What's new? The interaction between novelty and cognition

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General Conclusion

When a novel stimulus is encountered it elicits a cascade of effects in the brain, activating some of the major neuromodulatory systems, and affecting a wide range of cognitive processes. These effects were the focus of this dissertation. Two characteristics of novelty processing were found to be especially important for novelty's effects on cognition. First, the time-course of the brain's response to novelty can be very rapid, occurring in the order of milliseconds, but its effects can also play out on a slower timescale, lasting for tens of minutes. Consistent with the timing of such short-lived and longer-lasting responses to novelty in the brain, novelty's effects on cognitive processes also occur over different time-scales. Second, although novelty processing and its behavioral consequences were previously believed to be fully automatic and stimulus-driven (Escera et al., 1998, 2000; Naatanen et al., 1992), our findings suggest that they depend strongly on the circumstances in which a novel stimulus is encountered.

What is novelty?

A stimulus can be novel in various ways. Something can be novel compared to everything stored in long-term memory. This type of novelty is referred to as *stimulus novelty* (Courchesne, et al., 1975). Not only stimulus characteristics define novelty. Something can be familiar, but differ from everything else presented in a certain context. For example, when a picture of an apple is presented once in a series of pictures of other types of fruit, the apple is familiar to the observer, but it is new in that situation. In this case the picture of the apple is *contextually novel*.

Also related to context is *deviance*. When that same picture of the apple is repeatedly but infrequently presented in a series of pictures of tools, it is not stimulus novel nor contextually novel. However, it will still stand out because it *deviates* from the context in which it is presented. Findings discussed in this dissertation showed that some consequences of novelty processing are due to novelty itself, while others are actually the result of the novel stimulus deviating from its context.

Another aspect of the context that influences the processing of novel stimuli is *complexity*. Complex stimuli have many features (e.g. much detail, wide range of colors, high contrast), making it difficult to compress them (Rigau, Feixas, & Sbert, 2005). The complexity of the context determines how novelty is processed and how it affects other cognitive processes: When the context in which a novel stimulus is presented consists of highly complex stimuli, it is processed differently than when the context consists of only simple stimuli.

The brain's responses to novelty

The research presented in this dissertation suggests that novelty's effects can be grouped into at least three categories. The first two categories consist of effects that occur shortly after a novel stimulus is encountered. The third category involves longer-lasting effects. In **Chapter 1**, it was argued that these three types of effects are each linked to different responses of the brain to novelty.

First, the amygdala, mostly known for its role in processing of emotion, responds strongly to novelty as well (Blackford et al., 2010; Kiehl et al., 2005; Schwartz et al., 2003; Wright et al., 2003; Zald, 2003). Emotional stimuli are believed to enhance visual perception by eliciting an attentional response by activating the amygdala and the connected early visual cortical areas (Pessoa, 2013; Vuilleumier, 2005). Since novel stimuli can 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 it is not yet known what the exact time-course of these effects is, enhancements are typically reported to occur in the first few hundred milliseconds after presentation of an emotional stimulus (Sellinger, Dominguez-Borras, Escera, 2013).

Second, complex and novel stimuli can activate the locus coeruleus (LC; a brain stem area that is the exclusive supplier of norepinephrine to the forebrain), resulting in phasic norepinephrine (NE) release peaking around 200 ms following stimulus presentation (Aston-Jones & Cohen, 2005b; Mongeau, Blier, & de Montigny, 1997). This LC-NE system has been associated with arousal, but can also affect behavior more selectively. The adaptive gain theory 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 (Aston-Jones & Cohen, 2005a, 2005b). Novelty could thus potentially affect cognitive performance by activating this mechanism.

Third, the mesolimbic dopaminergic system is activated by novelty. In contrast with the short-lived LC-NE response, dopaminergic responses elicited by novelty are effective up to tens of minutes later (Kentros, Agnihotri, Streater, Hawkins, & Kandel, 2004; Li et al., 2003; Straube, Korz, Balschun, et al., 2003). After novelty detection, dopamine release from the substantia nigra/ventral tegmental area (SN/VTA) is believed to be triggered by a novelty signal from the hippocampus (Lisman & Grace, 2005). The mesolimbic dopaminergic system has been associated with several cognitive processes; most prominently with learning, memory, exploratory behavior, reward processing, and motivation.

Consistent with the timing of the short-lived and longer-lasting responses to novelty in the brain, novelty's effects on different cognitive processes also occur over different time-scales. As will be argued below, novelty has short-lived effects on perception and action, and longer-lasting effects on motivation, exploratory behavior, and learning and memory.

