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Predictive coding, multisensory integration, and attentional control: A multicomponent framework for lucid dreaming

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Lucid dreaming (LD) is a mental state in which we realize not being awake but are dreaming while asleep. It often involves vivid, perceptually intense dream images as well as peculiar kinesthetic sensations, such as flying, levitating, or out-of-body experiences. LD is in the cross-spotlight of cognitive neuroscience and sleep research as a particular case to study consciousness, cognition, and the neural background of dream experiences. Here, we present a multicomponent framework for the study and understanding of neurocognitive mechanisms and phenomenological aspects of LD. We propose that LD is associated with prediction error signals arising during sleep and occurring at higher or lower levels of the processing hierarchy. Prediction errors are resolved by generating a superordinate self-model able to integrate ambiguous stimuli arriving from sensory periphery and higher-order cortical regions. While multisensory integration enables lucidity maintenance and contributes to peculiar kinesthetic experiences, attentional control facilitates multisensory integration by dynamically regulating the balance between the influence of top-down mental models and the precision weighting of bottom-up sensory inputs. Our novel framework aims to link neural correlates of LD with current concepts of sleep and arousal regulation and provide testable predictions on interindividual differences in LD as well as neurocognitive mechanisms inducing lucid dreams.

sleep | lucid dreaming | sleep disorders | predictive processing | multisensory integration

Lucid dreaming (LD) is a peculiar oneiric experience during which we discriminate a dream from reality and hence, become aware of the fact that we are not awake but dreaming while asleep (1). Lucid dreams are heterogeneous in nature and involve various cognitive processes beyond the insight of being in a dream, such as agency and control over the dream plot, episodic memory, or unusual sensorimotor experiences. These lucidity dimensions may vary in occurrence and intensity across and within dreams, and they unfold into conscious experiences stretching along a continuum between nonlucid and lucid dreams (2). Interest in LD dates back thousands of years with likely roots in Eastern meditative practices (e.g., Dream Yoga) (3). Western philosophers and scholars inspired by their own lucid dreams documented the phenomena through introspection, highlighting distinctive features of lucid dreams, including self-awareness, volitional control, and access to real-life memories (4). Pioneering research showed that LD can be systematically studied by instructing trained lucid dreamers to signal their moments of lucidity with horizontal eye movements (5, 6). This signal-verified technique takes advantage of the fact that ocular movements persist during REM (Rapid Eye Movement) sleep, while motor atonia paralyses the body (7). Notwithstanding, early LD studies were received with skepticism due to low sample sizes, questionable reliability (8), and scarcity of well-defined physiological measures to characterize the LD state (9).

Nowadays, LD research enjoys its renaissance with novel insights into its neural aspects, evidencing neuroanatomical and neurofunctional differences between frequent and nonfrequent lucid dreamers (10, 11), neural correlates of LD experiences (12, 13), or the nature of sensorimotor processing during lucid dreams (14). Still using the eye movement signaling technique developed 40 y ago (5, 6), it shows that LD can be studied under laboratory conditions using neuroscientific tools and advanced neural data analysis (15). Studies indicate that lucid dreams usually emerge in REM sleep and that prefrontal–parietal neural networks characterized by reduced activity during nonlucid REM sleep become activated, resembling activity patterns observed in wakefulness (4). Wake-like neural activity in these regions and networks may reestablish the influence of cognitive functions (e.g., reflective self-awareness, attention, and control) shaping phenomenological aspects of lucid dreams (4, 9, 16). Although these studies are opening up new avenues in the neuroscience of consciousness (10), several questions remain regarding the neurocognitive mechanisms of LD. For example, what neurophysiological mechanisms are associated with the initiation, maintenance, or termination of lucidity within a dream? What leads to frequent lucid dreams in some individuals and none in others? Additionally, through which cognitive processes may LD induction practices facilitate this experience?

We address these questions by proposing a novel, multicomponent framework to explain and study the neural,

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cognitive, and phenomenological dimensions of LD. The model is based on five postulates. First, LD is associated with prediction error signals that arise during sleep at higher or lower processing levels, including bottom-up interoceptive pathways. Second, dispositional factors and state-like aspects of sleep regulation modulate sensitivity to prediction error signals. Third, compared with non-LD, prediction errors during LD are streamed forward to higher levels of the processing hierarchy and attenuated by updating mental self-representations or active inference accommodating bottom-up sensory signals (e.g., vestibular vs. proprioceptive) that convey contradictory information. Fourth, multisensory integration enables lucidity maintenance and contributes to peculiar kinesthetic experiences by integrating body-related inputs and dreamt self-representations. Fifth, top-down attentional control facilitates and stabilizes multisensory integration by regulating the balance between the generation of self-referent mental models and the gain of prediction error signals conveyed by incoming sensory stimuli. This way, attentional control stabilizes the current mental model (e.g., current LD scenario) against potentially violating sensory signals.

