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Research report

Predicting the unknown: Novelty processing depends on expectations

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ABSTRACT

Fulfilled predictions lead to neural suppression akin to repetition suppression, but it is currently unclear if such effects generalize to broader stimulus categories in the absence of exact expectations. In particular, does expecting novelty alter the way novel stimuli are processed? In the present study, the effects of expectations on novelty processing were investigated using event-related potentials, while controlling for the effect of repetition. Sequences of five stimuli were presented in a continuous way, such that the last stimulus of a 5-stimulus sequence was followed by the first stimulus of a new 5-stimulus sequence without interruption. The 5-stimulus sequence was predictable: the first three stimuli were preceded by a cue indicating that the next stimulus was likely to be a standard stimulus, and the last two by a cue indicating that the next stimulus was likely to be novel. On some trials a cue typically predicting a standard was in fact followed by an unexpected novel stimulus. This design allowed to investigate the independent effects of (violated) expectations and repetition on novelty processing. The initial detection of expected novels was enhanced compared to unexpected novels, as indexed by a larger anterior N2. In contrast, the orienting response, as reflected by a novelty P3, was reduced for expected compared to unexpected novels. Although the novel stimuli were never repeated themselves, they could be presented after one another in the sequence. Such a category repetition affected the processing of novelty, as evidenced by an enhanced anterior N2, and a reduced novelty P3 for novels preceded by other novels. Taken together, the current study shows that novelty processing is influenced by expectations.

1. Introduction

Generally, the visual world is highly structured, such that observers can form reliable expectations regarding upcoming stimulation. For example, a red traffic light can be expected to turn green at some point. Such expectations alter neural processing of information: Typically, stimuli expected by observers generate less neural activity than stimuli that are surprising (Summerfield and de Lange, 2014; Summerfield et al., 2008). It remains unclear, however, if the effects of expectations are generalizable to broader stimulus categories, when no specific sensory template can be activated by expectations.

A category of stimuli for which observers by definition cannot form specific expectations is novel stimuli. Truly novel stimuli, stimuli that have never been seen, are unknown and can therefore not be predicted. Nonetheless, forming expectations about novel stimuli may be important because new stimuli can be an unknown threat or source of reward, and therefore rapidly detecting and responding to novelty is essential for survival (Panksepp, 1998). Indeed, novel stimuli are typically prioritized over familiar stimuli by attracting attention (Escera et al., 1998; Escera et al., 2001; Friedman et al., 2001; Ranganath and Rainer, 2003; Yago et al., 2003), and generate differential neural activity very early during processing (Xiang and Brown, 1998). Orienting towards novel stimuli has been believed to be an involuntary process (San Miguel et al., 2008).

Predictions and expectations can also bias processing of subsequent stimuli, by activating sensory templates (Carlsson et al., 2000; Kok et al., 2017). This raises the possibility that enhanced responses to novel stimuli may in fact be due to their *unpredictability* (as they do not match with any active template) rather than their novelty per se. In fact, several studies have suggested that the event-related potentials (ERPs) traditionally believed to reflect novelty processing actually reflect a violation of expectations rather than the mere detection of novelty (Cycowicz and Friedman, 2007; Escera et al., 2001; Schomaker and Meeter, 2015; Schomaker et al., 2014).

The brain's response to novelty has been investigated since the seventies of the previous century using the ERP technique. This technique allows for the discrimination of different aspects of the orienting response towards novelty with a high temporal

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resolution. ERP studies of novelty typically use the three-stimulus novelty oddball paradigm (Courchesne et al., 1975; the current study's task differs in various ways from the novelty oddball task, as will be discussed below). In this paradigm, participants have the task to respond to an infrequent target stimulus, which in the visual version of the task typically is a simple geometric figure, such as a triangle. Targets are embedded in a random sequence of frequent standard stimuli (typically also geometric figures), and infrequent task-irrelevant novel stimuli. In the visual version of the task, novel stimuli typically consist of bizarre drawings or figures that the participants could not possibly have seen before. These novel stimuli evoke at least two novelty-associated ERP components, a frontally peaking negative-going component around 250–350 ms, referred to as the anterior N2 or N2b (Folstein and Van Petten, 2008), and a later positive-going frontro-central component around 300–550 ms, referred to as the novelty P3 (Friedman et al., 2001). The anterior N2 has been interpreted to reflect the automatic detection of novelty (Chong et al., 2008; Escera et al., 2001; Schomaker et al., 2014; Tarbi et al., 2011) or the strong neural responses generated by novel stimuli (Schomaker and Meeter, 2014; Schomaker et al., 2014), while the novelty P3 has been suggested to reflect the involuntary orientation towards and the conscious evaluation of novel events (Courchesne et al., 1975; Escera et al., 2000; Escera et al., 1998; Friedman et al., 2001). In terms of timing and topography, the novelty P3 is very similar to the P3a component which is elicited by deviant task-irrelevant stimuli (Squires et al., 1975). In fact, several studies have found that the two components cannot be distinguished (Combs and Polich, 2006; Goldstein et al., 2002; Simons et al.,2001), though see Barry et al. (2016). The novelty P3 has been traditionally associated with processing of stimulus novelty (Courchesne et al., 1975), but more recent studies have suggested it can is also be affected by top-down attentional factors (Chong et al., 2008), working memory load (Schomaker and Meeter, 2014; Tarbi et al., 2011; Lv et al., 2010), and stimulus complexity (Barkaszi et al., 2013).

