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Review

Short- and long-lasting consequences of novelty, deviance and surprise on brain and cognition

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ABSTRACT

When one encounters a novel stimulus this sets off a cascade of brain responses, activating several neuromodulatory systems. As a consequence novelty has a wide range of effects on cognition; improving perception and action, increasing motivation, eliciting exploratory behavior, and promoting learning. Here, we review these benefits and how they may arise in the brain. We propose a framework that organizes novelty's effects on brain and cognition into three groups. First, novelty can transiently enhance perception. This effect is proposed to be mediated by novel stimuli activating the amygdala and enhancing early sensory processing. Second, novel stimuli can increase arousal, leading to short-lived effects on action in the first hundreds of milliseconds after presentation. We argue that these effects are related to deviance, rather than to novelty per se, and link them to activation of the locus-coeruleus norepinephrine system. Third, spatial novelty may trigger the dopaminergic mesolimbic system, promoting dopamine release in the hippocampus, having longer-lasting effects, up to tens of minutes, on motivation, reward processing, and learning and memory.

Contents

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1. Introduction: Novelty's effects on cognition

When colleagues came to visit Pavlov's lab to see a demonstration of classical conditioning in his trained dogs, the animals failed to show the conditioned response over and over again. The unfamiliar visitors distracted the dogs so much that they 'forgot' to show the conditioned response to the conditioned stimulus. Pavlov called this distracted response of the dogs an 'investigatory reaction', or a 'What-is-it' reflex—this is now mostly known as the orienting response (Sokolov, 1963; Sokolov, 1990). He argued that such a response has biological significance (Pavlov and Anrep, 1927): The rapid detection and processing of novel stimuli is crucial to adapt to current demands and explore new opportunities. On one hand, new stimuli pose novel opportunities that may result in beneficial outcomes, and on the other hand new stimuli may pose a threat.

It is therefore not surprising that the detection of novelty results in a variety of brain responses, and has an immediate effect on cognition and behavior. The orienting response is one of the most important characteristics of mammalian behavior, and is assumed to occur automatically (Chong et al., 2008; Escera et al., 2000; Schomaker et al., 2014c; Tarbi et al., 2011). Recent findings in humans suggest that novelty elicits a wide range of additional effects on cognition. For example, novelty can strengthen reward processing (Bunzeck et al., 2012; Guitart-Masip et al., 2010), drive exploration (Düzel et al., 2010; Krebs et al., 2009), facilitate encoding of visual working memory (Mayer et al., 2011), enhance perception (Schomaker and Meeter, 2012), and speed up responses (Schomaker and Meeter, 2014a). Animal studies have shown that exploration of a novel environment promotes long-term potentiation (LTP) in the hippocampus, thereby improving memory encoding (Davis et al., 2004; Li et al., 2003; Sajikumar and Frey, 2004; Sierra-Mercado et al., 2008; Straube et al., 2003a).

Novelty thus simultaneously enhances many cognitive functions, allowing the brain to be optimally tuned to learn about and respond to novel events. These effects are the topic of this review. Which neural processes underlie them is not well understood yet. Here, we will first discuss neuroscientific evidence of the brain's responses to novel stimuli. Then we will review findings of novelty's beneficial effects, concentrating in turn on effects of novelty on attention, task performance, and learning. Tying together findings from a range of experimental findings, we will argue that these three classes of effects are induced by different aspects of novelty and are mediated by at least three different mechanisms in the brain. Fig. 1 provides an overview of the brain's response to novelty and the putative functional architecture.

2. The brain's response to novelty

2.1. Neural responses throughout the brain

Novel stimuli are processed differently than familiar ones. In nonhuman primates, single cell recordings have shown much stronger neural firing to novel as compared to familiar stimuli in the inferior temporal cortex (Li et al., 1993; Xiang and Brown, 1998). In humans, fMRI studies show stronger activity for novel compared to familiar stimuli across a wide range of areas, including limbic regions, frontal, temporal, parietal, and occipital areas (Hawco and Lepage, 2014; Tulvin et al., 1996).

A wide range of novel stimuli have been used in the literature, which have varied in ways from control stimuli that may reflect different aspects of novelty (see Section 2.2). Some areas are consistently activated by these different types of novel stimuli. For example, the fusiform gyrus, lingual gyrus and medial temporal cortex are especially strongly activated by a variety of novel compared to familiar stimuli (e.g., novel environments: Kaplan et al., 2014; novel fractals: Stoppel et al., 2009; novel pictures of landscapes, animals, buildings, etc.: Yamaguchi et al., 2004; surprising faces: Duan et al., 2010). Within the medial temporal lobe the hippocampus, associated with novelty detection (Knight, 1996; Lisman and Grace, 2005), is activated in particular by the exploration of novel spatial environments (Bast et al., 2009; Jeewajee et al., 2008; Kaplan et al., 2014; Lisman and Grace, 2005), with stronger stimulus-specific novelty signals in the adjacent perirhinal cortex (Staresina et al., 2012). Moreover, novelty can drive activity in the amygdala—on its own and in interaction with emotional content (Blackford et al., 2010; Kiehl et al., 2005; Schwartz et al., 2003; Wright et al., 2003; Zald, 2003).

New stimuli thus generate strong neural responses across many higher perceptual and multimodal areas. Several mechanisms have been invoked to explain why novel stimuli would elicit strong neural responses and familiar stimuli weaker ones. These include sharpening of representations with repeated presentation (which would reduce the population of neurons firing to familiar stimuli), predictive coding (in which predictions suppress firing for familiar, and thus predicted, stimuli), and a dominance of LTD over LTP in the first presentations of a stimulus, reducing neural responses (Bogacz and Brown, 2003; Meeter et al., 2005; Segaert et al., 2013). As yet it remains unclear to what extent these mechanisms underlie the brain's response to novelty.

2.2. Psychophysiological indices of novelty and deviance

Several psychophysiological indices of novelty processing have been identified using the novelty oddball task while the brain's response is measured using the electroencephalogram (EEG) technique. In the novelty oddball task frequent repeated *standard* stimuli, infrequent *targets* (the 'oddballs'), and infrequent deviant non-repeated *novel* stimuli are presented in random sequence (Courchesne et al., 1975). The stimuli can be presented in any sensory modality, but usually visual or auditory stimuli are used. The novel stimulus typically elicits several event-related potential (ERP) components associated with novelty processing, such as a large anterior N2 component (also referred to as N2b), and a large novelty P3 component peaking over frontocentral regions.