Predictive Coding

Predictive coding (PC) is a neural computational framework built upon scientific and philosophical traditions and comprehensive models of perception proposed by von Helmholtz (17–19). In this framework, the brain is a hierarchically organized system creating predictions (priors) of the external world and of its internal states, in close association with the incoming sensory stimuli (posteriors). Predictions are formed based on a generative model aimed at estimating the likely causes of incoming signals following Bayesian inference rules. Predictions are organized from bottom to top, corresponding to gradually more and more complex representational levels from simple, elemental details (e.g., colors, shapes) to complex, abstract representations (e.g., object categories, emotion, self-image, etc.). Predictions at each level of the processing hierarchy are streamed downward (top down) and matched with incoming bottom-up sensory signals. The difference between the prior of a given level (the model) and the posterior(s) of the level below (input) is called the prediction error (17, 18). Prediction errors are streamed upward to higher processing levels, becoming inputs that will be matched with predictions formed at higher levels. In turn, posteriors at one level will stream downward to shape predictions at the lower level. This way, information is shaped by a continuous and dynamic exchange between top-down predictions and bottom-up prediction error signals, along the hierarchically organized processing stream (19–21). Crucially, the system aims to minimize the amount of prediction error, eventually leading to predictions matching incoming sensory inputs: hence, providing accurate and adaptive models of the environment. Thus, statistical inferences are used to harmonize top-down predictions and bottom-up signals, attenuating prediction errors and surprise within processing levels (21, 22). Attenuation of prediction errors is accomplished by adjusting predictions to incoming stimuli (updating generative models) or by active inference (i.e., execution of actions [e.g., motor commands] to adjust sensory inputs to fit predictions). The balance between bottom-up and top-down influences is modulated by precision weighting regulating the gain of prediction errors. In other words, precision weighting determines if the incoming signal is considered precise or uncertain. If precision is high, bottom-up prediction errors force the system to update predictions or execute actions; if precision is low, prediction errors have less influence, and predictions are formed based on top-down models. Attention is central to precision weighting as it can increase the gain of prediction errors or (depending on the attentional focus) help in discarding certain prediction errors to favor others (23). Although PC was first introduced in relation to exteroception, it was extended to describe the processing of internal bodily signals (interoception), providing an essential reference for representing the own body (i.e., "the material me"), and lay the ground for more complex representations of the self (19, 24, 25).

Predictive Coding in Dreaming

Phenomenological aspects of dream experiences were studied in the PC framework (26–28). During sleep, the balance between top-down and bottom-up influences changes; sensory stimuli processing during sleep is attenuated, and attention is directed away from sensory afferents toward internally generated cognitive processes (26, 29), especially during phasic REM sleep (when the most intense forms of dreaming take place) (30). Attenuated precision on lower-level priors shifts the system toward top-down processes, and prediction errors are minimized mainly by higher-order predictions (more abstract, middle- to high-level priors), in contrast to wakefulness when perception is also constrained by sensory afferents (26, 28). Moreover, even if low-level prediction errors occur, they may not reach supramodal frontal and parietal cortices as these regions are relatively quiescent during REM sleep (31–34). Low precision assigned to sensory inputs leads to the dynamic creation of novel predictions to fit rapidly changing neural activations during dreaming (30). Given the lack of external constraints (feedbacks from sensorium), the brain will jump from one prediction to another, leading to bizarre, fragmented, and discontinuous dream narratives with vague, uncertain perceptual qualities (26). For instance, consider the following dream report.

> I was talking by phone with a woman whose personality was not immediately clear in the dream. I had to explain her how to find Georges Henry street in Brussels, and I remember walking the city streets. She repeated the street name, and I told her how great she could pronounce the French word so easily. Of course, I realized, because she is French. But then I felt puzzled, because I realized that I was speaking Hungarian with her, meaning she was someone else, not my French friend. Suddenly, I realized that I was talking to my sister, of course I was, that became so obvious in the dream!

This dream illustrates how high-level predictions can shape a dream narrative. The name of a Brussels street leads to the prediction that the dreamer is in Brussels, and

the pronunciation of a French name forms the prediction that the dreamer is talking to a specific French person, eventually leading to a prediction error: a mismatch between the language used in the dream (Hungarian) and the memory of the language (French) used by that person. To resolve the prediction error, an updated novel prediction is formed, changing the identity of the friend to fit the prediction with acoustic experience (model updating) (Fig. 1, *Upper*).

Prediction errors may also occur at lower levels of the processing hierarchy. Sleep sensory stimulation studies showed that external inputs can enter the processing stream and influence dream content, albeit that incorporation of incoming signals is quite arbitrary (35). Within the PC framework, interpretation of incoming sensory signals is mainly driven by top-down predictions (26). Albeit visual and acoustic stimulation outside the laboratory is rare under natural sleeping conditions, tactile and interoceptive stimuli may be incorporated into dreams in a similar manner, especially if they cause pain or discomfort (36). For instance, bedsheet wrinkles may incorporate into a dream as insects crawling on the skin. Proprioceptive feedback of the atonic body may also induce prediction errors and model updating (i.e., new priors shaping the dream plot: "I am unable to run quickly, my legs are in water"). Alternatively, if further attention is directed toward bodily signals and thus, higher precision is tagged to interoceptive stimuli, the representation of the real body can be partially reinstated in alignment with lower-level interoceptive processing. In this case, interoceptive feedbacks producing prediction errors may be attenuated by active inference, leading to increased sympathetic activity (e.g., increased heart rate), brief movements, arousals, or awakening (active inference) (Fig. 1, *Lower*).

