiro, 2021)). The two signatures are characterized broadly either by high or low activity (in mammals, rapid eye movement or REM sleep and non-REM sleep). Sleep signatures in birds have also been identified with REM and non-REM sleep, but in other taxa high and low activity sleep signatures do not map directly into REM and non-REM mammalian sleep. Hereafter to facilitate discussion across taxa, we refer in mammals and birds to REM and non-REM sleep and in all other taxa to high or low activity sleep signatures, where "activity" refers either to brain activity measured by EEG or to behavioral activity. High activity sleep, with various specifications of definition, variously has been termed paradoxical sleep, active sleep, propagating wave sleep, and high-cortical activity sleep (Leung et al., 2019; Ma et al., 2019) and low-activity sleep termed slow wave sleep, slow bursting sleep, and quiet sleep (Libourel & Herrel, 2016; Siegel, 2005). Our general terms indicate only that these sleep signatures share either neural or behavioral similarities of high or low activity. We do not imply the states lumped under either term are evolutionarily or functionally homologous, nor that sleep within these signatures is itself homogeneous.

In addition to higher frequency cortical activity similar to that when awake, mammalian REM sleep is characterized by more behavioral activity including rapid-eye-movements, muscle twitches, lack of muscle tone (atonia), variability of respiratory and cardiovascular activity, fluctuations in body temperature, and an elevated arousal threshold (Peever & Fuller, 2017; Siegel, 2005).

In addition to lower frequency cortical activity, mammalian non-REM sleep is characterized by the absence of rapid-eye move-ments, relaxed muscles but not complete atonia and consistant cardiovascular activity similar to the waking state (Peever & Fuller, 2017).

Lizards and fish also exhibit two sleep signatures (Kavanau, 2002; Libourel & Barrillot, 2020; Shein-Idelson, Ondracek, Liaw, Reiter, & Laurent, 2016). Muscle atonia and eye twitching occur during *both* sleep phases in these lizards (Libourel & Barrillot, 2020). In fish, high-activity sleep signatures showed awake-like EEG readings with muscle atonia (Leung et al., 2019). There is however no rapid eye movement during sleep of zebra fishes (Árnason, Þorsteinsson, & Karlsson, 2015) or lizards (Libourel & Barrillot, 2020). Zebra fish thus indicate that basal vertebrates have two sleep signatures (Leung et al., 2019).

Similarly, the two sleep signatures also occur among several species of the Ecdysozoa (those invertebrates that shed a cuticle). Arthropods (including fruit flies, honey bees and crayfish) as well as the nematode *Caenorhabditis elegan* each have variable sleep states. High-activity sleep signatures of *Drosophila melanogaster* exhibit higher wave frequency and lower stimulus threshold for arousal (a high-activity signature) that was not like waking wave frequencies of the fly and was only present at the beginning of sleep (Yap et al., 2017), while honeybees have short bursts of high activity in the mushroom bodies accompanied by antennal twitching or swaying (Schuppe, 1995; Zwaka et al., 2015). In both fruit flies and honeybees, low-activity sleep states are characterized by decreased brain activity. Sleeping crayfish exhibit reduced wave frequency (low-activity sleep signature) (Mendoza-Angeles et al., 2010) but have two distinct phases of sleep (Osorio-Palacios et al., 2021).

Among cephalopods, high-activity sleep behaviors have been at least anecdotally described for both *Octopus vulgaris* (Meisel et al., 2011) and the cuttlefish *Sepia officinalis*. There is a neural recording of a single *O. vulgaris* during low-activity sleep behaviors which shows activity spikes in the vertical lobe, which is the learning and memory center of octopuses. Medeiros et al. (2021) found that *O. insularis* exhibited both quiet and active sleep, during each of which the octopuses were less responsive to stimuli. Active sleep episodes were short in duration and characterized by dynamic skin patterns and increased eye movement.

3.2. Measuring animal dreaming

We begin our consideration of what may be known about animal dreaming with the two more neurological lines of evidence (neural correlates and the relationship of replay with memory). We conclude by exploring the use of sleep behaviors of animals as evidence for dreaming. All three lines of evidence, beyond the mere fact of dreaming, perhaps may also offer hints of dream content. Of these, perhaps most plausible is dream-enacting behaviors.