These components may reflect responses to different forms of novelty. When a stimulus has never been seen, felt, or heard before by the observer it is novel, but a stimulus may also be novel only in the context of the experiment—the first is referred to as *stimulus novelty* and the latter as *contextual novelty*. Moreover, an environment can be novel, even though it contains only objects familiar to the observer (e.g., a never-visited classroom will be novel to a student, even though it may look like other classrooms (s)he knows). There are reasons, discussed below, to assume that *spatial novelty* has different consequences for brain and behavior than stimulus or contextual novelty.

Novel stimuli may also deviate from the other stimuli presented in the same experiment, and may therefore be *surprising* to the

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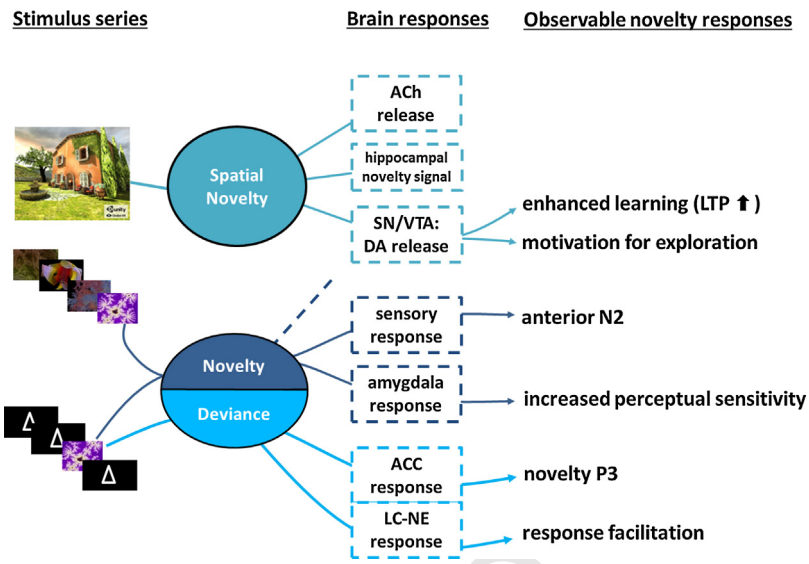

Fig. 1. Overview of the effects of novel stimuli on the brain and cognition. A stimulus can be deviant in addition to novel when it deviates from other stimuli in the context (e.g., as in an experiment in which a fractal is presented between simple standard triangles. See for example Schomaker et al., 2014d). Some of the effects of a novel stimulus are due to novelty itself, while other effects are more sensitive to deviance. Other effects of novelty have mostly been observed in nonhuman animals and humans during and after exploring novel environments (spatial novelty–here exemplified by a scene from a virtual reality environment). It is an open question, whether these effects are specific to spatial novelty, or whether they can also be elicited by novel stimuli (as indicated by the dashed line). See main text for further explanations. ACC = anterior cingulate cortex; DA = dopamine; LC–NE = locus coeruleus norepinephrine system; SN/VTA = substantia nigra/ventral tegmental area; Ach = acetylcholine.

observer. Stimuli can deviate from other stimuli without being novel—e.g., a picture of dog is a *deviant* in an experiment in which observers categorize images of furniture, but that does not make it necessarily novel (see Table 1 for a summary of these concepts). Although the concepts of deviance and surprise are thus readily dissociable from novelty, in typical visual novelty oddball experiments they are confounded: Novel stimuli also deviate strongly from the standard stimuli with which they are compared, and they are usually presented at low frequencies which may make them unexpected or surprising to the observer. The question therefore remains which aspect – novelty, deviance, or surprise – actually elicits neural responses usually ascribed to novelty.

The anterior N2, an early ERP component elicited by novel stimuli, peaks over frontal scalp regions around 250–300 ms for visual stimuli. It is not affected by the context set up by standard stimuli or by the frequency with which novel stimuli occur, suggesting that it is a response to novelty, not deviance, and that it is not sensitive to context, task relevance or expectations (Schomaker et al., 2014d; Chong et al., 2008; Tarbi et al., 2011; Schomaker and Meeter, 2014a). Although it is affected by attention, it may be so in an untypical way: When attention is engaged in a difficult working memory task, the anterior N2 to task-irrelevant novel stimuli is larger than when attention is available, suggesting that attention is required to suppress the initial processing of novel stimuli (Schomaker and Meeter, 2014b). This suggests that the anterior N2 Q5 is a reflexive response to novelty, reflecting an automatic novelty detection process (Chong et al., 2008; Tarbi et al., 2011). Alternatively, it may simply reflect the stronger neural response to novel stimuli elicited in higher perceptual areas. In line with the latter idea, a perceptual response to novel stimuli that are not attended has been found in the lingual gyrus, a brain region in the ventral visual stream (Stoppel et al., 2009). This perceptual response may be related to the increased firing rate seen in electrophysiological responses to stimulus novelty. It may thus be that a novel stimulus is a 'loud' stimulus in terms of neural firing, and that this is the basis of the anterior N2. A reason for this could be that stimuli typically have to be complex to be novel, as simple stimuli probably have been encountered before or will at least resemble previous sensory input to some extent. The lingual gyrus thus may be related to the early perceptual processing of novelty, however, rigorous source localization studies linking the anterior N2 and lingual gyrus are still needed.

A somewhat later ERP component elicited by novel stimuli is the novelty P3 (Courchesne et al. (1975). Another component, the P3a elicited in response to unexpected stimuli, has very similar characteristics as the novelty P3; it peaks frontally and in the same time-window (Squires et al., 1975). In fact, using a factor analysis the two components could not be distinguished, suggesting they

Table 1
Concepts related to novelty, with a description and examples of stimuli.