Fig. 1. Schematic illustration of PC and dream phenomenology. The dream narratives (thought clouds) are shaped by the updating of middle- to higher-level priors or active inference that may lead to arousals or awakening. Blue triangles indicate the mental space of more specific lower-level predictions (*Lower*) and more abstract middle- to higher-level predictions (*Upper*). (*Upper*) A prediction is formed about having a conversation with a French friend (the first time point). Low precision weighting (lines ending in green circles) on auditory perception does not trigger strong prediction errors (red arrows pointing upward); however, at a later (second) time point the top-down expectations increase the precision of lower levels regarding the auditory input, predicting a conversation in French. This way, the auditory content recognized as Hungarian produces a stronger prediction error as it deviates from the expected language. The prediction error is then attenuated by a novel prediction (the red contoured box) that changes the identity of the talking partner (to a Hungarian person) to match the higher-order model with the auditory input. (*Lower*) A motor plan to run away is streamed downward to lower levels and impinges with bottom-up proprioceptive information of an atonic, paralyzed body (the first time point). The prediction error produced at this lower level is attenuated by a new prediction at different levels: the mental scheme of the legs that move slowly (despite the motor command) and a higher-level prior updating the visual scene and predicting that the legs move slowly because they are standing in water (the second time point). At later time points, increased precision on proprioceptive information leads to new predictions and model updating or to active inference producing motor activity that may break out of muscle atonia and lead to arousals or even awakening (time point 3). To sum up, in *Upper*, the model update was sufficient to reduce prediction errors in the system; thus, dreaming could continue. In contrast, *Lower* illustrates a scenario when the model update is not sufficient to reduce prediction errors, and active inference reached the peripheral effectors, eventually leading to arousals and awakening.

Prediction Errors, Multisensory Integration, and Dynamic Attention Guide Lucid Dreams

PC mechanisms were also proposed to account for LD experiences (26, 37, 38). In LD, prediction errors trigger updating of predictions that, at some point, reach a metacognitive self-model explaining the ongoing mental representations as dream images (37). We assume that in LD, prediction errors are streamed forward through the processing hierarchy, reaching supramodal, prefrontal, and parietal cortical regions [in contrast to non-LD when activity is largely attenuated in these areas (16, 31–33)]. The insight of being in a dream breaks the constant flow of new predictions since it provides a superordinate prediction fitting the internally generated sensorimotor experiences of dreaming. Otolithic sensations involving experiences such as flying or levitating, hallucinatory-like experiences surpassing the perceptual intensity of nonlucid dreams, or strange bodily illusions are frequent features that contribute to the saliency and memorable quality of lucid dreams. We assume that the intensification of such low-level perceptual processing is increased because precision weighting of prediction errors arising from periphery, including bodily signals, is higher during lucidity moments. Notably, increased gain on interoceptive signals does not imply that the dreamers will be aware of (have conscious access to) their real body image, but the contribution of interoceptive signals to the mental representation of the self (24) will be stronger in LD compared with non-LD. Bottom-up signals conveying real body information will enter into the processing stream as inputs that will be matched with current predictions of bodily states. For instance, a dreamer may experience running within the dream. Such higher-level body-state priors shape priors at lower levels to predict heavy muscle work. On the other hand, a bottom-up proprioceptive signal conveys the contradictory information of a fully relaxed, atonic body. The mismatch between the prediction of a moving body and proprioceptive feedback of an inert body creates a prediction error, resolved by a superordinate self-model integrating both body representations: "my real body is immobile, lying in bed, while I am dreaming that I am running."

Integrating ambiguous bodily representations may lead to peculiar kinesthetic experiences of LD (Fig. 2). In the PC framework, flying, levitating, or out-of-body experiences [often reported in LD (39, 40)] are updated predictions attenuating prediction errors (e.g., a flying body is a good proxy for the inconsistency between a body image moving within the dream but at the same time, felt as inert and weightless due to muscle atonia). We do not claim that prediction errors triggering lucidity are restricted to lower levels in the processing hierarchy. Prediction errors that appear at higher levels (for instance, in the context of a mismatch between higher-level priors within the dream narrative ["I failed my graduation exam"] and an episodic memory for a specific event ["but I am already full professor"]) may also trigger a metacognitive LD insight ("this is not possible, I must be dreaming"). On the other hand, we propose that even if prediction errors inducing lucidity occur at higher levels, once the superordinate model of the sleeping and dreaming self is established, higher precision weighting is assigned to lower levels of the processing stream. Higher precision weighting on lower-level priors leads to more fine-grained perceptual details within the dream, resembling wakeful perception. Additionally, superordinate metacognitive predictions of "dreaming while asleep" will be streamed downward to lower-level priors. Simultaneously, reengaging attention toward sensory periphery, including interoceptive signals, will also assign high precision to bottom-up sensory afferents from the external environment. Importantly, prediction errors are assumed to occur at the same rate in LD and non-LD in lower levels of the processing hierarchy. In LD, however, the brain must not reinterpret each sensory signal at higher (more abstract) levels and must not jump from one prediction to another, explaining the immersive perceptual experiences of dreaming. In other words, in LD, prediction errors are generated (at a similar rate as in nonlucid dreams) but attenuated at lower levels of the processing hierarchy, while higher-order priors remain stable as compared with non-LD. We propose that this reorganization of precision weighting contributes to some LD peculiar features. LD is often highly vivid and includes overwhelming visual, acoustic, and kinesthetic hallucinatory-like experiences with fine-grained details resembling wakeful perception (2). Similarities between LD and wakeful perception were evidenced in a groundbreaking study (14) showing that smooth pursuit eye movements can be elicited in LD and wakefulness, while participants were only capable of producing saccadic eye movements in wakeful imagery. We may speculate that during waking visuomotor imagery, higher-level priors (modeling a moving target) are not efficiently streamed downward to produce precise lower-level perceptual representations of the object, in turn compromising smooth eye tracking. Lower-level perceptual representations may also form in dreaming and waking imagery, allowing smooth pursuit movements in both conditions (14, 41), but less efficiently than in LD. Noticeably, LD is rated less bizarre than non-LD (42), despite the immersive perceptual quality and hallucinatory-like nature. We surmise that lucid dreams are experienced as less bizarre because prediction errors occur and are resolved at lower levels. Hence, surprise is minimal at higher levels, and the self can passively reflect on the contents of consciousness, as if the dreamer thought, "Anything strange can happen, because I am in a dream."

