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What's new? The interaction between novelty and cognition

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INTRODUCTION

The Orienting Response

Novel stimuli are typically prioritized over familiar stimuli by attracting attention (Friedman et al., 2001; Ranganath & Rainer, 2003; Escera, Alho, Schröger, & Winkler, 2000; Escera, Yaho, & Alho, 2001; Escera, Alho, Winkler, & Näätänen, 1998; Näätänen, Teder, Alho, & Lavikainen, 1992). This was already known by Pavlov in the 1920's. When colleagues came to visit his lab to see a demonstration of conditioning in the 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 & 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 may pose new opportunities that may result in beneficial outcomes, and on the other hand new situations 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. How novelty affects the brain and behavior is the main topic of this dissertation.

When an organism involved in a task encounters a novel stimulus, the orienting response can have different consequences for task performance. Task-irrelevant novel information can attract attention at the expense of task-relevant information, even when this competing information is relevant. But novel information can also have the opposite effect - improving performance.

The onset of a novel stimulus can elicit a general alerting response. Such alerting may be the result of novelty triggering norepinephrine (NE) release from the locus coeruleus (LC), a brain stem area that is the exclusive supplier of the neurotransmitter NE to the forebrain. This novelty-induced LC response peaks around 200 ms after presentation, putatively resulting in NE release around that time. It has been suggested that at the height of this response task-relevant behavioral responses could be facilitated (Aston-Jones & Cohen, 2005b; Nieuwenhuis et al., 2005; Schomaker & Meeter, 2014a). In addition, novelty detection may result in an unspecific call for attentional resources (Filion, Dawson, Schell, & Hazlett, 1991; SanMiguel, Morgan, et al., 2010; Zimmer, 1992). Typically, novelty attracts attention to itself, but some superfluous attentional resources could spill over to the processing of subsequently presented stimuli, facilitating their processing (Schomaker & Meeter, 2012). This effect may be triggered by novelty activating the amygdala (Blackford,

Buckholtz, Avery, & Zald, 2010; Kiehl et al., 2005; Schwartz et al., 2003; Wright et al., 2003; Zald, 2003).

The effects of novelty on arousal and attention occur on the course of milliseconds, but novelty can also have longer-lasting effects. Exploration of a novel environment has been reliably shown to promote learning and memory in animals lasting up to tens of minutes (Kentros et al., 2004; Li et al., 2003; Straube, Korz, Balschun, et al., 2003). Also in humans, exposure to novelty can enhance memory processes (Fenker et al., 2008; Wittmann, Schiltz, Boehler, & Düzel, 2008). Furthermore, it can strengthen reward processing (Wittmann, Bunzeck, Dolan, & Düzel, 2007; Wittmann et al., 2005), and promote exploratory behavior (Düzel, Bunzeck, Guitart-Masip, & Düzel, 2010). These effects have been argued to be mediated by a bidirectional connection between the hippocampus and substantia nigra/ventral tegmental area (SN/VTA) of the mesolimbic dopaminergic system. A novelty signal from the hippocampus activates dopaminergic neurons in the SN/VTA, which in turn increases plasticity in the hippocampus and improves motivation through striatal connections.

What is new?

What can be considered new is a matter of definition. A percept is never exactly the same as what has been experienced before, and never completely different. Heraclitus already wrote: “No man ever steps in the same river twice, for it's not the same river and he's not the same man”. Every time, when passing a river that you have seen many times before, you will see the river from a different perspective, under different lighting conditions, and with a different state of mind. In this sense, you will always see the river in a way that you have never seen it before. On the other hand, while passing a different river, in a place you have never been before, you will recognize it as a river, even when being on the other side of the world. Novelty is thus a matter of degree - a stimulus is more, or less novel. The stimuli used in the studies of this dissertation have utilized the extremes: Novels are new stimuli of a category that most observers are unfamiliar with, which are compared to familiar stimuli that are repeated hundreds of times within the experiment. With such repeated exposure the novelty of any stimulus wears off, and with this increased familiarity the orienting response is reduced. This process is called habituation (Sokolov, 1963b; Sokolov & Paramonova, 1961). Since habituation cannot have occurred for something that we have never encountered before, the orienting response towards novelty may thus actually reflect the absence of habituation

(Habib, 2001). This can provide an operational definition of novelty: Something is novel, when we have not habituated to it yet.