Concept	Description	Example
1. Stimulus novelty	Unfamiliar, never experienced before. Different from anything stored in long-term memory	Unfamiliar stimuli, like fractals or objects that are difficult to categorize (Courchesne et al., 1975; Daffner et al., 2000a,b; Stoppel et al., 2009; Schomaker and Meeter, 2012)
2. Contextual novelty	Differs from other stimuli shown in the context (e.g, the experiment), but has been seen pre-experimentally	Non-repeated images of familiar scenes, letters, well-known symbols (Polich and Comerchero, 2003; Friedman and Cycowicz, 2007; Barkaszi et al., 2013)
3. Spatial novelty/environmental novelty	Novelty of the environment rather than of a single stimulus	Unfamiliarized (virtual) environment (Straube et al., 2003a,b; Schomaker et al., 2014b)
4. Deviance	Infrequent category that is dissimilar to other stimuli	Stimuli such as infrequent grating patterns, that typically elicit visual mismatch negativity (vMMN; e.g. Czigler et al., 2002; Liu and Shi, 2008)
5. Surprise/unexpectedness	Violates expectancies, due to deviations from explicit predictions	Unanticipated stimulus sequence, such as unpredicted action effects (Waszak and Herwig, 2007; Iwanaga and Nittono, 2010)

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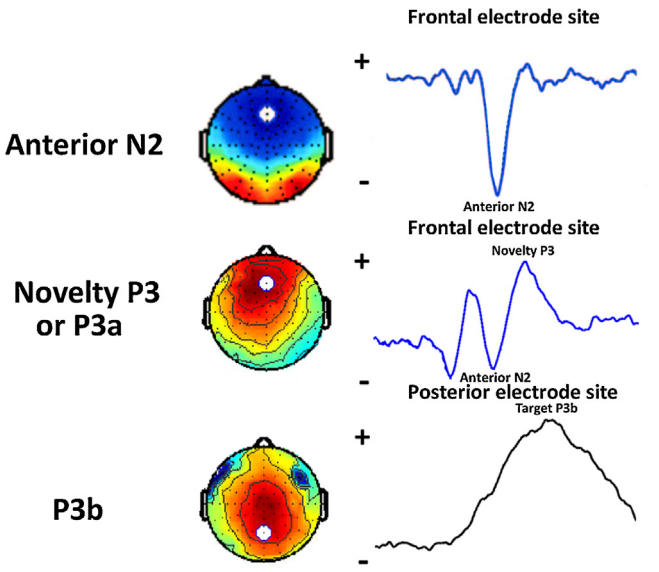

Fig. 2. Anterior N2 and P3 Subcomponents. The anterior N2 and novelty P3 (or P3a) peak over frontal regions, whereas the target P3b peaks somewhat later over posterior regions. Topographic plots reflect data from a principal component analysis parsing the novelty P3 and P3b elicited by novels and targets respectively in a visual novelty oddball paradigm, and the corresponding grand-average ERPs from Schomaker and Meeter (2014b).

reflect the same process (Simons et al., 2001). The novelty P3 can be distinguished, however, from the somewhat later P3b (or P300) component (Spencer et al., 1999, 2001). This component peaks over posterior regions and has been associated with memory-related processes (Polich, 2007; Polich and Criado, 2006), although others have argued that it reflects task-related decision-making processes rather than memory (Verleger, 2008). In an oddball paradigm, especially targets elicit a large amplitude P3b. Novel stimuli also elicit a P3b, but with a smaller amplitude (He et al., 2001). Fig. 2 shows the characteristics of the novelty-related ERP components.

The novelty P3 has previously been suggested to be a psychophysiological index of the involuntary orienting response (Escera et al., 2000; Escera et al., 2001). Others, however, have argued that it reflects the voluntary orienting of attention to deviant or novel information (Berti, 2008; Chong et al., 2008; Chong et al., 2008). Recent findings have suggested that the novelty P3 is elicited only when the novel stimulus is potentially task-relevant, and must thus be evaluated (Schomaker and Meeter, 2014b). Moreover, other recent findings showed it is strongly dependent on the context in which the novel stimulus is presented. Schomaker et al. (2014d) presented novel images of impossible objects either in in a task dominated by complex dot clouds or in a task dominated by simple geometrical figures. They found that the novel images elicited a much smaller novelty P3 when presented in the context of complex dot clouds, than in the context of simple geometrical figures. A similar reduced novelty P3 was observed when novel stimuli (in this case complex fractals) were the most frequent stimulus category (see Fig. 1). This suggests that the novelty P3 is not a response to novelty per se – as the impossible objects and fractals were novel in all situations – but to *deviance*; to be exact, the novelty P3 is only elicited by stimuli deviating from a context of stimuli that are equally or less complex than the deviants (also see Barkaszi et al., 2013). Note that stimulus complexity can be defined in many ways, but all definitions have in common that more complex stimuli have a large variety of features that cannot be easily compressed (e.g., Rigau et al., 2005).

With this reconceptualization of the novelty P3, the similarity between the novelty P3 and the P3a component becomes even more striking, as the P3a is elicited by non-novel stimuli that deviate from other stimuli in an experiment (e.g., a blue square amongst blue circles; Conroy and Polich, 2007). Interestingly, the P3a has been sourced to the same anterior cingulate and prefrontal cortex network that is also involved in error processing (Wessel et al., 2012, 2014), suggesting that deviance detection is in some ways similar to the detection of errors. It has been suggested that responses to deviance actually reflect prediction errors: Standard stimuli set up a prediction that is violated by deviant stimuli. This violation would then result in a brain response that underlies the novelty P3 (Schomaker et al., 2014a,d).

Overall, recent psychophysiological evidence thus suggests that the brain generates dissociable responses to novelty and deviance. This is an important result, since especially in clinical studies, the psychophysiological responses to novelty as elicited in visual novelty oddball tasks have been proposed as a tool for diagnosing neuropsychiatric disorders (Bruder et al., 2001; Stevens et al., 2007). For example, in schizophrenia the novelty P3 to novel stimuli is often reduced, which is interpreted as a disturbance of the orienting response towards novelty (Cortinas et al., 2008; Devrim-Ucok et al., 2006). The evidence presented above suggests that this reduction could be due not only to an impaired orienting response, but also to a failure to form predictions of events. Indeed, it has been argued that schizophrenic patients have trouble anticipating upcoming events, and that this deficit may underlie their misperceptions of the world, possibly, contributing to some of their psychotic symptoms (Ford and Mathalon, 2012; Frith et al., 2000).