While prediction errors may trigger lucidity moments, they are likely not sufficient to sustain LD. The transient LD state can easily shift back into a nonlucid state or end in abrupt awakening (43). Skilled lucid dreamers, however, can remain in the state for longer periods. We propose that multisensory integration at higher levels is a critical process to sustain lucidity. During LD, sensory inputs from the external world, including surroundings and the body, are integrated with stochastic activations of higher-order sensorimotor areas (31, 33, 34). For example, proprioceptive and vestibular stimuli may interfere with visual body representations within the dream, but the latter does not overwrite low-level sensory signals (44). Increased gain of bodily signals during LD enables maintenance of an egocentric reference frame, a sense of the body within the dream, and the perception of dream scenes from a first-person perspective. Sense of the real body and dreamt

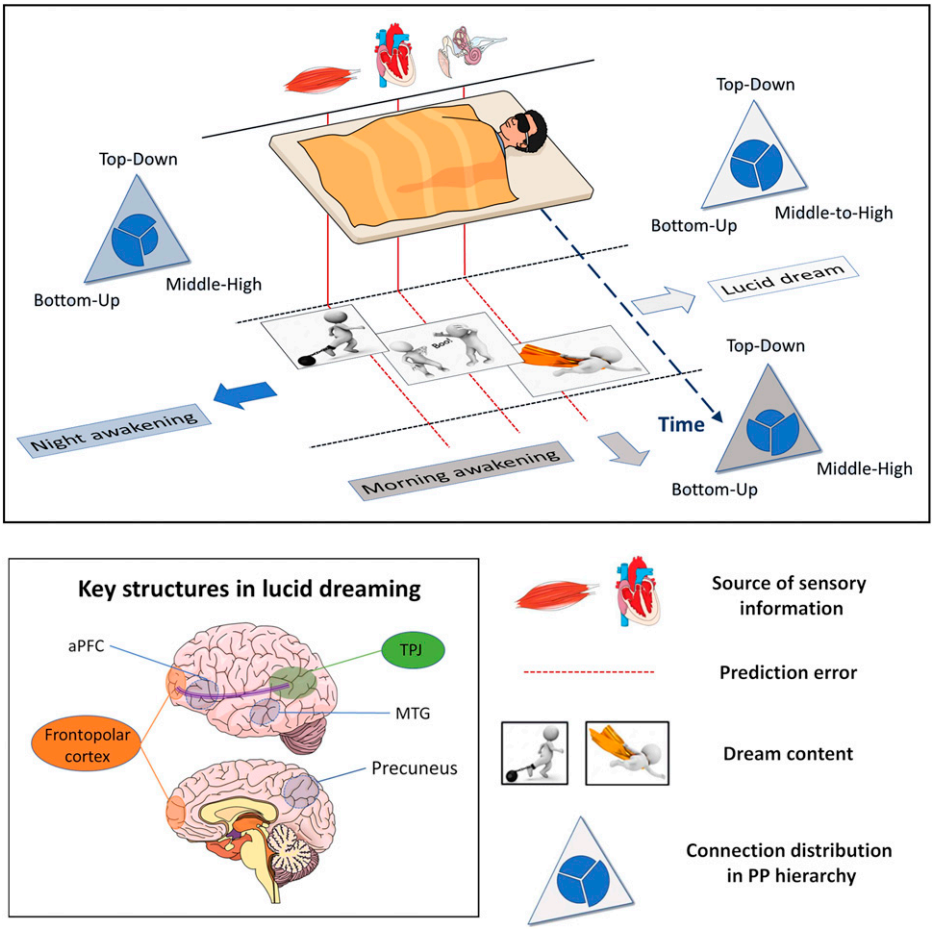

Fig. 2. A multicomponent framework for LD. In this example, interoceptive (e.g., proprioceptive, cardiac, vestibular) inputs create prediction errors under increased alertness conditions during sleep. Prediction errors are attenuated during dreaming by updating middle- to high-level priors leading to dream incorporation or by active inference provoking arousals and abrupt awakenings. Alternatively, attenuation of prediction errors can be achieved by a metacognitive, superordinate self-model (i.e., LD "I am dreaming while I am asleep"). This model integrates ambiguous inputs arriving from lower (e.g., sensory periphery) and higher (e.g., sensorimotor cortex) processing levels. Importantly, LD may also be triggered by prediction errors occurring at higher levels of the processing stream (e.g., mismatch between dream events and episodic memory for specific events). Active inference and abrupt awakenings would result from higher precision weighting on bottom-up signals and lower influence of higher-level predictions. Top-down influences are stronger in the case of LD maintained by multisensory integration, itself underpinned by TPJ and medial temporal gyrus activity, and by recollection of episodic memories, subtended among others by the precuneus. Attentional control and dynamic precision weighting rely on activity in frontopolar regions and frontotemporoparietal connections. aPFC, anterior prefrontal cortex; MTG, middle temporal gyrus; PP, predictive processing.

sensations are far from being stable, as prediction errors are constantly monitored and resolved by model updating and active inference. More specifically, interoceptive and exteroceptive stimuli can be incorporated into dream imagery (model updating), and dream imagery can induce changes in the periphery (active inference) to match higher-order predictions. Active inference in LD is exemplified by findings showing that congruent changes in respiration or heart rate accompany voluntary dream activities (e.g., physical exercise or controlled respiration) (45, 46).