Many aspects of a stimulus can make it novel, and many factors (like the context in which it occurs, and where the focus of attention is) determine whether it will draw attention. For example, most people have probably never seen a picture of the aye-aye animal, making it novel. However, if the aye-aye is presented amongst pictures of other unfamiliar animals, it will not stand out from its context. Although it is still novel, it is less salient in such a context (see Figure 1 for a picture of the aye-aye presented in different stimulus contexts). Other factors of influence are the complexity – the physical salience - of the stimulus and the context in which it is presented. The different types of novelty and the factors impacting its processing will now be discussed.

The extreme opposite of familiarity is something that has never been experienced before. This type of novelty has been called (1) *stimulus novelty* (Courchesne, Hillyard, & Galambos, 1975). Most visual input is novel in the sense that we have not experienced that exact configuration. But most visual input resembles past experiences sufficiently to easily categorize it. Stimulus novelty thus refers to stimuli that cannot be recognized or readily categorized or labeled.

As with stimulus novelty, stimuli may deviate from everything stored in long-term memory, but may also deviate from their more immediate stimulus context. This concept may be referred to as (2) *contextual novelty*. Contextually novel stimuli might be familiar, but differ substantially from other stimuli experienced within the context; in an experiment, this usually means that a stimulus differs in a recognizable way from all other stimuli in the experiment (for examples see Barkaszi, Czigler, & Balazs, 2013; Cykowicz & Friedman, 2007; Polich & Comerchero, 2003). Contextually novel stimuli are thus non-repeated throughout an experiment, but may belong to a well-known category (such as animals or geometric forms). By definition, stimulus novelty implies contextual novelty; stimulus novelty is thus a subcategory of contextual novelty.

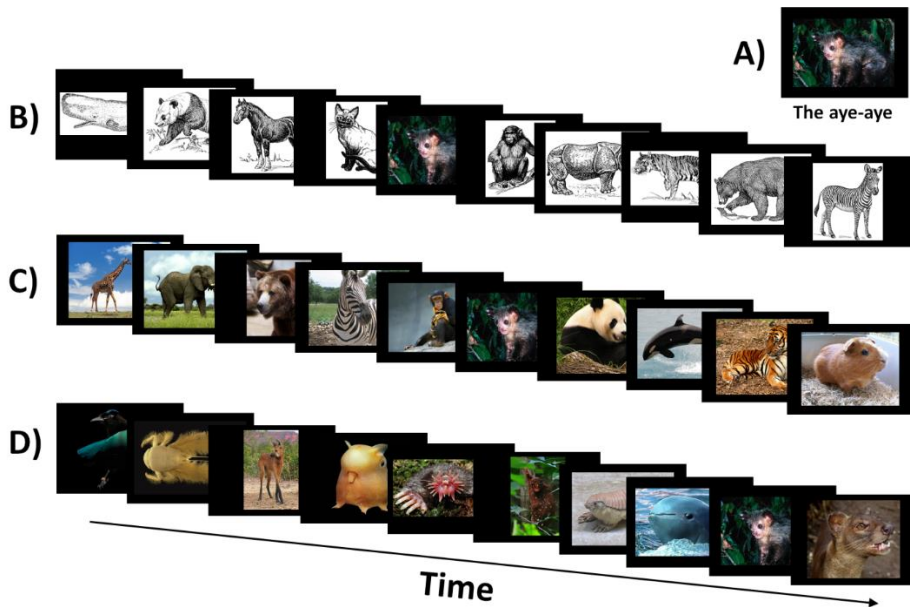


Figure 1. A) The aye-aye is a rare animal that many people may never have seen, making it novel in itself. This is an example of stimulus novelty. B) When a picture of the aye-aye is presented among line-drawings of familiar animals it will not only stand out because of its stimulus novelty, but also because it deviates from the context¹. C) In contrast, when presented amongst pictures of familiar animals it will not stand out so much, even though it is still contextually and stimulus novel, it does not physically deviate from its context. D) Similarly, when presented amongst pictures of only rare and unfamiliar animals it will not stand out, and may therefore draw less attention, albeit still contextually and stimulus novel. Sources: Google Commons (for the familiar animals) and BoredPanda.com (for the unfamiliar animals).