Factors influencing novelty processing and novelty's effects on cognition

In ***Part 1*** of this dissertation the rapid detection and evaluation of novelty, and the perceptual and behavioral consequences of detecting different types of novelty were investigated. In **Chapter 2**, novel stimuli were shown to enhance visual perception relative to familiar stimuli, presumably by eliciting a transient attentional response in a similar way as emotional stimuli. In two experiments participants performed a tilt detection task in which a target Gabor pattern was either vertically oriented or somewhat tilted to the left or right. Each target was preceded by a familiar or novel fractal image that acted as a cue. Novel cues were found to increase perceptual sensitivity relative to familiar cues. This effect became more pronounced when the familiar stimulus became more familiar with every repeated presentation. The novel and familiar stimuli were from the same category of fractal stimuli, and did not deviate strongly from one another. The observed effect was thus caused by stimulus novelty and not deviance (in contrast with some of the findings that will be discussed below). Since novelty can activate emotional brain circuits, these effects were suggested to be mediated by novel stimuli activating the amygdala, enhancing early sensory processing via its connections with the visual cortex.

In **Chapter 3**, complex deviant stimuli were found to transiently facilitate behavioral responses to an auditory target, between 0 and 200 ms after their presentation. Facilitation occurred irrespective of whether the visual stimuli were novel or repeated, but did not occur when deviant stimuli were simpler than the non-deviant stimuli. It was thus not an effect of novelty per se, but rather of a combination of deviance and complexity. That is, only stimuli that were infrequent and more complex than the stimulus context in which they occurred caused facilitation. These effects on responses were suggested to be mediated by the complex deviant stimuli eliciting a LC-NE response; a response known to peak around 200 ms as well. The finding that novel stimuli did not result in facilitation when presented in an equally complex stimulus environment were replicated in **Chapter 4**. Adults did not show facilitation of behavioral responses when novel images were presented. Positive mood, however, was shown to induce facilitatory effects of novelty in children. Children who saw a happy video were generally faster in responding to the auditory target than children that saw a neutral video. This facilitation was seen especially when the auditory target was presented together with a novel fractal. Children were thus faster in responding in the context of novelty, but they also adopted a more liberal response criterion, consistent with increased arousal (Posner, 1978). Responsiveness to novelty thus changes with age, and can be affected by mood.

In **Chapter 5** the brain's response to novelty was measured using EEG. Two event-related potential (ERP) components, associated with novelty (the anterior N2 and the novelty P3), were used to investigate the effects of stimulus context on novelty processing. In two experiments in which the complexity of the stimulus context and the occurrence of novels were varied, no

differences were observed for the early processing of novelty, as indexed by the anterior N2. In contrast, later processing, as indexed by the novelty P3, was strongly affected by context. Novel stimuli only elicited a novelty P3 when the stimuli were deviant and complex, that is, when they were infrequent and complex relative to the context in which they occurred. This set of conditions is very similar to the conditions in which facilitation of responses was observed in **Chapter 3**. Since the same stimuli were presented in similar stimulus contexts in these two chapters (however, with slightly different frequencies) it seems safe to assume that if EEG had been measured in the studies of **Chapter 3**, a novelty P3 would have been observed in the conditions in which facilitation of responses was found. Interestingly, the LC-NE response has been linked to both the novelty P3 (Murphy, Robertson, Balsters, & O'Connell R, 2011; Nieuwenhuis, De Geus, & Aston-Jones, 2010), and to facilitatory effects on behavior (Aston-Jones & Cohen, 2005b; Nieuwenhuis, Aston-Jones, & Cohen, 2005; Nieuwenhuis et al., 2010; SanMiguel, Morgan, Klein, Linden, & Escera, 2010; Sara, 2009; van Mourik, Oosterlaan, Heslenfeld, Konig, & Sergeant, 2007). This supports the idea that the LC-NE response underlies the facilitatory effects observed in **Chapter 3**, however, future research investigating this link directly is required.

As stated above, the results in **Chapter 5** show that processing of novelty is affected by the stimulus context: When complex or novel stimuli were frequent, the novelty P3 was strongly reduced. An explanation for this pattern might be that the later evaluation of novelty, as indexed by the novelty P3, is sensitive to expectations. Possibly, a novel stimulus only generates a novelty P3 when novel or complex stimuli are not expected. In line with this suggestion, in a recent unpublished study we found that the novelty P3 is indeed sensitive to expectations: The novelty P3 was smaller when a novel stimulus was presented at a predictable relative to an unpredictable position in a sequence.

In contrast to the novelty P3, the earlier processing of novelty, as indexed by the anterior N2, depended on stimulus characteristics and was unaffected by the complexity of the stimulus context. The anterior N2 has been linked to the detection of novelty (Folstein & van Petten, 2008; Tarbi, et al., 2011). Alternatively, as argued in **Chapter 1**, the anterior N2 may simply reflect the perceptual part of novelty processing, rather than a specific detection process (Stoppel et al., 2009; Prox, Dietrich, Zhang, Emrich, & Ohlmeier, 2007).

In the experiments of **Chapter 5**, novel stimuli also elicited a P3b, an ERP component that has been associated with the updating of working memory (Donchin & Coles, 1998). Using principal component analysis (PCA) we were able to disentangle the novelty P3 and P3b, confirming that they reflect different processes in the brain. The P3b was smaller when novel stimuli were frequent. This is consistent with the idea that the P3b reflects the updating of expectations, since novel stimuli do not violate expectations when the chances of seeing a novel stimulus are high. The novelty P3 may

reflect the violations of expectations, whereas the P3b may reflect the updating of (working memory) templates.