2.3. Neuromodulatory responses to novelty

Some of the major neurotransmitter systems have been associated with novelty processing. Unexpected novel stimuli can activate the locus coeruleus (LC), releasing norepinephrine (NE; Vankov et al., 1995; Sara et al., 1994), and novel environments and pictures of unknown scenes (which are novel but not deviant) are known to stimulate both dopaminergic neurons in the substantia nigra and the ventral tegmental area (SN/VTA) promoting dopamine (DA) release (Bunzeck and Düzel, 2006; Li et al., 2003). Moreover, novel environments and exploration are known to increase acetylcholine (ACh) efflux (Giovannini et al., 2001). It is not yet clear, however, how novelty stimulates the release of DA, ACh and NE: Novel stimuli could directly activate the noradrenergic, cholinergic, and dopaminergic neurons, or indirectly through a novelty signal generated in other regions. Several computational models have proposed that the hippocampus generates a novelty signal, which then drives the medial septum to release ACh (Hasselmo, 2006; Meeter et al., 2005), and/or the VTA to release DA (Lisman and Grace, 2005). The central idea in these models is that the hippocampus, through a functional loop, regulates its own plasticity in response to novelty. Little direct empirical evidence has so far been found to support this conjecture; however, it still enjoys support, perhaps because alternative models have not yet been proposed.

While a hippocampal novelty signal could possibly drive ACh and DA release in response to novelty, it almost certainly does not drive NE release. The LC responds very swiftly to stimuli, at about 110 ms in primates (Bouret and Richmond, 2009). A hippocampal response to stimuli is often detected not before 200 ms (Jutras and Buffalo, 2010), which would be after the LC response. A simpler explanation is suggested by findings that the LC is strongly driven by responses that are simply loud or complex: loud noises, bright flashes (Grant et al., 1988; Rasmussen et al., 1986). As has been discussed above, novel stimuli are typically complex and generate stronger responses across a wide set of perceptual areas than familiar stimuli. It may be that it is this neural loudness that drives LC

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activity: LC may simply respond to any surge in cortical input it receives.

These three neuromodulators (DA, ACh, and NE) are released widely through the brain, can stimulate learning, and could plausibly be related to some or all aspects of the brain's novelty response (ACh: Hasselmo, 1995; Meeter et al., 2004; DA: Lisman and Grace, 2005; NE: Nieuwenhuis et al., 2005). Nevertheless, it has never been established whether they, in isolation or in combination, underlie novelty's consequences for cognition and behavior. We will now discuss these consequences in turn, starting with the effects of novelty on attention.

3. Attention to novelty

The central characteristic of the orienting response is that the organism orients towards the stimulus that elicits it. Novel stimuli thus attract attention, also when there is no incentive to pay attention to them, and even when performance on ongoing tasks suffers. Consistent with novel stimuli attracting attention, novel stimuli are encoded better into visual working memory than familiar ones (Mayer et al., 2011, 2014). Mayer and colleagues suggested that this effect was mediated by more efficient allocation of attentional resources to novel than to familiar items, rather than to low-level stimulus characteristics. Another line of research has shown that when participants have to report the location of a probed word in an array, they respond faster and more accurately to novel as compared to repeated familiar words. This has been called the *novel popout* phenomenon (Johnston and Schwarting, 1997; Reicher et al., 1976), and is also believed to rely on attentional processes (Strayer and Johnston, 2000). The reliability of the effect, however, has been questioned and the results have also been explained as effects of cognitive load (for a critical view see Christie and Klein, 1996), or inter-item associations (Diliberto et al., 1998).

The fact that novel stimuli capture attention has consequences for task performance. The orienting response to novel stimuli can pull attention away from task-related processes, resulting in distraction (Naatanen, 1992). Distraction by task-irrelevant novel sounds has been shown to, for example, prolong reaction times and reduce accuracy on a task in which images had to be categorized (Wetzel et al., 2013). Such effects occur across as well as within sensory modalities, and have been reported for the visual modality (Bendixen et al., 2010; Berti and Schroger, 2006), auditory modality (Berti and Schroger, 2004; Escera et al., 2000; Parmentier and Andres, 2010; Parmentier et al., 2011a,c; Wetzel et al., 2006, 2013), and tactile modality (Ljungberg and Parmentier, 2012; Parmentier et al., 2011b).

Through its effects on attention, novelty can also sharpen perception. These effects on perception have interesting similarities to those of emotional stimuli. In a typical emotional cueing paradigm, images of faces acting as cues are followed by a low contrast stimulus that is difficult to see. Faces with a negative emotional relative to a neutral expression have consistently been shown to enhance perception of a subsequently presented target (for a comprehensive review see Phelps, 2006). Although much remains to be clarified, emotional stimuli are believed to enhance perception through activation of the amygdala, then strengthening sensory processing via the amygdala's connections with the visual cortex (Anderson and Phelps, 2001; Morris et al., 1998). In an adapted version of such a paradigm emotionally neutral novel or familiar fractal images acted as cues. The novel images increased sensitivity to shortly presented (low contrast) visual targets compared to familiar images (Schomaker and Meeter, 2012). Novel iamges also led to a more conservative response criterion, which is consistent with known effects of attention (Rahnev et al., 2011). Notably, the novel images in this experiment were not deviant (i.e., they did not deviate as a category from the familiar images in the experiment), suggesting that the effects on perception were a response to novelty, not deviance.

The orienting response towards novelty has been associated with the same motivational circuits that underlie the attentional response to emotionally significant information (Bradley, 2009; Weierich et al., 2010). Indeed, although the amygdala is mostly known for its role in processing emotional stimuli, it also responds to neutral novel images (Blackford et al., 2010; Kiehl et al., 2005; Schwartz et al., 2003; Wright et al., 2003; Zald, 2003). Moreover, amygdalar responses to emotional stimuli are strongly modulated by the novelty of those images, suggesting that novelty is integral to the amygdala's function (Weierich et al., 2010). Novelty could thus enhance perception via the same mechanisms as by which emotional stimuli are thought to enhance perception.

4. Facilitating task performance

Novelty's distracting effects on behavior, through capture of attention as discussed above, are well established. However, the orienting response can also have exactly the opposite consequence. The orienting response has been suggested to include a call for processing resources (Filion et al., 1991; SanMiguel et al., 2010b; Zimmer, 1992), eliciting a general increase in arousal and attentional resources. Such increases could be stimulus-aspecific and spill over to other stimuli presented in the temporal and/or spatial vicinity, enhancing their processing (Aston-Jones and Cohen, 2005b). A variety of studies have suggested that the transient increase in arousal and/or attention due to novelty can indeed have a range of positive effects on task performance (DiGirolamo, 1998; SanMiguel et al., 2010a,b; Wetzel et al., 2012; Schomaker and Meeter, 2012, 2014a). These effects will now be discussed.