¹ Note, throughout this thesis the term deviance is used to refer to an infrequent category of stimuli that also physically differs from the other stimuli presented in an experiment. For example, an infrequent photo amongst frequent line-drawings.

A more short-term aspect of novelty is (3) *deviance*, which applies to an infrequent stimulus category that physically deviates from the current context. Deviance is relatively independent from the other types of novelty: Deviant stimuli are not necessarily unique. An infrequently repeated picture of a giraffe would not be stimulus novel or unique, but it would be deviant when presented among frequent line-drawings of a bear. Similarly, the infrequent deviant stimuli used in typical mismatch negativity studies are repeated throughout the experiment (see for example Czigler, Balazs, & Winkler, 2002; Liu & Shi, 2008). In addition, novel stimuli are not necessarily deviant (as when a picture of the aye-aye is presented amongst pictures of other unfamiliar animals), though in typical studies of novelty they are. The counterparts of deviant stimuli are frequent ‘standard’ stimuli. As will be seen later on, deviance is a very important concept that explains many aspects of novelty processing.

A fourth concept is that of (4) *unexpectedness* and its consequence, *surprise*. An example of an unexpected outcome (for most people) is when pressing the ‘y’ on a keyboard with German settings, and seeing that a ‘z’ is presented on the screen (also see Iwanaga & Nittono, 2010; Waszak & Herwig, 2007). Novel and deviant stimuli will always be surprising to some extent (a deviant stimulus breaks the expectations set by frequent standard stimuli and a novel stimulus can by definition not be predicted). Nevertheless, surprise can be manipulated relatively independently from the other concepts. For example, a cue can foretell that the next stimulus is novel, making it less surprising without changing its novelty.

Also *stimulus context complexity* affects how a stimulus is processed. Stimulus context complexity refers to the complexity of the immediate context in which a stimulus occurs, and does not imply any stimulus characteristics of the stimulus itself. Complexity can be defined in multiple ways, but these will usually be highly correlated. Complex stimuli are those that have a large variety of features that cannot be easily compressed (for an information-theoretical approach to complexity see Rigau, Feixas, & Sbert, 2005). In Figure 2 the different concepts related to novelty that are relevant for the research in this dissertation are shown in a Venn diagram.

There are more factors that influence novelty processing, such as individual differences or difficulty of the task at hand. However, these factors were not investigated in this dissertation, and are thus not discussed further.

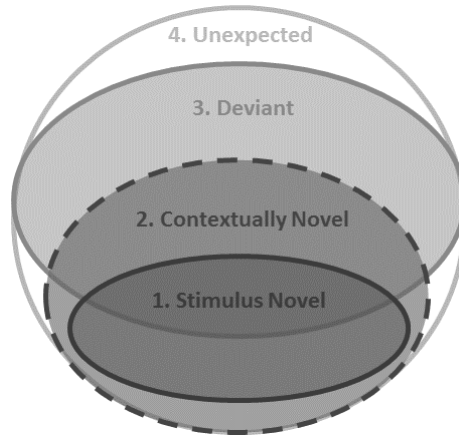


Figure 2. Venn diagram depicting the relation between different aspects of novelty, deviance from the context, and expectations. Stimulus novelty is a subcategory of contextual novelty. Although novel stimuli often deviate from the context, this is not necessarily the case, nor are deviants necessarily stimulus novel (see the ‘What’s new’ paragraph for more detailed descriptions). All novel and deviant stimuli are unexpected, although they can be more or less unexpected depending on the context in which they occur.

Novelty oddball paradigm and psychophysiological indices of novelty processing

The brain’s response to novelty is often investigated using the novelty oddball paradigm while the electroencephalogram (EEG) is measured (Courchesne, Hillyard, & Galambos, 1975; Squires, Squires, & Hillyard, 1975). In this task infrequent deviant *novel* stimuli are presented amongst frequent repeated *standard* stimuli, and an infrequent *target* (the ‘oddball’). The stimuli are presented in a random sequence, while participants respond only to the infrequent target. The stimuli can be presented in any sensory modality, but the most frequently used are the visual and auditory versions of this task. In this dissertation only visual versions of the novelty oddball paradigm were used.

