Box 1. The Setup of the Study

The study [1] comprised four experiments, each with two conditions that were chosen to preclude behavioural predispositions of ravens: token exchange with humans and tool use (ravens are non-tool users in the wild). Before the experiments, the ravens learned to use the tool not through associative learning but from a single observation, and repeated this successfully five times (the only times they had ever used tools). They learned to exchange the correct token in less than 30 trials. The training deviated from the testing, as they never selected the items among distractors and the apparatus or exchanging human was present. Importantly, they never experienced the problem they had to plan for until after training: a situation where an item was needed but they had none [7,8]. The experiments replicated previous studies with primates, but also included new controls. Experiment 1 tested decision-making for 15 min into the future while Experiment 2 tested for 17 h. Experiment 3 tested self-control in a 15-min setting and Experiment 4 in a <1-min setting. The results of these experiments were compared to evaluate the value of the items. All individuals performed significantly above chance *per* planning criteria in all experiments and conditions.

value. Further, one would have to assert that in the 15-min delay experiment the ravens associatively learned – in a handful trials each week – that the item was more rewarding than the immediate reward and that this learning had no signature learning curve, such that they instantly became 100% successful with the short delay. Such learning – if there were any trace of it – sounds like learning used in planning, which involves forming associations between long-term memories of events. This is no lean learning explanation, and hardly any alternative to planning.

The other alternative explanation provided by Redshaw and colleagues was that the ravens used memory-mediated reinforcement, or mnemonic associations. This is a peculiar argument, as mnemonic associations are dependent on episodic memory and are regarded as one alternative to Mental Time Travel planning, but not as an alternative to planning *per se* [10]. Mnemonic associations occur where the animal at the future situation recollects the actions that led to that situation (actions initially driven by goal-directed associative learning or innate propensities) and so learns this connection, which later drives planning behaviour in similar situations.

Such a planning mechanism does not work, however, with respect to past actions not directed towards the future reward: in this case, selecting the immediate reward. Then, the animal must already know that the selection event is future related, otherwise it could have associated any action, at any time, that failed to lead to the reward [11]. So, if mnemonic associations were used, the ravens must have known the item–outcome relationship before the self-control experiments, making our control valid anyway. Given the results it is improbable that such associations were at play, but if they were they are still no alternative to planning.

The fact that ravens exert future-oriented behaviours, apparent in apes and mature humans but not in monkeys or young children, does not vanish with attempts to recharacterise planning terminology. That merely diverts from the intriguing theoretical consequences that arise from the discoveries that some avian dinosaurs parallel the complex behaviours of our closest relatives and us.

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Forum

Stressful Events as Teaching Signals for the Brain

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Stressful events are better remembered than mundane events. We explain this advantage by reconceptualizing stress in terms of cumulative prediction errors (PEs) that promote rapid learning of events. This proposal integrates the effects of stress on perception and memory, and provides exciting new perspectives for research on stress and cognition.

Stress is ubiquitous in our daily life and can have a major impact on our mental health and wellbeing. This impact may in part be driven by stress-induced changes in cognition. In particular, it is well documented that stressful events are typically much better remembered than mundane events. Enhanced memory for stressful events may be highly adaptive as it prepares us for similar scenarios in the future. However, the memory boost may also contribute to stress-related mental disorders such as post-traumatic stress disorder [1]. So far, superior memory for stressful events has mainly been related to increased arousal and the operation of adrenaline, noradrenaline, and glucocorticoids [2]. While this 'arousal view' is well supported by empirical evidence, we introduce here a novel hypothesis that may stimulate new research and enhance our understanding of memory formation under stress. In particular, we argue that acutely stressful events, mainly characterized by their unpredictability, elicit a PE that acts as a teaching signal for the brain and promotes rapid learning of the ongoing events (Figure 1).

Box 1. PE: Learning from Deviation of Expectation

A PE is a mismatch between prediction and real sensory input and can therefore signal false beliefs about the structure of the world. Consequently, a PE contributes to the updating of internal models to increase the accuracy of future predictions.

Nowadays, the idea of a 'predictive brain' spans basically all domains in cognitive science: perception, action, reinforcement learning, language, affective and social neuroscience, and clinical psychology [11].

Not relying only on bottom-up information provides great computational advantages. Prior information in perception can disambiguate sensory input and fill in where noise and clutter prevent unequivocal and fast recognition. In the framework of predictive coding, it is assumed that each sensory input is interpreted based on expectations. Corticocortical feedback connections are suggested to provide such top-down predictions and only residual errors (PE) are fed forward in the visual hierarchy to be further processed.

Important to note is that not only do PEs support the formation of new learning to improve future predictions, but surprising feedback generally improves memory for the event and, in the context of reward learning, a PE has also been shown to boost episodic memory for the event, although the underlying systems likely differ [4].