4.1. When distraction becomes facilitation: Requirements for novelty's short-lived beneficial effects on behavior

Whether new information results in distraction or facilitation of performance depends on several factors. First, behavioral distraction typically occurs when the novel stimuli are informative about target occurrence and time of appearance, but not when they are uninformative (Parmentier et al., 2010; Wetzel et al., 2012, 2013). For example, when a deviant novel sound (i.e. a burst of white noise) provides information about the onset of a visual target digit, further processing of the novel sound is required, resulting in behavioral distraction (Parmentier et al., 2010). In contrast, when the same sound is entirely task-irrelevant such further processing is not required—and distraction does not occur.

Second, whether distraction or facilitation occurs depends on the attentional demands of the task at hand: When demands are low novelty results in facilitation, while when demands are high novelty results in distraction (Lv et al., 2010; SanMiguel et al., 2010a; Schomaker and Meeter, 2014a,b). In one study, novel sounds resulted in faster classification (of face vs. scrambled face), and better recognition memory when working memory load was low (no memory load, or remebering a single face; SanMiguel et al., 2010a). When working memory load was high (remembering three faces), novel sounds decreased performance. A reason for this could be that in a task with low attentional demands, attention may wander (Forster and Lavie, 2009; Lavie, 1995). Novel stimuli may improve performance by refocusing attentional resources or by eliciting a general alerting response. In this case any distracting effect of novelty, the 'orienting cost', is outweighed by an 'alerting benefit' (SanMiguel et al., 2010a). In contrast, when demands are high, all attentional resources are already used to perform the task (Kahneman, 1973), leaving no room for a novelty-induced alerting

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benefit. Furthermore, the depletion of attentional resources may result in a failure to suppress task-irrelevant (novel) stimuli (Lv et al., 2010; Schomaker and Meeter, 2014b), resulting in increased distraction by the novel stimuli.

A third variable of importance is the context in which the novel stimulus occurs. In a task by Schomaker and Meeter (2014a) participants responded to an auditory target while viewing a stream of novel and standard visual stimuli. Novel visual stimuli facilitated responses to the auditory targets, but only when they were infrequent, deviant, and visually more complex than other stimuli in the stream (the *stimulus context*). When the stimulus context was as complex as the novel stimuli or more so, no such facilitation was found, even though novel stimuli can enhance perception under these circumstances (see Section 3; Schomaker and Meeter, 2012). It thus seems that novel stimuli always elicit an attentional response (enhancing perception, possibly contributing to speeded responses as well), but have a more prominent arousing effect when they deviate from a simple stimulus context. This suggestion of differential effects on attention and arousal is supported by an analysis of response bias, which has been argued to be differently affected by attention and arousal (Rahnev et al., 2011). Novel stimuli engender a more conservative response criterion, associated with increases in attention (Rahnev et al., 2011), when the stimulus context is complex (Schomaker et al., 2015), but a more liberal one, associated with arousal, when the context is simple (Experiment 3 in Schomaker and Meeter, 2014a). A reason for such discrepant effects may be related to differences in processing demands for simple versus complex stimuli. As described above, the effects of arousal become more prominent when task demands are low. Simple stimuli have lower processing demands than complex stimuli, which may have the same effect as low task demands: leaving more room for an alerting benefit.

Interestingly, the conditions in which novelty results in facilitation of responses are strikingly similar to those in which the novelty P3 is elicited: Only deviant, complex stimuli elicit facilitation and the frontal novelty P3 (Barkaszi et al., 2013; Schomaker et al., 2014d). Indeed, although in the literature the novelty P3 has often been associated with behavioral distraction (Berti et al., 2004; Berti and Schroger, 2001, 2004; Escera et al., 2001; Munka and Berti, 2006; SanMiguel et al., 2008, 2010b; Schroger et al., 2000; Schroger and Wolff, 1998), some studies have instead hinted to a dissociation between the two. Wetzel et al. (2013) found that the novelty P3 is automatically elicited by environmental novel sounds and deviant bursts of white noise, but that consequences for behavior depend on whether target-related information is conveyed (i.e. distraction only occurs when the deviant/novel provides info regarding the time and probability of target occurrence in a visual classification task). Moreover, the novelty P3 has been associated with improved task performance. SanMiguel et al. (2010b) found that responses to visual targets on a simple classification task (face/scrambled face) were facilitated during the presentation of novel sounds that also elicited a novelty P3. In other words, the novelty P3 does not always reflect distraction (an 'orienting cost'), but can also reflect alerting effects that underlie the facilitation of target processing (SanMiguel et al., 2010b). One other study directly linked the novelty P3 to beneficial effects. In a visual two-choice task, the novelty P3 was enhanced in children with attention deficit hyperactivity disorder (ADHD) compared to the normal control group, while at the same time omission errors were reduced for the children with ADHD (van Mourik et al., 2007). The authors argued that "distraction can have beneficial effects". Wetzel et al. (2013) found that a frontal novelty P3 for novel stimuli resulted in facilitation, while no facilitation was found for deviants that elicited a more central P3 component. Thus, the same mechanism may underlie both the frontal novelty P3 ERP component and novelty's beneficial effects on behavior.

4.2. Facilitation: The novelty P3 and the role of the LC–NE system

Indeed, both novelty's facilitating effects and the P3 have been associated with the LC–NE system (Donchin, 1981; Nieuwenhuis et al., 2005, 2010; Wetzel et al., 2012). The P3 has been shown to depend on NE in several ways. For example, a P3-like response in monkeys was fully attenuated when the LC was lesioned (Pineda et al., 1989), and by a psychopharmacological intervention that depletes NE (Swick et al., 1994a,b). In turn, novelty can drive LC phasic activity. For example, strong bursts of activity were seen in a large population of noradrenergic neurons of the LC in rats that were placed in a novel environment (Sara et al., 1994; Vankov et al., 1995). In humans the P3 has been related to pupil diameter (Murphy et al., 2011), which itself is believed to reflect LC activity (Murphy et al., 2014; Nieuwenhuis et al., 2005; Phillips et al., 2000). Prestimulus pupil size and P3 exhibited an inverted U-shape relation, with large P3 amplitudes being associated with intermediate pupil diameter and optimal task performance on a visual oddball task (Murphy et al., 2011). Similarly, several genes affecting noradrenergic pathways have been related to P3 amplitude using an independent component analysis, linking genotypes to psychophysiological data (Liu et al., 2009).