At the neuroanatomical level, the temporoparietal junction (TPJ) plays a critical role in multisensory integration, supporting the sense of body and self-location to maintain an egocentric reference frame (47–49). It is also involved in (non-lucid) dreaming; TPJ lesions were associated with global dreaming cessation (50), and individuals with frequent dream recall show increased TPJ activity, indicating its involvement in dream imagery generation (51). Whereas TPJ activity appears critical to establish self-referent, internally generated mental simulations of the environment during dreaming and waking cognition (also termed self-projection) (52), we propose that such simulations integrate a broader range of processing levels in LD. As mentioned above, dreaming and waking imagination mainly relies on computing high-level priors. In LD, lower-level priors of earlier sensory processing steps are streamed upward, having a stronger influence on conscious experience. Accordingly, activity in temporoparietal regions is higher in LD than non-LD (4).

Another peculiar feature of LD is the sense of control during dreaming. Skilled lucid dreamers can monitor the contents of their dreams, flexibly change attentional focus, access episodic memories, and even partly control their dreams narrative (16). In our framework, these abilities result from the dynamic precision assignment to lower- and higher-level priors, enabling balance between top-down and bottom-up influences. Such dynamic weighting may also stabilize and extend lucid dreams for longer periods and maintain lucidity in a sleep state featuring neurocognitive components of wakefulness. A stronger focus on prediction errors originating from bodily signals (i.e., higher precision on low-level processing steps) may also elicit active inference and awakening, whereas a shift toward high-level predictions may reestablish non-LD. However, executive functions are partially reinstated in LD, facilitating top-down control over the dream plot, in contrast with non-LD in which these are strongly deactivated (2, 9, 13, 16). Executive functions allow lucid dreamers to flexibly shift attention from one stimulus to another (e.g., from sensory inputs [proprioception, visual, acoustic stimuli …] to internally generated visual imagery [body image within the dream …]) or voluntarily recall episodic memories contradicting the unfolding dream scenes. Such cognitive mechanisms may generate new prediction errors, forcing the system to reupdate mental models and reinstate metacognitive self-awareness. Such cognitive operations may be linked to increased activity in frontopolar

areas and more specifically, functional interactions between frontopolar and temporoparietal regions (4, 16). Accordingly, frontopolar areas exhibit larger gray matter volume in frequent vs. nonfrequent lucid dreamers and increased activation in metacognitive thought-monitoring tasks (11, 53). Moreover, lucid dreamers exhibited higher functional connectivity between frontopolar and temporoparietal association cortices in resting wakefulness (10). Simultaneously monitoring a wide range of diverse and ambiguous stimuli without becoming focused on one resembles a self-awareness state promoted by meditation practices (54, 55). For instance, in mindfulness meditation, exteroceptive and interoceptive events are constantly monitored but not interpreted by affective value or subjective meaning. Expert meditators develop enhanced awareness of bodily states (i.e., increased bottom-up processing), leading to perceptual clarity and subtle interoception replacing top-down, interpretative, or narrative accounts of bodily sensations (56). Notably, increased gray matter volume in frontopolar regions features expert meditators (similarly to lucid dreamers) (56).

As an intermediate summary, we propose that LD requires a wide range of cognitive operations (Fig. 2), including 1) resolving prediction errors by generating a superordinate self-model (lucidity moment), 2) enhanced processing of bottom-up signals and attenuation of prediction errors at lower levels of the processing hierarchy, 3) multisensory integration of ambiguous stimuli from the sensory periphery and higher-order regions, and 4) dynamic precision weighting and flexible monitoring of contents of consciousness.

Regulation of Sleep and Arousal: Gating Lucidity

Sleep is a remarkably heterogeneous state, fluctuating between deep, stable sleep periods characterized by sensory disconnection and fragile, aroused states during which environmental alertness is temporarily reinstated (57). Deeper sleep states reflecting sleep homeostatic pressure predominantly feature low-frequency (1- to 10-Hz) electroencephalographic (EEG) activity (58); whereas transient, vulnerable periods feature wake-like, faster EEG frequencies, sympathetic arousal, and increased muscle tone (59). The interplay between sleep-like and wake-like activities during sleep provides a balance between two antagonistic but fundamental roles of sleep: sensory disconnection facilitating restorative properties of sleep (60) and environmental monitoring transiently restoring alertness (57). Crucially, the sleeping brain limits arousals duration; longer periods of wake-like activity may lead to awakenings and sleep fragmentation. Regulation of wake-like activities also occurs at the spatial level; wake-like, high-frequency activity often occurs at specific brain locations and localized networks, while sleep-like activity persists in widespread brain regions (61).