Brain responses on the novelty oddball paradigm measured by the EEG can be time-locked to the onset of the stimuli using the event-related potential (ERP) technique. When observing the grand-averaged waveforms elicited by visual novel stimuli typically a negative wave peaking over frontal regions around 250-300 ms post-stimulus can be identified. This ERP component, called the anterior N2 (sometimes also referred to as N2b; Folstein & Van Petten, 2008; Näätänen & Picton, 1986; Szucs, Soltesz, Czigler, & Csepe, 2007), is believed to reflect the early detection of novelty. Its

amplitude is affected by a variety of factors, such as viewing time (Chong et al., 2008; Daffner et al., 1998; Nittono, Shibuya, & Hori, 2007), physical characteristics such as stimulus complexity (Shigeto, Ishiguro, & Nittono, 2011), and template mismatch (Folstein & Van Petten, 2008). Some findings have suggested that focal attention is required for the elicitation of the anterior N2 (Folstein & Van Petten, 2008), while other studies have suggested that it is elicited outside the focus of attention, but that attention may enhance it (Folstein, Van Petten, & Rose, 2008; Fu, Fan, & Chen, 2003; Wang, Cui, Wang, Tian, & Zhang, 2004). More recently it has been argued that it reflects an automatic process, entirely unaffected by attention (Chong et al., 2008; Tarbi et al., 2011; Schomaker, Roos, & Meeter, 2014).

The anterior N2 is typically followed by a frontocentral component peaking around 300-550 ms post-stimulus, that has been termed the P3a (Squires, Squires, & Hillyard, 1975). In the same year that the P3a was first described, Courchesne, Hillyard, & Galambos' (1975) found that bizarre, novel stimuli elicit a positive component in the same time-range and with the same frontal topography as the P3a. They termed this component novelty P3. Although the P3a and novelty P3 were long seen as two separate components, more recent findings suggest there is little reason to distinguish them (Combs & Polich, 2006; Goldstein, Spencer, & Donchin, 2002; Polich & Comerchero, 2003; Simons et al., 2001). The novelty P3 is believed to reflect the orienting or switching of attention and is often taken as a psychophysiological index of the involuntary orienting response (Escera et al., 2000), however, others have argued it reflects the voluntary orienting of attention to deviant or novel information (Berti, 2008; Chong et al., 2008). The novelty P3 probably reflects the recruitment of a large brain network concerned with processing and orienting attention towards unexpected information. This network probably comprises part of the (pre)frontal lobes (Daffner, Mesulam, Holcomb, et al., 2000; Daffner, Mesulam, Scinto, Acar, et al., 2000; Schröger et al., 2000; Verbaten, Huyben, & Kemner, 1997; Knight, 1984), anterior cingulate cortex (Dien et al., 2003), and orbitofrontal cortex (Lovstad et al., 2012).

The novelty P3 can be differentiated from the P3b (also referred to as P300). The P3b peaks later than the novelty P3 and typically has the largest amplitude over parietal or posterior rather than frontocentral electrodes (Soltani & Knight, 2000). It has been associated with the updating of working memory (Donchin, 1981b; Donchin & Coles, 1988). Target-relevant stimuli typically elicit a P3b (He et al., 2001; Spencer et al., 2001), and it has been argued that events must be task-relevant and involve a decisional process to evoke the P3b component (Friedman et al., 2001; Verleger, 2008). Task-irrelevant novel stimuli, however, can also elicit a P3b component, but with a smaller amplitude (He et al., 2001). The novelty P3 and P3b overlap in time (Dien et al., 2003;

Dien, Spencer, & Donchin, 2004; He et al., 2001; Spencer et al., 1999, 2001), and additional analyses, like factor analysis or principal component analyses, are required to distinguish them.