As noted above, there are different P3 subcomponents that have different neural generators and are associated with different processes. Polich (2007) suggested that a parietal noradrenergic system underlies the P3b, whereas the dopaminergic system was proposed to play a role in the generation of the frontal novelty P3/P3a. However, there are reasons to believe the novelty P3 is also related to the noradrenergic LC–NE system. The LC is connected to the anterior cingulate cortex (ACC), orbitofrontal cortex (OFC; Aston-Jones and Cohen, 2005a,b), and prefrontal cortex (Sara, 2009), which are all suggested to be sources of the novelty P3 (ACC: Dien et al., 2003; prefrontal cortex: Knight, 1984; OFC and ACC: Lovstad et al., 2012)—supporting a role of the noradrenergic system in eliciting the novelty P3.

It is thus possible that the LC–NE response to novelty is both related to the novelty P3 and underlies novelty's subsequent facilitatory effects on behavior. The strongest arguments in favor of such a link are the similarity of conditions eliciting facilitation and the novelty P3, and the timing of the effects. Effect of NE have been argued to peak 100–200 ms post-stimulus (Aston-Jones and Cohen, 2005a,b; Nieuwenhuis et al., 2005), which is exactly the time frame in which novelty facilitates responses (Schomaker and Meeter, 2014a). However, direct evidence for the putative relations between LC–NE, the novelty P3 and facilitatory effects of novelty is still lacking.

5. Effects on learning and exploration

Since a novel stimulus or novel environment by definition provides opportunities for learning, many theories have suggested that novelty elicits a learning signal (Hasselmo et al., 1996; Meeter et al., 2005; Recce and Harris, 1996; Tulving and Kroll, 1995). Indeed, it seems that spatial novelty triggers exploration and facilitates neuroplasticity, although such effects have been more scarcely reported for stimulus novelty.

5.1. Novelty's exploration bonus: The lure of the unknown

Exploring new opportunities and environments is a crucial aspect of mammalian behavior. In fact, foraging species must have a drive to explore new environments, in order to survive (Panksepp, 1998). Also in present day lifestyles curiosity may help survival: Senior citizens with higher curiosity were found to have better chances of being alive and healthy five years later (Swan and

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Carmelli, 1996), and openness to actions has been associated with longevity (Jonassaint et al., 2007). An interest in the new can thus be beneficial, and may also be required to detect potential threats and avert harm. To optimally adapt behavior to the current situation the brain has to make a trade-off between exploiting well-known sources of reward on the one hand, and exploring new objects and situations on the other that may signal more profitable outcomes—or an unknown source of threat.

It has been suggested by computational theories of reinforcement learning that novelty may promote exploratory behavior novelty by eliciting an 'exploration bonus' (or novelty bonus), motivating exploratory behavior in search for reward (Düzel et al., 2010; Kakade and Dayan, 2002; Knutson and Cooper, 2006). This idea has been worked out in a theory: NOvelty-related Motivation of Anticipation and exploration by Dopamine or NOMAD (Düzel et al., 2010). NOMAD suggests that perceiving a novel stimulus results in both temporally specific phasic bursts of DA, which increases plasticity both for storage of the novel stimulus itself and of stimuli that follow it, and an increase in tonic DA levels. Moreover, the mere anticipation of novelty would already lead to an increase in tonic DA levels. This increase in tonic activity would in turn enhance reward anticipation and promote exploratory behavior.

Empirical evidence for this theory has shown that novel stimuli and anticipation of novel stimuli can indeed activate the dopaminergic reward system, enhancing reward prediction responses (Bunzeck et al., 2012; Wittmann et al., 2007), and ensuring that novel opportunities are evaluated and potential risks are assessed until the outcome is known (Krebs et al., 2009). Moreover, novelty increases phasic DA release in the striatum to reward (Bunzeck et al., 2007; Guitart-Masip et al., 2010; Krebs et al., 2011; Lisman and Grace, 2005). In addition, VTA activity caused by reward anticipation was found to be correlated with better episodic memory, suggesting that DA release can indeed boost memory (Murty and Adcock, 2014). In the other direction, reward can accelerate novelty processing (Bunzeck et al., 2009), a process believed to be controlled by DA, that also modulates memory retrieval performance (Apitz and Bunzeck, 2013; Eckart and Bunzeck, 2013; for a review on the link between dopamine and memory see Shohamy and Adcock, 2010).

However, the link between novelty and learning has also been associated with other neuromodulatory systems. In particular, NE has also been implicated in novelty-induced learning benefits, specifically in nonhuman animals (Straube et al., 2003b; Sara, 2009; Harley, 2007; Madison and Nicoll, 1986). NE increases the excitability of neurons in the dentate gyrus and promotes long-term potentiation (LTP; Kitchigina et al., 1997; Kemp and Manahan-Vaughn, 2008; Klukowski and Harley, 1994), a mechanism believed to underlie the formation of memories (Cooke and Bliss, 2006).

5.2. Novelty's long-lasting beneficial effects: Promoting memory

Animal studies have repeatedly shown that exploration of a novel compared to a familiar environment can promote learning. Neurophysiologically, it can increase LTP in the hippocampus, thereby improving memory encoding (Davis et al., 2004; McGaugh, 2005; Uzakov et al., 2005). In one example, after exploring new environments early LTP in rats was turned into long-LTP in the hippocampus, specifically in the dentate gyrus, whereas it was not after exposure to a familiar environment (Straube et al., 2003b). Behaviorally, an effect of novelty on learning has been shown for example for taste memory: A strong novel taste can facilitate memory formation for a different weak taste in rats (Merhav and Rosenblum, 2008). The beneficial effects of exploring a novel environment on learning and memory may also be partially caused by effects on arousal: Exploration of novel environments results in increases in arousal and locomotor acitivity (Moser et al., 1994), which in turn can promote LTP and learning as mediated by noradrenergic activity (Sara et al., 1994; Vankov et al., 1995; Cahill and McGaugh, 1998).

