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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., 2012; 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