The coexistence of sleep-like and wake-like patterns is accentuated in NREM (non-Rapid Eye Movement) parasomnias (e.g., sleep terrors, sleep walking, and confusional arousals) (62); local arousals duration and intensity in deep sleep increase, while sleep-like patterns continue in other cortical regions (63). Intracerebral studies capturing NREM parasomnia episodes observed local wake-like electrical patterns within motor, cingular, insular, and amygdalar cortices, while frontal- and frontoparietal-associative areas featured deep sleep patterns (64, 65). Hence, the balance between sleep- and wake-like states exhibits a pathological shift toward wake-like activities in some regions, while sleep regulation is preserved in frontoparietal associative cortices (63). Such imbalance between sleep-like and wake-like patterns during sleep appears to be a common denominator of a wider variety of pathological sleep states (*SI Appendix*, Table S1). In particular, relatively increased wake-like EEG activity was also observed in nightmare disorders (66, 67), insomniac complaints (68–70), and sleep paralysis (71, 72).

LD features signs of reduced sleep regulation (4). Lucid experiences arise under low homeostatic sleep pressure; they more likely occur at early morning hours during the last cycle of nighttime sleep or daytime naps (1, 8). Frequent lucid dreamers self-report more sleep–wake transitions, suggesting a higher sense of alertness during sleep that might not necessarily lead to poor sleep quality (73). Moreover, objectively verified wake–REM transitions (73) and manipulations facilitating environmental alertness seem to provide favorable conditions for LD experiences (8). We propose that reduced sleep pressure and shift toward wake-like states during sleep (especially REM sleep) enable the processing of environmental inputs otherwise attenuated during sleep. That is, transient intrusion of wake-like activity patterns can facilitate a gain of bottom-up afferent signals.

Although exteroceptive inputs are reduced during sleep, the body still provides a rich source of information (74). Cortical processing of such interoceptive signals is intimately linked with arousals; interoceptive processing is enhanced in increased arousal conditions (75, 76). In turn, interoceptive processing facilitates further arousals during sleep, shifting the brain into a more vigilant state (29, 36). For example, in an aroused sleep state, attentional resources are partially reinstated, allowing for the processing of proprioceptive or vestibular bottom-up afferents with higher precision that in the PC framework, would lead to prediction errors in the processing stream. Notably, we do not claim that higher precision on bodily signals would lead to the perception of the real body during sleep, as changes in interoceptive processing are not necessarily perceived (77–79). These signals may give a momentum for LD, provided that multisensory integration and flexible model updating are established. Importantly, prediction errors can force the updating of mental models without necessarily involving lucidity. For example, imagine you have a nightmare in which you are dreaming of being chased by an angry dog and trying to run away. Due to increased arousal and enhanced interoceptive processing, the proprioceptive feedback loop conveys information of the failure to execute motor commands under REM-related muscle atonia. Here, the prediction error may be attenuated by a new self-model escalating the nightmare: "I want to run away from the dog, but I cannot move because I realize I have prison balls on my legs." Alternatively, prediction error signals facilitated by enhanced interoceptive processing may be attenuated by active inference provoking a motor command breaking muscle atonia, interrupting REM sleep, and leading to abrupt awakening from the nightmare. Another example is poor sleep quality; under reduced sleep-depth conditions, proprioceptive signals may restore to some extent the mental representation of the real body (model updating) and the experience of being

awake while asleep (e.g., "I am not asleep, just lying in my bed"). Attention toward bodily signals reallocates cognitive resources to monitor further the external environment (25), a mechanism leading to hyperarousal and sleep-state misperception in insomnia (80). Again, prediction errors may even trigger the execution of motor commands, leading to arousals or in severe cases, awakenings and sleep fragmentation.

Whereas wake-like EEG activity was evidenced in sleep disorders, evidence for wake-like EEG activity during LD is based on scarce, underpowered, and somewhat inconsistent findings (4). Besides small population samples, studies featured methodological differences and a small number of scalp recording sites, and they often focused on specific (e.g., alpha) or narrow frequency ranges (4). The few sleep EEG studies consistently reported reduced sleep regulation signs and to some extent, increased wake-like activity in LD vs. non-LD, such as reduced power (71, 81, 82) and synchrony (82) in (1- to 4-Hz) low frequencies or increased alpha (83), parietal beta (84), or gamma (13) activity; however, the increase in fast frequencies (beta and gamma) was questioned more recently (82, 85). Interestingly, lucid dreams were mainly observed (1) during phasic REM (i.e., REM periods with increased ocular activity). In nonlucid REM, environmental alertness is largely reduced, and wake-like EEG activity in alpha and beta ranges diminished during phasic REM periods (29). Reduced low-frequency activity reflecting diminished sleep regulation in LD may index transient periods when exteroceptive processing and interoceptive processing are partially reinstated. On the other hand, these transient periods might alternate with enhanced sleep regulation and sensory attenuation after bottom-up signals are integrated in new self-models generated during LD. Future studies should further examine the dynamics of sleep-like and wake-like EEG activity in LD episodes.

Individual Differences in LD: Neurocognitive Factors

The neurocognitive factors contributing wide interindividual differences in LD frequency are scarcely investigated. Our model suggests that frequent lucid dreamers should be characterized by increased sensitivity toward sensory (including interoceptive) signals during sleep. Accordingly, increased vestibular sensitivity measured by caloric stimulation was found in frequent lucid dreamers (86). In addition, these authors observed better static balance performance in frequent vs. nonfrequent lucid dreamers, suggesting that lucidity may be associated with stronger reliance on vestibular cues (87). These early findings were corroborated to some extent recently (88). Indeed, vestibular cues contribute to the representation of the own body (bodily self), and their integration with other signals (e.g., visual) is essential to build the egocentric reference frame (48). Interestingly, the role of vestibular signals appears more relevant in the supine position (89) and presumably, during LD that often features otolithic sensations, such as flying, floating, and elevation (90). Out-of-body experiences (also reported in lucid dreams) are also peculiar subjective phenomena arising from the integration of vestibular inputs with ambiguous tactile, proprioceptive, and visual stimuli. Such sensations can be induced experimentally or appear after focal lesions (89). For instance, a case study described a patient with peripheral vestibular damage who experienced frequent out-of-body experiences and lucid dreams (91).