3.2.1. Neural correlates of dreaming in animals

Animals do not verbally report dreams as do humans, as far as we know. In parallel with humans, however, animals exhibit two sleep signatures marked in many cases both by neural signature and by changes in sleep behavior. Human verbal ability allowed identification of neural correlates of dream reporting, an avenue not available with animals. However, the various neural signatures described above and correlated with behavioral sleep lend credibility to the notion that if dream experiences occur in animals, they may be marked by particular neural signatures. In mammals in particular, it is conceivable that brain imaging may in future allow identification of specific conscious experiences during sleep. For instance, the methodology that allowed Siclari et al. (2017) to observe activity in sleeping brains for face perception, movement, and spatial settings, and finding that these activities matched dream experiencing, could be applied to non-human animal research, comparing neural signature of specific waking experiences with matched neural firing patterns during sleep. With a more complete map of the human brain when it is dreaming – on which research already has made significant progress – we may be able to undertake similar neural imagining in those non-human animals that possess similar brain anatomy (e.g. mammals such as primates, cats, and dogs).

3.2.2. Replay and learning in animal sleep

When waking neural patterns of particular activites recur in sleep, this constitutes replay. A function of replay is the consolidation of memories, and this appears to be so in animals as well as humans. When rats are exposed to an arena, place neurons are selectively activated in relation to particular spatial areas. During sleep, rats replay these patterns of place neuron activation. Experiments disrupting this replay impaired the consolidation of memories of a recently explored arena (Buhry, Azizi, & Cheng, 2011; Foster, 2017; Van de Ven, Trouche, McNamara, Allen, & Dupret, 2016). More generally, the memory function of replay during sleep identified in mammals seems to be conserved in low-activity sleep across animal taxa. The memory function of replay has been demonstrated in zebra finches (Dave & Margoliash, 2000), and context odor presentation during sleep (presumably eliciting replay) enhanced memory in honeybees *Apis mellifera* (Zwaka et al., 2015). Dave and Margoliash (2000) found that these replay patterns in zebra finches often included the single- or dual-cell burst order evoked by ordered syllables in their own song. Memory researchers have supported the hypothesis that replay may evidence dreaming and dream content (see above references on replay in humans).

When rats replay in Slow Wave Sleep the neural firing patterns that occurred during novel waking experiences, the replay is not necessarily an exact replica of the original firing patterns: replays may be sped up (Euston, Tatsuno, & McNaughton, 2007; Nádasdy et al., 1999), and it may involve new, imagined routes (Gupta et al., 2010). Replay can occur during wakefulness too, and may occur in temporally reversed order (Foster & Wilson, 2006). Findings such as these may support the argument that animals dream. While changes in neural activity are not necessarily reflected in the conscious experience of the animal, such reactivation nevertheless could be evidence supporting such a change. Dreaming requires the creation of "patterns that have never been experienced before…in the absence of environmental stimulation" (Foulkes, 1999, p.11). The novel changes in neural patterns during replay, which are not elicited by the specific environmental stimulation previously encountered in waking experience, may be reflected in the sleeping experience of the animal.

Replay has also been observed in REM sleep (Louie & Wilson, 2001). Neuronally, replay occurs not only in the hippocampus, but also in the visual cortex, which may "directly relate to the perceptual imagery experienced during sleep and dream states" (Ji & Wilson, 2006), and the basolateral amygdala, perhaps indicating a reactivation of the affective state experienced during initital encoding (Girardeau et al., 2017). Again, these lines of evidence may point towards some conscious experiencing during replay, which may be conceptualised as a form of animal dreaming, particularly in reference to the visual and affective characteristics of human dreaming. This may be especially likely in REM sleep, which is very often accompanied by dreaming in humans.

Thus, while we do not suggest that all neuronal replay in non-human animals indicates conscious experiencing, with a more complete understanding of how neuronal replay relates to dream experiencing in humans, such as through the use of targeted memory reactivation (in which a sound, odor, or other stimulus associated with training while awake is presented again during sleep; e.g. Picard-Deland & Nielsen, 2021), we may begin to be able to map from human replay-dreaming to animal replay-dreaming in non-human animals such as mammals, birds, and insects.