Stress as a Cumulative PE

The failure to accurately predict events results in a so-called PE, a key concept in psychology and cognitive neuroscience with particularly strong influence in reinforcement learning (RL) and perception (Box 1).

In RL, the concept of PE is used to explain dynamic learning, which ultimately relies on predictive processes. Crucially, learning is a function of the strength of PE; that is, the greater the deviation from expectation the greater the adjustment of internal predictions and thus new learning. Multiple studies have demonstrated that unexpected rewards result in an increase of phasic dopamine firing in the ventral tegmental area and substantia nigra [3]. It is proposed that learning is mediated by dopamine, as it induces synaptic changes in various brain regions [3]. In this way, faulty assumptions about reward predictions in the environment can be modified and more accurate predictions formed. Importantly, spillover effects of PEs have been reported as well, in that not only reward predictions but also episodic memories are improved [4]. Crucially, dopamine neurons can also transmit signals related to aversive events, manifesting either as a decrease in signed reward PEs or, in some dopamine neurons, as an increase in activity, which may be especially associated with early stimulus-driven responses [3].

Unpredictability is also a core feature of a stressful event. Examples such as sudden exposure to extreme temperatures or an explosion in the supermarket illustrate that in an acute stressful episode, we usually experience a lack of predictability [5]. Although rather neglected in stress research, a release of dopamine is also commonly observed during stressful episodes [6]. We therefore propose that stressful events represent a PE to the organism and argue that it is the PE that ultimately contributes to the memory boost for stressful events. If stress capitalizes on predictive processes, one would expect interactions with reinforcement learning. Indeed, stress can reduce the acquisition of reward-related information and attenuate neural responses to reward [7] as well as directly influence PE signals [8].

Obviously, even for the shortest acute stressor, the timescale is different from that of the rapid PE, which operates within milliseconds [3]. We therefore suggest thinking about stress as an accumulation of PEs; that is, in a situation that is not predictable, stress will develop. An average of PEs across a period of time would essentially become a proxy or approximate measure of uncertainty [9]. One could argue that stress also occurs when an upcoming aversive event is fully predicted. However, well-predicted events can engage metacognitive processes that attenuate the physiological and subjective stress response [10] and experienced stress may result instead from imprecision in the prediction. Moreover, there may be 'hard-coded' expectations of organisms that are not cognitively penetrable and that ultimately serve to maintain homeostasis, such as expecting temperature in a specific range or a certain amount of food. Such PEs may still result in a stress response, even when consciously expected. Moreover, it should be noted that, beyond the mere prediction of upcoming events, stress may also result from the appraisal of these expected events [11].

Stress not only boosts memory for circumscribed episodes, it also modifies the way we perceive the world. For example, stress reduces the attentional blink, indicating amplification of sensory processing [12]. The concept of PE is also a dominant explanatory route to understand and formalize perception. Here, it is assumed that information from bottom