Another factor that was found to influence the magnitude of the novelty P3, is context-derived expectations (Cycowicz and Friedman, 2007; Schomaker et al., 2014). For example, Schomaker et al. (2014) found that the novelty P3 component was strongly reduced when novels were frequent rather than rare. Still, each individual novel stimulus was presented just once – rather it was the frequency of *novel stimuli as a category* that affected the size of the novelty P3 component. A similar effect was found when the standard stimuli in an novelty oddball paradigm were complex, though not very novel, dot clouds as opposed to simple geometric figures (Schomaker et al., 2014). Interestingly, the anterior N2 was unaffected by these experimental manipulations, suggesting it more closely reflects the novelty of the stimulus itself (called *stimulus novelty* in Schomaker and Meeter, 2015), and is less dependent on contextual factors. Schomaker et al. (2014) explained their findings by changes in participants' expectations about upcoming stimuli. In conditions in which complex stimuli were frequent, upcoming stimuli were also expected to be complex. If the novelty P3 is mostly a response of *surprise* by unexpectedly complex stimuli (as hypothesized by Schomaker et al., 2014), a complex novel stimulus would elicit less of a novelty P3 in contexts that led participants to expect complex novel stimuli. Others have suggested, however, that it is in fact the later P3b component that reflects predictive surprise, and the following positive slow wave prediction updating, while the P3a (or novelty P3) was suggested to reflect belief updating Kolossa et al. (2017). If this is the case, expectations would modulate the P3b and/or positive slow wave rather than the novelty P3.

However, expectations were not directly manipulated in this previous study, nor in any other study showing effects of expectations (Cycowicz and Friedman, 2007), making it difficult to rule out alternative explanations. In particular changing the frequency with which stimuli occur not only manipulates expectations, it also alters the likelihood of a repetition (e.g., if 70% of stimuli in an experiment are novels, a novel is much more likely to be preceded by a novel than when only 10% of stimuli are novels). It could thus be that repetition suppression, rather than expectation, is the factor that reduces the novelty P3.

Previous studies thus suggest that novelty processing consists of a part that is a response to stimulus novelty itself (indexed by the anterior N2), but also of a part that is sensitive to expectations, indexed by the novelty P3. However, expectations were never experimentally manipulated, and findings were potentially confounded by the likelihood of repetitions (Cycowicz and Friedman, 2007; Schomaker et al., 2014). In the current study, we aimed to investigate the effects of expecting something new on novelty processing, and to rule out possible effects of repetition. We directly manipulated participants' expectations and investigated the brain's response to novel stimuli under such different conditions using ERPs. We used a task inspired by the novelty oddball task, including frequent standards, less-frequent novels, and infrequent targets. In contrast with the traditional novelty oddball task, expectations were actively manipulated: Each stimulus was preceded by a cue that predicted that the next stimulus would either be a standard or a novel stimulus. Additionally, stimuli were presented in an almost predictable sequence. On a few trials, novel stimuli were unexpectedly presented when both the cue and the position in the sequence would lead the observer to expect a standard stimulus. We investigated whether such unexpected novels were processed differently from expected novel stimuli, and whether these effects superseded those of repetition (i.e., of two novels following one another).

2. Methods

2.1. Participants

24 participants volunteered to take part in the study, but three were excluded due to noisy EEG data and one due to technical problems (see EEG analyses for details). Data of the remaining 20 participants was included in the analyses (5 male; age 21–29, mean = 23.4, sd = 2.2; 16 right-handed). All of them had normal or corrected to normal vision. Participants either received course credit or 8 Euros per hour per compensation. The study was performed in accordance with the ethical standards of the 1964 Declaration of Helsinki and in accordance with the ethical committee of the faculty of Behavioural and Movement Sciences at the Vrije Universiteit Amsterdam, the Netherlands. Participants all signed informed consent before their participation.

2.2. Stimuli

Two types of cues were presented: a green and yellow fixation cross that predicted standard or novel stimuli respectively (which color predicted what stimulus category was counterbalanced across participants). In addition, a rare non-cued target was presented on 12.5% of the trials in order to make sure that participants would attend all presented stimuli. The target could occur at any position in the sequence with equal probability. Novel stimuli were randomly drawn from a large set of fractal images, that were generated using the open-source program ChaosPro 4.0 (http://chaospro.de). The novel fractals were colorful, complex images without any semantic meaning. Both the standard and target stimulus were simple geometric forms, and consisted of triangles pointing in opposite direction (either upwards or downwards).

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