3.2.3. Dream enactment by animals

Do animals also exhibit sleep behaviors that might have parallels to dream-enactment behaviors in humans? A pioneering series of experiments on cats by Michel Jouvet suggests that they do; indeed, this work illustrated apparent dream-enacting behaviours in cats many years before the same was observed in humans in REM Sleep Behaviour Disorder (Jouvet & Michel, 1959; Jouvet, 1962). Jouvet (1979) reported that following pontine lesions, no alterations were observed during wakefulness or Slow-Wave Sleep, but during REM sleep typical atonia was absent, and cats were observed performing complex behaviors during sleep such as stalking (as if pursuing prey), attacking behaviors, flight behaviors, and grooming. Subsequent research has confirmed these findings (Henley & Morrison, 1974, Hendricks, Morrison, & Mann, 1982). Jouvet termed this apparent dream-enactment "oneiric" behaviour.

Comparable results have been found also in experiments with rats. When pontine tegmental lesion is performed in rats, oneiric behavior is similarly observed of the kind observed in humans in REM Sleep Behavior Disorder: Sanford et al. (2001) observed behaviors ranging from exaggerated jerking movements to more complex, perhaps dream-enacting behaviors, including "headlifting, treading limbs as if walking in place, full locomotion, and explosive leaps and jumps" (p.3).

Thus, rats have been shown during sleep to replay their neural firing patterns but in ways that are different to the original firing patterns that occurred when awake, involving hippocampus, visual cortex, and amygdala activity, which enhance memory consolidation. Rats also display oneiric-like behavior following lesions to pontine areas responsible for muscle atonia. The same can be said for humans, as discussed earlier. The sole difference between humans and rats is this scenario is that in humans we can acquire verbal

dream reports, and in rats we cannot. Therefore, it seems reasonable to make the inference that rats are dreaming, and by extension other mammals in which similar behaviors have been observed, such as cats.

In non-mammalian animals, too, documented sleep behaviors have increased complexity that may parallel dream enactment in humans. Although vocalization by sleeping birds appears not yet to have received scientific attention, examples are available on YouTube, for example, in which pet birds exhibit stereotypical sleep postures while vocalizing.

Sleeping octopuses at times may rapidly twitch eyes, suckers or arms, exhibit increased ventilation rates, tightly curled arms, or show rapid changes in body pattern unrelated to the environment where sleeping (Meisel et al., 2011; Medeiros et al., 2021). Similarly, body colouration and arm twitches have been observed in cuttlefish during a quiescent state accompanied by rapid eye movements, which may be analogous to REM sleep (Frank, Waldrop, Dumoulin, Aton, & Boal, 2012). Further, the body patterns demonstrated by octopuses may be representative of patterns correlated with waking activities. Although untested, such a finding would be evidence for replay and possible dream experience, similar to ways dream enactment may reveal dreaming and dream content in humans.

High-activity sleep behaviors in *O. vulgaris* and *O. insularis* include a "half and half" body pattern display during sleep (Meisel et al., 2011; Medeiros et al., 2021). In awake cephalopods, similar differences in right-side and left-side body pattern displays function in social interactions and camouflage (e.g., *O. tetricus*, Scheel, Godfrey-Smith, & Lawrence, 2016; squid & cuttlefish e.g., Brown, Garwood, & Williamson, 2012). In the 2019 BBC documentary The Octopus in My House (also as PBS Octopus: Making Contact[2]), *O. cyanea* was shown in sleep passing through a number of body patterns (Fig. 1), reminiscent of changes that might be displayed while awake and active. While this film was not analyzed in detail, a published study Iglesias, Boal, Frank, Zeil, and Hanlon (2019) reported that during sleep body patterns of cuttlefish (*Sepia officinalis*) represented only portions of normal patterning seen in the waking state.

A difficulty posed by many animal models in investigating dream-enacting behaviors is the typical muscle atonia that accompanies REM sleep; as in humans, paralysis of muscles during REM sleep appears to prevent dream-enacting behaviors. The octopus, in this way, is a particularly promising model to observe dream-enacting behaviors naturalistically and without the need to perform lesions as is required in mammals. Fig. 2 illustrates the argument that the octopus is an excellent candidate that exhibits sleep behaviours potentially revealing of dream content that also do not draw attention or put the animal in danger (e.g. vocalization, large-scale body movements), as such behaviours would be under selection pressure to be supressed during normal sleep.