We have proposed that lucid dreamers efficiently integrate inputs from the sensory periphery with activations produced at higher-order processing levels and dynamically adjust precision weighting of different processing levels by increased attentional control. Whereas differences in multisensory integration (e.g., visuovestibular or visuotactile integration) between frequent and nonfrequent lucid dreamers were not directly examined, an early study observed better performance in frequent ones in the rod and frame test (92), requiring multisensory integration (93). In this task, participants must set a linear line, embedded in a square, to the subjective vertical position, discarding the position of the surrounding frame. Reliance on proprioceptive and vestibular inputs reduces the bias induced by the visual frame, improving performance (44). Frequent lucid dreamers were better at disregarding irrelevant visual signals, presumably relying more on vestibular and proprioceptive information in their responses (92). In our framework, precision of interoceptive signals was flexibly increased at the expense of visual inputs, a mechanism likely essential in maintaining lucidity.

We also hypothesized that attentional control [depending on integrity of prefrontal, mainly frontopolar structures (11) and frontopolar–temporoparietal connections (10)] can flexibly modulate precision weighting and balance top-down and bottom-up influences in LD. Few studies have examined cognitive functions in relation to LD, but two reported relatively enhanced attentional control in lucid dreamers in tasks requiring them to resolve conflicting information (94, 95). Future studies are needed to replicate and extend these intriguing findings to determine whether individual variability in LD is associated with attentional control differences.

Becoming Lucid: Lucid Dream Induction Techniques

Several techniques have been developed to increase LD frequency. Evidence supporting their success is admittedly not robust, but lucid dream induction seems a learnable skill, whose frequency can be modified (8). External stimulation during (REM) sleep by visual (light), acoustic, vestibular, and tactile stimuli was commonly used in early LD studies. Such sensory signals are expected to be at least partially processed and appear in the dream, eventually being identified as cues from the external environment (8). External stimulation generates specific bottom-up signals likely exceeding other inputs arriving from the sensory periphery. We have argued that such bottom-up signals may be associated with prediction errors that can be attenuated by model updating (nonlucid dream incorporation) or active inference (awakening) or provide LD momentums. Accordingly, external stimulation induces lucid dreams in some cases under laboratory conditions, but stimulation often provokes awakenings or is incorporated into dreams without becoming lucid (8). Sensory stimulation during REM sleep transiently shifts sleep into a more vigilant state of increased environmental alertness (96). Relatedly, other practices apply sleep disruption to induce LD: for instance,

sleep fragmentation or forced awakening before going back to sleep (97). Such state change may increase the gain of bottom-up sensory inputs, increase prediction errors, and thus, provide favorable conditions for LD.

Cognitive training promoting metacognition and different mnemonic practices (8) may also facilitate prediction errors and their attenuation during dreaming at higher levels of the processing stream. For instance, "reality check" is a common practice in which participants ask themselves during wakefulness whether they are awake or dreaming, a self-reflective training that seems to transfer into dreaming and trigger lucidity (98). Developing habits of self-reflection on its cognitive state (whether the mind is awake or dreaming) may draw the dreamer's attention to elements of the dream environment (e.g., events, feelings, thoughts) and increase the precision of middle- to higher-order priors. Accordingly, cognitive techniques often involve monitoring the environment to identify surprising or discrepant elements. Other cognitive techniques instruct participants to recall their intention of becoming lucid and to rehearse this objective, especially before falling asleep (99). These practices use prospective memory to increase the probability of the prediction (prior) of being in a dream against the alternative prediction of being awake (37).

In our view, prediction errors are important components of LD. Nonetheless, they are not sufficient to establish and maintain lucidity. In line with a multicomponent framework, studies indicate that combining different lucid dream induction procedures is more efficient than using a single technique (8). For instance, external stimulation appears to have a higher success rate if repeatedly applied during longer intervals and combined with cognitive training (8). Repeated use of external stimulation with the intention of gaining lucidity may strengthen episodic memories of specific cognitive practices (e.g., increasing metacognition) and previous LD episodes. Reactivating these memories about lucidity inductions and lucid dream experiences (as middle- to higher-order priors) may promote lucidity during dreaming. Accordingly, a study combining targeted memory reactivation with LD induction resulted in an unprecedented rise in lucid dream experiences (100). The procedure involved external stimulation (and presumably, sleep disruption), cognitive training, and cued reactivation of specific memories related to lucidity. It also indicates that beyond interindividual differences in LD frequency, most humans are potentially susceptible to LD when multiple lucidity components are boosted simultaneously.