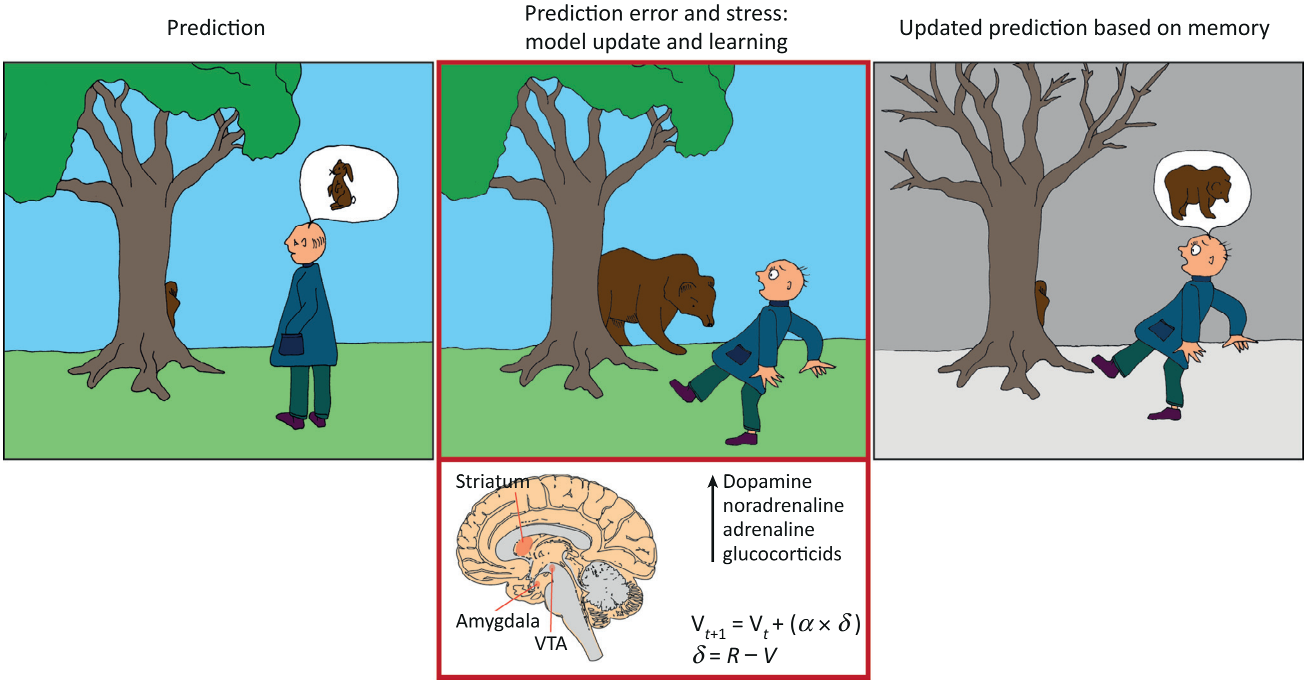

Figure 1. Stressful Events as Teaching Signals for the Brain. Unpredictability is a key feature of most stressful events. For example, one may expect a (harmless) rabbit behind a tree and be surprised by the discovery of a dangerous predator instead. Such a surprising, affectively laden scenario elicits a stress reaction, resulting in the release of adrenaline and glucocorticoids and enhanced activity of the amygdala, a core region for processing affectively relevant events. There is broad evidence that this neuroendocrine stress reaction promotes enhanced encoding of this event. We here propose that acute stress elicits a prediction error (PE) that contributes to the memory advantage. PE is a key concept in reinforcement learning and is inherently linked to dynamic learning. On a neuronal level, PE is associated with dopamine release, which increases synaptic plasticity and ultimately promotes updating of predictions (this process is formalized in the delta rule, depicted above). Similar mechanisms may also contribute to learning of the stressful event. VTA, ventral tegmental area.

up, the sensory input, is interpreted based on top-down expectations [13]. PEs promote more weight on bottom-up information to adjust (faulty) expectations. How do stressed individuals process incoming sensory information? According to our hypothesis, stress is elicited by PEs and should therefore be associated with a focus on bottom-up information. Indeed, such a shift towards networks that are specialized in processing saliency has recently been proposed in response to acute stressors [12].

New Avenues for Research on Cognition under Stress

Here we propose a reconceptualization of stress as elicited by PEs. One implication of this proposal is a stronger focus on the role of dopamine, a key player in the context of predictive processes, in stress effects on cognition. While stress research to date focuses mainly on the (well-described) actions of adrenaline, noradrenaline, and glucocorticoids, future research may use specific pharmacological manipulations or genetic variations to test the role of dopamine in cognition under stress. This reorientation may also be beneficial for our understanding of stress-related mental disorders, such as schizophrenia or depression, that are associated with dysregulation of the dopamine system.

Moreover, in RL a rich repertoire of computational approaches has been developed, the use of which may be highly beneficial for stress research. The advantage of computational models is the formulation and test of formalized cognitive hypotheses. The incorporation of such methodologies in stress research has only recently begun; for example, by demonstrating how stress changes the weight of PE signals in a reversal learning task [14]. By reconceptualizing stress paradigms as tasks that implement learning via error, one may also use RL and Bayesian frameworks to describe and explain behavior and neural mechanisms underlying stress effects on cognition.

Concluding Remarks and Outstanding Issues

Over the past decades, a plethora of studies has demonstrated the impact of stress on various cognitive functions. However, a unifying framework that links these findings – particularly across cognitive domains – is still missing. We propose that the reconceptualization of stress as driven by PEs provides such integrative power.

While we focused here mainly on acute stress, the proposed cumulative nature of the relationship between stress and PEs may also bridge the distinction between acute and chronic stress. Specifically, as the organism encounters more and more unexpected affectively relevant outcomes, stress will accumulate, and ultimately may become chronic. Furthermore, while the present PE hypothesis focuses on the encoding of ongoing events, it is also important to note that glucocorticoids can act on memory consolidation long after the actual event [15]. Another important issue is whether the PE signal triggers arousal under stress or whether PE-related processes and arousal are elicited independently. Stress reactions for strong positive PEs or interindividual differences in prediction and stress reactions are more examples for exciting new questions that this novel perspective raises.

In sum, by conceptualizing stress as mediated by PEs, three outstandingly developed, yet so far rather unrelated, fields of neuroscientific research are linked: stress and cognition, reinforcement learning, and perception. The synergy between these fields may stimulate novel methodological approaches and generate new predictions for research on cognition under stress.

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