4. Do animals possess the ability to dream?

Edelman (1989) suggested that there are two types of consciousness, primary and secondary. Primary consciousness may be described as "the direct experience of percepts and feelings, and thoughts and memories arising in direct response to them" (Farthing, 1992, p. 12). Secondary is "thoughts about one's own conscious experience" (ibid., p.13). It is also generally agreed that mammals (and probably birds) have primary consciousness (e.g. Edelman, Baars, & Seth, 2005). While Edelman considered octopuses "a distant case and major challenge", others have considered that octopuses may have primary consciousness also (e.g. Denton 2005, Godfrey-Smith, 2013; Mather, 2008).

Many dream researchers conceive of dreams in terms of primary vs secondary consciousness. For example, in terms of wake (may include secondary vs dream (mostly primary), or non-lucid (primary) vs lucid (secondary) dreams (Cicogna & Bosinelli, 2001; Hobson & Voss, 2010, 2011; Mutz & Javadi, 2017), or in terms of the features of dreams such as "perceptual, experiential, cognitive, and memory-based recognition" vs "noticing positive and negative feelings and by personally defined oddities", which may illustrate that primary and secondary consciousness may both occur in dreaming (Kozmová & Wolman, 2006). Dreaming in these accounts requires primary consciousness, but secondary consciousness is only required for specific dream features like lucidity or self-reflection. Thus, animals possess the necessary prerequisite form of consciousness required for some forms of dreaming.

We argue that at least two of three types of evidence of human dreaming, one of them behavioral, also bear on whether animals dream. A dream-capable animal will exhibit behavioral sleep, show evidence of replay either in neural recordings or in memory tasks, and exhibit behavior affected by the content of dreams, just as humans will sleep, dream of events, and consolidate memories through 'replay' during sleep. While animals likely also display neural correlates of dreaming, these logically could only be identified in context of replay studies or dreaming evidenced by sleep behavior to provide the context to which neural recordings correlate.

It appears that all animals may sleep, so that behavioral sleep comprised of regular reversible quiescent periods of decreased responsiveness occur and that if deprived of these the animal must recover by sleeping longer. Thus behavioral sleep itself is likely to occur in any animal considered for evidence of dreaming.

It does not appear that a dream-capable animal must have behavior affected by the dream to have experienced the dream (Dennett, 1976, and as discussed above), any more than a person must relate the dream to experience it. None-the-less, where behavior is unaffected by the dream, we would have no evidence of the dream itself, unless we were the dreamer. Two types of behavior might be affected by dreaming – first, if dreams function as practice and memory consolidation, then dreamers might learn tasks with fewer repetitions than non-dreamers, so that dreaming may affect learning (e.g. as suggested in Melnattur et al., 2015, and evidenced in Wamsley et al., 2010). Second, some animals may have behaviors that relate dream content, such as people discussing a dream. In the former case, an experiment that disrupted sleep might affect rates of learning, providing behavioral evidence of the effects of sleep (and possibly dreams related to replay) on learning. Neural recordings during sleep might allow replay specifically to be disrupted, providing more focussed evidence. In the latter case, for example, a dog's legs may cycle in sleep as though it were running. However, if