Outline of this dissertation

This dissertation presents seven studies on novelty and the consequences of novelty for cognition. The first chapter presents a framework in which these consequences are systematized. The rest of this dissertation is divided into two parts. In **Part I** (Chapters 2-6) on one hand studies are described in which both novelty's effects on attention and arousal and on the other factors influencing novelty processing were investigated. In **Part 2** (Chapters 7 and 8) studies are discussed demonstrating novelty's longer-lasting effects on memory.

Chapter 1 reviews recent empirical findings of novelty's beneficial effects on cognition. It is suggested that novelty-induced perceptual enhancements are caused by novelty activating the amygdala and recruiting attentional resources. The other consequences of novelty are linked to the noradrenergic and dopaminergic systems. Tying together findings from a wide range of studies, it is proposed that short-lived facilitatory effects of novelty are mediated by the LC-NE system (see for example Krebs, Fias, Achten, & Boehler, 2013; Murphy, Robertson, Balsters, & O'Connell R, 2011), and longer-lasting effects on learning and reward-processing are mediated by dopamine through a bidirectional connection between the hippocampus and SN/VTA (see for example Chowdhury, Guitart-Masip, Bunzeck, Dolan, & Düzel, 2012; Lisman & Grace, 2005; Rangel-Gomez, Hickey, van Amelsvoort, Bet, & Meeter, 2013).

Chapter 2 is an adaptation from Schomaker, & Meeter (2012). Emotional threat stimuli are known to enhance perception by activating the amygdala and eliciting an attentional response. Novel stimuli can also activate the amygdala, and could therefore also possibly enhance perception via the same mechanism. In two experiments novelty's effects on visual perception were investigated using a tilt detection task. Novel or familiar stimuli cued the onset of a target that was either tilted or not. Novel cues increased perceptual sensitivity, especially towards the end of the experiments when the familiar stimulus became more and more familiarized (through repeated presentation). These effects were not caused simply by a shift in bias towards a more liberal response criterion. In fact, participants tended to adopt a more conservative criterion after novel rather than familiar cues, which is consistent with the idea that novel cues enhanced perception by eliciting an attentional response.

Chapter 3 was based on Schomaker, & Meeter (2014a). In a series of experiments it was investigated whether different types of novel visual stimuli resulted in distraction or facilitation when performing an auditory detection task, relative to standard visual stimuli. Facilitation of responses was observed when the auditory target was presented together with deviant complex stimuli (either novel/non-novel), but not for deviant or complex stimuli per se. The effect could not be explained by the complex deviant stimuli re-orienting attention back to the task due to surprise. The facilitatory effects peaked 200 ms post-stimulus. The timing of the effects observed is consistent with the adaptive gain theory of the LC-NE system (Aston-Jones & Cohen, 2005b). The conditions under which facilitation was observed are very similar to the conditions under which the novelty P3 is elicited (see Chapter 5).

Positive mood can affect a range of cognitive processes. It can increase cognitive flexibility and control, and promote curiosity and exploratory behavior. Furthermore, watching a happy movie can increase sympathetic arousal. In **Chapter 4** it was investigated whether positive mood interacts with novelty in inducing facilitatory effects on behavior. This could occur by positive mood further increasing arousal or potentiating novelty's effects on attention. To induce a positive mood, half the participants viewed a happy movie before performing the experimental task. The other half watched a neutral movie. The task was similar to the ones used in Chapters 2 and 3. While viewing complex novel and familiar images, participants performed an auditory detection task. Processing of novelty is known to change with age, therefore also its consequences may be different in children versus adults. A large sample of children and adults was tested in order to obtain a developmental perspective on the facilitatory effects of novelty and mood. Children were slower and less accurate than adults on the auditory detection task. Positive mood resulted in response facilitation in the children, but also induced a more liberal response criterion in them. The facilitatory effects were somewhat stronger for the novel than for the standard stimuli. No effects of mood were observed in the adults. Taken together, these results suggest that the effects of positive mood were stronger in children, inducing facilitatory effects of novelty.