Conclusions

We proposed five postulates to provide a multicomponent mechanism for the initiation and maintenance of LD, encompassing neural, cognitive and phenomenological levels. Since no idea is without antecedents and science is incremental in essence, our assumptions are built on previous theoretical considerations and empirical findings on LD. More specifically, peculiar characteristics of dreaming cognition were explained in the context of predictive processing by Hobson and Friston (28) and further elaborated on by Bucci and Grasso (26). Additionally, the assumption that LD is initiated by recognizing inconsistent, bizarre, or counterfactual dream elements was proposed in the first LD studies (43). Recently, others argued that (37) the insight of being in a dream is a result of a reasoning process involving Bayesian inference (the hypothesis of being in a dream vs. of being awake) to solve dream plot inconsistencies. Our first postulate is based on these assumptions and observations; however, we extend these considerations, arguing that such inconsistencies may produce prediction error signals not only at higher levels but also, at lower levels originating from bottom-up interoceptive inputs. Studies on LD neural correlates concluded that prefrontal and fronto-temporoparietal networks support increased awareness, self-reflection, and control in LD (4). Building on these findings, our fifth postulate hypothesizes that the role of top-down attentional control (supported by prefrontal and fronto-temporoparietal networks) is to regulate the balance between the generation of self-referent mental models and the gain of prediction error signals conveyed by incoming sensory stimuli. This way, attentional control stabilizes current mental models against potentially violating sensory signals, leading to increased control over the dream plot in skilled lucid dreamers. Additionally, we postulate that individual differences and intraindividual fluctuations in sleep-arousal regulation modulate sensitivity to prediction error signals (the second postulate). These signals are streamed forward to higher-processing hierarchy levels and attenuated by updating mental self-representations or active inference accommodating bottom-up sensory signals conveying contradictory information (the third postulate), leading to multisensory integration enabling lucidity maintenance and contributing to peculiar kinesthetic experiences by integrating body-related inputs and dreamt self-representations (the fourth postulate).

To our knowledge, our theoretical model is the first to provide such a mechanistic explanation for LD. Our assumptions offer testable predictions with regard to the neurocognitive aspects of—and interindividual differences in—LD (*SI Appendix* has more details). Although the relevance of interoceptive sensitivity and especially, the vestibular pathway was investigated in early and recent studies (86–88), future investigations should corroborate findings in sufficiently larger samples and diversify interoceptive domains (e.g., proprioception, cardiac interoception). Moreover, we argue that the influence of interoceptive afferent pathways is just one component of multiple potential mechanisms establishing lucidity. Therefore, interoceptive processing assessments should be combined with tasks involving perception and/or imagery. Experimental manipulations involving ambiguous sensory stimuli and inducing body illusions may also provide fruitful working models to examine differences in multisensory integration between frequent and nonfrequent lucid dreamers. Research combining visual tasks with interoceptive challenges [for instance, virtual reality simulations (101)] with galvanic vestibular stimulation may model the proposed mechanisms of PC and multisensory integration taking place in LD, providing valuable insights on the background of otolithic experiences in LD. Similarly, including attentional control as an additional variable in such cognitive tasks (e.g., flexibly shifting between interoceptive and exteroceptive focus) and neuroimaging assessments may help in delineating the role of

fronto-temporoparietal networks in attentional control and dynamic precision weighting. The multicomponent framework of LD may also facilitate lucid dream studies in relation to development (and aging) and psychopathology (*SI Appendix*). While the view of LD as a sleep state featuring a mixture of EEG components of wakefulness and sleep is intuitively appealing, it should be confirmed by more robust evidence in larger samples and higher EEG density coverage (4). Data-driven procedures taking into consideration the whole broadband EEG spectrum by parameterizing periodic and aperiodic components provide statistically more valid quantifications of EEG activity than consensual analyses of power in specific frequency bands. For instance, the spectral slope of the transformed EEG spectrum (including low and high frequencies) attenuates the influence of nonneural sources and other confounders (102, 103) while remaining a powerful technique to distinguish different states of vigilance (103) or pathological sleep conditions overlooked by traditional techniques (68). Moreover, different types of LD experiences or the temporal evolution of becoming lucid within a dream might rely on different neural correlates (104). Instead of comparing averaged EEG power between nonlucid and lucid episodes, more dynamic approaches, such as time–frequency analyses, may offer novel insights into the temporal evolution of lucidity. Efficient LD induction procedures, like the targeted lucidity reactivation technique (100), would provide an excellent experimental context for such advanced EEG analyses of sleep recordings collected during the experimental manipulations.

Finally, preliminary studies indicate that practicing lucid dream techniques may help in overcoming nightmares (105) and insomnia (106). The efficacy of LD in ameliorating these sleep disorders would be particularly interesting since both nightmares and insomnia feature increased arousal (70, 107) and may thus provide favorable conditions for LD. Nevertheless, as compared with lucid dreams, oneiric experiences during nightmares and insomnia are highly stressful, and self-reflection is also compromised. In the case of nightmares, individuals experience perceptually vivid and emotionally absorbing dysphoric dreams and perceive these oneiric experiences as real without having the ability to control and change the unpleasant dream plot. In contrast, insomnia sufferers often perceive that they are awake while they are actually sleeping; in other words, they dream that they are unable to sleep (108). Although bottom-up influences might be enhanced in these conditions, both are characterized by rigid and narrow attentional focus and lack of control. It is thus tempting to speculate that multisensory integration and attentional control achieved during LD are key factors in transforming nightmares and insomniac dream mentation. Future studies should corroborate the efficacy of lucid dream therapy and provide insightful information on the treatment mechanisms relating phenomenological and neural levels.

Data, Materials, and Software Availability. There are no data underlying this work.

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