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[2] Nature on PBS, "Octopus dreaming" https://www.pbs.org/wnet/nature/octopus-dreaming-trept6/19376/
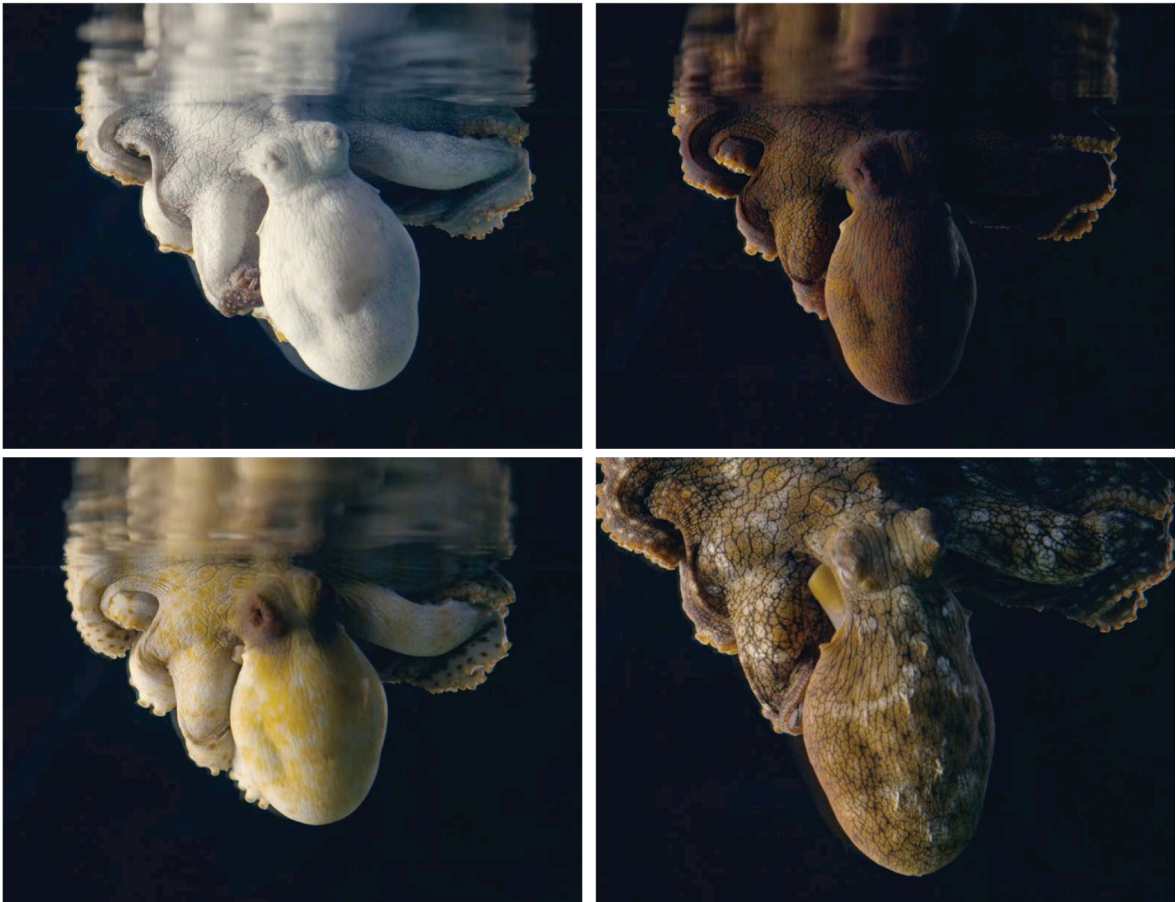
Fig. 1. Body patterns displayed by sleeping *Octopus cyanea* within a short period of time. All images were recorded without change in lighting conditions. If body pattern sequences during sleep vary and more closely resembled ecologically relevant sequences than random sequences, this may constitute evidence of dream content. Photography by E. Kovacs used with permission of PBS Nature and Passion Planet Production. Video sequence appears in the PBS Nature production Octopus: Making Contact.

the behavior is sufficiently similar to waking behavior (the dog actively runs in its sleep) we may be unable to distinguish a sleep behavior from a waking one. Generally during sleep, motor responses are inhibited but not always completely extinguished. These partial motor responses possibly provide behavioral evidence of dreaming.

5. Conclusions

We have argued that human dream science is not wholly dependent on verbal reports of dream experience, but may utilise alternative measurements such as neural correlates of dreaming, neuronal and conscious "replay" of newly-acquired material (that enhance memory consolidation/assimilation and may affect subsequent behavior), and dream-enacting behaviors. With respect to the first two of these alternatives, we have argued that mammals especially, but perhaps also birds and potentially even insects, may provide feasible non-human animal models in which to study dreaming.