In humans the idea that novelty can enhance memory for unrelated information is less extensively researched, but several studies hint towards such an enhancing effect as well. Wittmann et al. (2007) found that anticipation of novelty activated both the hippocampus and SN/VTA; in a separate behavioral experiment they also found that anticipated novel items were remembered in a way that yielded better recollection a day later, relative to unanticipated novel items. One functional magnetic resonance imaging (fMRI) study provides evidence for the idea that experiencing (in addition to anticipating) novelty can enhance memory in humans. Participants were first exposed to a series of either novel or familiar scenes, and then had to study a list of words. When participants had been exposed to the novel scenes, they had better recollection and free recall of the words than when exposed to familiar scenes (Fenker et al., 2008). Novelty co-activated both the SN/VTA and hippocampus; however, this did not correlate with the memory enhancements. Recently, we investigated whether active exploration of a novel environment also enhances learning on an unrelated task in humans. In a within-subjects design participants explored a novel and a previously familiarized virtual environment, after which they performed a word learning task. Exploration of a novel as opposed to familiar environment enhanced recall, believed to be hippocampus-dependent, but not recognition memory, a type of memory believed to be relatively hippocampus-independent (Schomaker et al., 2014b).

Several studies have also looked at novelty's effects on encoding at the level of single items. One such study, using pupillometry, found that pupil constriction during encoding was stronger for complex natural visual scenes that were later remembered, and for novel compared to familiar scenes at retrieval (Naber et al., 2013). Remarkably, pupil constriction was also strong for familiar items that were misjudged as novel. Therefore the authors argued that pupil constriction reflects subjective novelty, which itself has been argued to be associated with the strength of memory formation (Kishiyama et al., 2004; Knight, 1996; Lisman and Grace, 2005).

Two item-level effects also seem to point to a beneficial role of novelty on encoding. The *Novelty Effect* consists of better recognition memory for new items than for items that were previously familiarized in a preceding phase (Kormi-Nouri et al., 2005; Tulving et al., 1994; Tulving and Kroll, 1995). The second is the *Von Restorff* effect, which denotes better memory for words presented in a deviant, novel font than for words presented in a standard font (Bruce and Gaines, 1976; Geraci and Manzano, 2010; Von Restorff, 1933; Schmidt, 1985), and for objects presented in novel rather than standard colors (Kishiyama et al., 2004, 2009). Interestingly, the Von Restorff effect is further enhanced by the D1/D2 receptor agonist apomorphine in humans (Rangel-Gomez et al., 2013), and is reduced in Parkinson's patients that have abnormalities in dopaminergic functioning (Schomaker et al., 2014a).

Several neuromodulatory systems have been suggested to underlie the effects of novelty on learning, such as dopaminergic inputs (Lemon and Manahan-Vaughan, 2006; Li et al., 2003; Lisman and Grace, 2005; Roggenhofer et al., 2010; Sajikumar and Frey, 2004), noradrenergic inputs (Kitchigina et al., 1997; Straube et al., 2003a; Uzakov et al., 2005; Vankov et al., 1995) through beta-adrenoreceptors (Kemp and Manahan-Vaughan, 2008), and cholinergic inputs (Barry et al., 2012; Bergado et al., 2007; Hasselmo, 1999; Meeter et al., 2004). The dopaminergic and noradrenergic systems have also been suggested to mediate these effects in concert, working through their reciprocal connections (Briand et al., 2007; Harley, 2004; Sara, 2009). All three neurotransmitters are known to be released in response

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to novel stimuli, and have been linked to plasticity in the brain.

Involvement of NE in eliciting novelty's benefits seems inconsistent with the pupillometry results of Naber et al. (2013). Typically, pupil dilation has been linked to NE release (de Gee et al., 2014; Gilzenrat et al., 2010; Jepma and Nieuwenhuis, 2011; Murphy et al., 2011, 2014). The data of Naber et al. (2013) thus suggest that subjective novelty correlates with low NE release, and low NE release with better encoding, however, they explained their findings in terms of variations in ACh.

Another reason to believe that NE nor ACh is crucial for novelty's effects on memory is the time scale on which the effects occur. Effects of ACh release have been argued to peak some two seconds after release (Hasselmo and Fehlau, 2001), while effects of NE release may act on shorter time scales (Mongeau et al., 1997). In contrast, exploring a novel environment can facilitate LTP induction minutes after a return to the home cage. If novelty would affect memory on a time scale of seconds it would support a role for norepinephrine or acetylcholine, while effects that last minutes would favor involvement of the dopamine system. Indeed, effects of novel environments one LTP induction have been argued to depend on the activation of dopaminergic D1/D5 receptors (Li et al., 2003).

Effects of novelty on human memory have been reported for both short and long time scales. The Novelty Effect and the Von Restorff effect play out at the time scale of individual word presentations (i.e., seconds), consistent with fast short-lived responses of ACh or NE. However, both effects can be explained by mechanisms that have little to do with novelty itself. The Von Restorff effect has been argued to be an effect of distinctiveness at test, rather than novelty during study (Dunlosky et al., 2000; Rangel-Gomez and Meeter, 2013). The Novelty Effect may simply be proactive interference: Items that are studied repeatedly for separate lists may lead to source discrimination problems, with memories from different lists then interfering with one another at test (Dobbins et al., 1998). In fact, the procedure followed in studies of the Novelty Effect is equivalent to that of studies of proactive interference.

Effects that are more clearly linked to encoding all play out at a longer time scale. Novelty-induced memory enhancements seen in nonhuman animals depend on a long-lasting state that may last up till 30 min after exposure to a novel environment (Li et al., 2003; Straube et al., 2003a). Exploration of novel versus familiar virtual environments has been shown to improve recall in humans, up to 15 min after exposure, indicating that the positive effects of novelty on learning also linger for some time in humans (Schomaker et al., 2014b). Similarly, seeing novel scenes positively affected learning ten minutes afterwards (Fenker et al., 2008), but a recent attempt to find a similar effect on an item-by-item basis failed (Rangel-Gomez and Meeter, in submission). Such longer-term effects of novelty are most consistent with the idea that DA modulates the novelty-induced benefits for memory, as proposed by, among others, Lisman and Grace (2005). Also other evidence has accumulated for an important role of DA in increasing plasticity in the hippocampus (Jay, 2003; Lemon and Manahan-Vaughan, 2006; Li et al., 2003; Lisman and Grace, 2005; Roggenhofer et al., 2010; Sajikumar and Frey, 2004). Together, these findings suggest that the same mechanism underlies both the benefits of novelty for learning, and the exploration bonus (Düzel et al., 2010; Blumenfeld et al., 2006; Lisman and Grace, 2005).