In **Chapter 5** the brain's response to different aspects of novelty was investigated in an ERP study using a visual novelty oddball paradigm. It has previously been argued that the orienting response to novel stimuli is a fully automatic stimulus-driven process. Manipulating the stimulus context should then have no effect on novelty processing. To test this, two experiments were performed in which novel stimuli remained the same across conditions, but the context was changed to either manipulate the complexity of the stimulus context (Experiment 1) or deviance from the context (Experiment 2). In Experiment 1, the novel stimuli (line-drawings of unknown

objects) were either presented in a stimulus context of simple geometric forms, or in a context of complex scrambled images. It was found that when the stimulus context was complex the novelty P3 component, believed to be a psychophysiological index of the orienting response towards novelty, was attenuated. No effect was found on the anterior N2, a component believed to reflect novelty detection. A similar effect was obtained in Experiment 2, where the novelty P3 was reduced for novels that were frequent, rather than deviant. Again, no effect was found on the anterior N2. In conclusion, these results suggest that novelty detection is a relatively automatic process depending on stimulus characteristics, whereas the further evaluation of novelty depends strongly on deviance of the stimulus and the complexity of the context in which it is presented: When novelty is expected the brain's orienting response towards it is reduced. Interestingly, the conditions under which a novelty P3 was elicited are very similar to the conditions under which complex deviant (novel) stimuli induced facilitation in Chapter 3. Since the novelty P3 has been associated with the LC-NE response, these findings further suggest that such a response may underlie the observed facilitatory effects in those experiments.

In **Chapter 6** we investigated the role of attention in the early detection of novelty. In two tasks the amount of attention available for novel stimuli was manipulated. Participants either performed an easy visual novelty oddball task or a more difficult working memory task while the same types of stimuli were presented. In the visual oddball task participants responded to an infrequent target, while these stimuli could be ignored in the working memory task. In the difficult working memory task six items had to be rehearsed, while the visual oddball stimuli (novels, standards, or targets) were presented. When attention was occupied by the working memory task the novel stimuli received less attention, as reflected by a smaller novelty P3 than in the visual oddball task. In contrast, the anterior N2 component to the visual oddball stimuli was enhanced in the working memory task. The initial detection of novel stimuli was thus enhanced (as indexed by the large anterior N2) when few attentional resources were available. In a second experiment, a condition was added in which working memory load was low, but the visual oddball stimuli were task-irrelevant. Results from this experiment showed that the novelty P3 was mainly affected by task relevance, and the enhanced anterior N2 was caused by the high working memory load. Together, these results suggest that suppression of task-irrelevant novelty is reduced when attention is otherwise engaged, resulting in enhanced novelty detection.

In **Part II** studies are described evidencing novelty's beneficial effects on memory. Exposure to novel environments is known to enhance plasticity and learning in the hippocampus in animals. In **Chapter 7** we addressed the question whether active exploration of a novel environment would enhance learning on an unrelated task performed after exploration in humans as well. In a

within-subjects design participants explored a novel and a previously familiarized virtual environment after which they performed an unrelated word learning task. Exploration of a novel environment enhanced recall, but not recognition memory. In addition, more words were recalled by participants that reported higher levels of presence in the virtual environment. After exploring a novel compared to a familiar environment participants reported stronger experiences of presence, suggesting that participants paid more attention to the novel environment. This was an additional effect, however, that could not explain the novelty effect on learning.

Parkinson's disease (PD) is characterized by a degeneration of nigrostriatal dopaminergic cells, resulting in dopamine depletion. This depletion is remediated through dopamine replacement therapy (DRT). Since dopamine is known to affect novelty processing and memory, these processes may be implicated in PD and DRT may affect them. **Chapter 8** describes a study in PD patients (on and off DRT) and a matched healthy control group investigating the effects of dopamine on novelty processing and memory formation. Participants performed a Von Restorff task, in which memory is typically better for salient events (i.e. words presented in deviant rather than standard font). Patients with PD remembered notably fewer words than controls. Furthermore, healthy controls, but not patients with PD exhibited the typical Von Restorff effect, suggesting that especially memory encoding for novel font words was impaired in the patients with PD. In line with this suggestion, psychophysiological indices of memory encoding and novelty, the P2 and P3 event-related potential components, were reduced in the patients with PD. But no effects of DRT were observed, indicating that the abnormalities in learning and memory in PD are not resolved by dopaminergic medication.