With respect to dream-enacting behaviors, we have argued that octopuses and other cephalopods are one animal group for which waking and sleep behavior might be sufficiently related to reveal not only dream experiencing, but potentially even dream content. This is because during ecologically relevant waking behavior (such as hunting, contesting, or mating), octopus motor responses include not only those relevant to locomotion but also to camouflage and display through muscularly controlled body pattern displays. Because their expression would not interrupt sleep by causing movement (unlike other animals which may at first appear to be a better candidate, such as rats or cats), body pattern displays may be only partially suppressed during sleep; and body-pattern changes may represent specific behavioral sequences due to their ecological relevancy. Thus, body patterns during dreaming of hunting may be predictably different than those during dreaming of mating, thereby exhibiting behavior affected by the content of the dream. This is an empirical supposition, at least in principle testable by comparing sleep body pattern behavior with waking body pattern behavior. Such a comparison has been conducted for a single cuttlefish species (Iglesias et al., 2019) but not to our knowledge for octopuses.

These propositions offer potential novel methods for the study of dreaming not only in non-human animals, but also in humans for
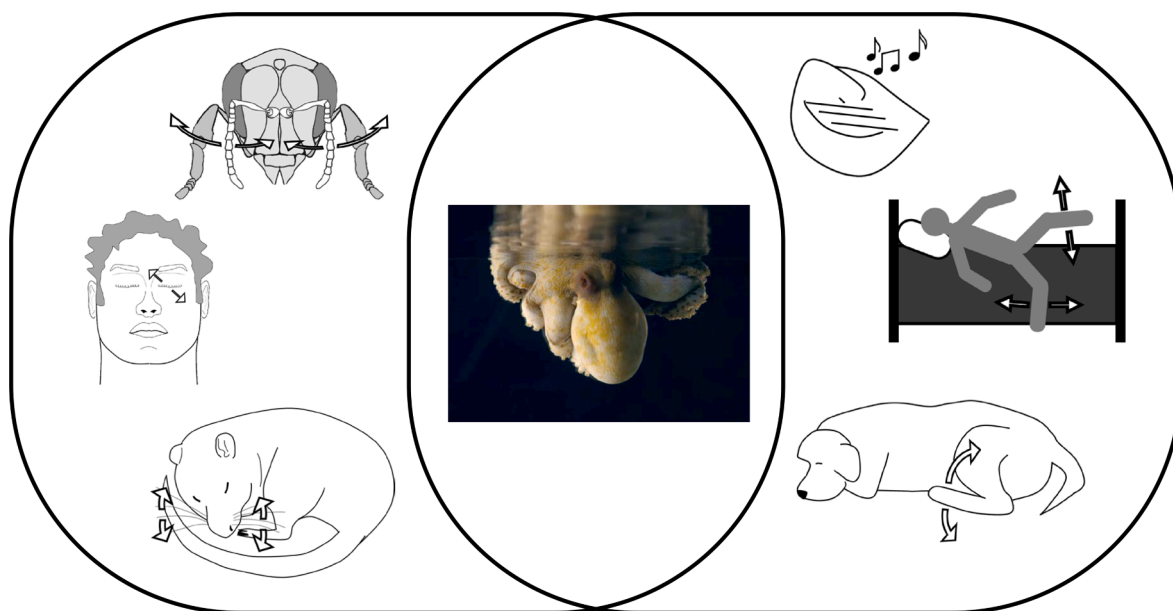
Fig. 2. Can sleep behaviors reveal animal dreaming? In the left oval, normal sleep postures are illustrated of example animals (bee, rat, human) with active sleep behaviors (arrows). In the right oval, candidate dream-enactment behaviors are illustrated for a sleep-singing bird, a dog 'running' during sleep, and a human exhibiting violent sleep behavior. These may be symptomatic of disordered sleep. In the overlap of the two ovals (center), octopuses (representing cephalopods including cuttlefish) illustrate candidate non-human dream enactment behaviors that are typical of normal sleep, and potentially could evidence dream content. Illustration by MM (bee, humans, rat, dog), DS (sleeping bird), octopus as in Fig. 1.

whom verbal reports of dream experience cannot be elicited, such as non-verbal humans and humans who have little to no dream recall.

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CRediT authorship contribution statement

J.E. Malinowski: Conceptualization, Writing – original draft, Writing – review & editing. **D. Scheel:** Conceptualization, Writing – original draft, Writing – review & editing. **M. McCloskey:** Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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