6. A framework for organizing novelty's effects on brain and behavior

In summary, novelty elicits strong responses across a wide variety of brain areas, and stimulates several neuromodulatory systems, affecting many aspects of cognition. Here, we argued that the neurophysiological responses to novelty play out on different time-scales, and that this can explain the differences in the timing of novelty's effects on different cognitive processes. The research reviewed here suggests that these effects can be grouped into at least three categories. The first two consist of effects that occur shortly after a novel stimulus is encountered. The third contains longer-lasting effects.

First, the amygdala, mostly known by its role in processing of emotion, responds strongly to novelty as well (Zald, 2003; Blackford et al., 2010). Emotional stimuli are believed to enhance visual perception by eliciting an attentional response by activating the amygdala and its connections with early visual cortical areas (Vuilleumier, 2005). Since novel stimuli can reliably activate the same brain circuits as emotional stimuli, novelty could potentially enhance perceptual processes via the same pathways. The effects of emotion on visual perception are very fast; although the exact time-course of these effects is not yet known, enhancements are typically reported to occur in the first few hundred milliseconds after presentation of an emotional stimulus (Sellinger et al., 2013). Novel stimuli have been shown to have similar enhancing effects on perception (Schomaker and Meeter, 2012). Although much remains uncertain, we argued that the orienting of attention towards novel stimuli may result from amygdalar activation affecting early sensory processing regions in the brain.

Second, novel stimuli can activate the LC (a brain stem area that is the exclusive supplier of NE in the forebrain), resulting in phasic NE release peaking around 200 ms following stimulus presentation (Aston-Jones and Cohen, 2005b; Mongeau et al., 1997). This LC–NE system has been associated with arousal, but can also affect behavior more selectively. The adaptive gain theory (Aston-Jones and Cohen (2005a) posits that phasic NE release from the LC acts as a temporal filter, facilitating task-relevant behavior by boosting decision-making processes and suppressing non-target-related brain activity. Novelty could thus potentially facilitate task performance via this mechanism. Recent studies showed that new stimuli can indeed facilitate responses, but that the effects depend strongly on other factors. In fact, the speeding of responses seems to be a response more to deviance than to novelty per se (Schomaker and Meeter, 2014a). The same has been argued to be the case for the novelty P3 ERP component (Schomaker et al., 2014c), suggesting a possible common mechanism.

Third, mesolimbic dopaminergic system can be activated by novelty. In contrast with the short-lived LC–NE response, dopaminergic responses elicited by novelty can be effective up to minutes later (Li et al., 2003). After novelty detection, DA release from the SN/VTA is believed to be triggered by a novelty signal from the hippocampus (Lisman and Grace, 2005). Behaviorally, especially spatial novelty has been shown to have enhancing effects on memory in animals (Davis et al., 2004; McGaugh, 2005; Uzakov et al., 2005; Straube et al., 2003b), and humans (Fenker et al., 2008; Schomaker et al., 2014b). These effects can be observed tens of minutes after exposure.

7. Open issues

The framework discussed above summarizes many of the findings on novelty processing. However, some links in the framework are tentative, and many gaps remain.

In the current review we have linked distinct neuromodulatory mechanisms to different behavioral effects of novelty. However, direct evidence in humans linking these systems and their cognitive effects is mostly lacking. More research is thus required to validate our suggestions that the longer-lasting effects of novelty may be mediated by DA, and the short-lived effects by NE, ACh, or a mechanism activating limbic regions. Moreover, in many studies novelty,

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deviance, and surprise are confounded: New stimuli are often also deviant or unexpected, or animals are unexpectedly placed in a new environment. Therefore it is unclear whether novelty-induced DA, NE or ACh release is truly related to novelty, or is actually released in response to deviance or to surprise. Future studies should thus take care to separate effects of novelty, deviance, and surprise.

Second, we have argued that effects of deviance are more in line with an arousal response (possibly associated with the LC–NE system), whereas the effects of stimulus novelty are more in line with an attentional response. It has been argued that arousal is characterized by an increase in response readiness (Kahneman, 1970; Posner and Boies, 1971) while attention is characterized by an increase in perceptual sensitivity. If stimulus deviance indeed affects behavior through arousal, it should not ameliorate perceptual sensitivity, however, this has not yet been tested.

Third, some effects of novelty have been found mostly or exclusively in studies investigating exploration of novel environments. This raises the question whether either spatial novelty or the act of exploring is qualitatively different than other forms of novelty, or whether spatial novelty is merely a stronger novelty manipulation than the presentation of a novel stimulus.

Fourth, we have linked both the novelty P3 and arousal responses to deviance from the context. However, it is unclear why the brain responds differently to a deviant stimulus than to a nondeviant one. Two established mechanisms could mediate the effects of deviance. The first is frequency of occurrence. The magnitude of the P3b to targets is known to decrease as targets are spaced closer together in time, presumably through some process of adaptation to the target stimulus (Gonsalvez and Polich, 2002). It could be that similar adaptation processes operate at the category level. Since a deviant category of stimuli is per definition less frequent in an experiment than standard stimuli, the brain could be less adapted to stimuli from the deviant category, resulting in a larger brain response to those stimuli. Alternatively, standard stimuli could set expectations that are violated by the deviant stimuli. Responses to deviant stimuli could thus actually be responses of surprise, caused by violations of expectations. Recent data from our lab suggests that both processes, adaptation and violation of expectations, independently contribute to the novelty P3 component (Meeter et al., 2014).

8. Conclusion

Novel stimuli set off a cascade of responses in the brain, which generate a plethora of effects on cognition. Here, we have argued that these effects can be grouped into three categories: An attentional response to novelty, possibly mediated by the amygdala, an arousal-like response to deviance, which could be mediated by the noradrenergic system, and a slower upregulation of exploration, motivation and learning, mediated by the dopaminergic system. However, many questions remain unanswered, providing fertile ground for years of future research investigating novelty and its effects on brain and cognition.

Q7 Uncited references

Bocanegra and Zeelenberg (2009, 2011), Chowdhury et al. (2012), Harley (1987), Kentros et al. (2004), Phelps et al. (2006), Redgrave et al. (2008), Wittmann et al. (2005, 2008).

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