In **Chapter 6**, we investigated the role of attention in eliciting the electrophysiological responses to novelty. In two ERP experiments the task requirements were manipulated while the same sequences of stimuli were presented. Participants were shown novel, standard and oddball stimuli while they either engaged in a difficult working memory task, an easy working memory task, or a visual oddball task. When attention was engaged in a difficult working memory task the anterior N2 was larger than when participants engaged in either the easy working memory task or the visual oddball task. This suggests that when participants paid attention to the visual stream, this suppressed the early processing of the *task-irrelevant* novel stimuli. When attention was already engaged in a difficult working memory task, suppression was reduced, resulting in enhanced early processing of the novel stimuli. In contrast, the further evaluation of novelty was reduced when attention was occupied, as reflected by a reduction in the novelty P3 when participants were engaged in the difficult working memory task. Unlike the anterior N2 that was influenced only by a high working memory load, the novelty P3 was affected both in the condition with a high and with a low memory load. In both conditions, the part of the visual stream in which the novel stimuli were presented was entirely task-irrelevant, while the novel stimuli elicited a typical novelty P3 when visual oddball stimuli were the relevant part of the sequence. This suggests that it is not so much attentional load that determines whether a stimulus elicits a novelty P3, but rather whether it is potentially task-relevant. The evaluation of novelty may thus be strongly affected by task relevance. Possibly, participants formed a clear concept of the oddball when it required a response, but not when it was irrelevant. In the latter case the novel stimuli did not violate their expectations, since there were no clear expectations, reducing the novelty P3.

Previously, it has been argued that novelty reflexively attracts attention (Escera et al., 1998, 2000; Naatanen et al., 1992). In summary, findings of the current dissertation suggest that the early processing of novelty indeed occurs relatively independently of the complexity of the context in which novel stimuli are encountered. However, the subsequent evaluation of novelty is reduced when participants were involved in a difficult task, and when complex or novel stimuli can be expected. The findings in these studies suggest that both the task requirements and stimulus context are crucial in determining how novelty is processed by the brain and what the consequences are for behavior. Stimulus novelty can enhance perception of subsequently presented information, by eliciting a transient attentional response. Possibly by violating expectations, complex deviant (non)novel stimuli facilitate behavioral responses, by eliciting a LC-NE response. However, direct evidence for the relations between LC-NE, the novelty P3 and facilitatory effects of novelty is lacking. Ideally, the novelty P3 and indexes of LC activity (e.g., pupil dilation) should be measured concurrently while novelty-induced facilitatory effects are observed.

Novelty processing during learning and novelty-induced memory enhancements

In ***Part 2*** novelty's longer-lasting effects on memory were the topic of investigation. To learn how to optimize behavior it is crucial to learn the specific conditions under which beneficial and detrimental outcomes are encountered (Fu & Anderson, 2008). Since novel environments by definition provide an opportunity for learning, it would be advantageous if learning is specifically promoted when exploring them. Findings from animal studies have shown that encoding of new information is indeed enhanced during and after animals explore a novel compared to a familiar environment (Straube, Korz, & Frey, 2003; Merhav & Rosenblum, 2008). Also in humans, stimulus novelty can promote learning (Wittmann et al., 2007; Murty et al., 2013; Fenker et al., 2008). In line with these findings, memory improvements on an unrelated word learning task were observed after active exploration of a novel relative to a familiar virtual environment in **Chapter 7**. Only hippocampus-dependent recall was enhanced, but not recognition memory, believed to be a more hippocampus-independent process (Yonelinas et al., 2002; Aggleton & Brown, 1999; Fernandez, et al., 2002). Learning took place about ten minutes after exploration, suggesting that novelty's memory enhancing effects are generalizable and can occur over extended periods of time. This is one of the first studies showing such temporally extended enhancing effects of environmental novelty in humans.

Not only novelty of the environment, but also the novelty of the to-be-learned information itself can ameliorate learning. Memory is typically better for words presented in a deviant novel font rather than a standard font. This is known as the Von Restorff, isolation or distinctiveness effect (Von Restorff, 1933; Bruce & Gaines, 1976; Dunlosky et al., 2000; Geraci & Manzano, 2010; Geraci & Rajaram, 2004; Rangel-Gomez & Meeter, 2013; Schmidt, 1985). In **Chapter 8**, such a Von Restorff effect of better memory for words presented in novel fonts was observed in healthy controls, but not in patients with Parkinson's disease (PD). Especially, recall memory of novel font words was impaired in the patients with PD. This effect was accompanied by a reduction in the P3 to novel compared to standard font words in patients with PD compared to healthy controls. This ERP component was correlated with successful memory encoding, raising the possibility that a process aiding the encoding of novel words was compromised in PD patients. PD is characterized by a degeneration of dopaminergic cells in the SN, resulting in dopamine depletion throughout the brain. The observed abnormalities in learning and memory for novel font words in patients with PD were not resolved by dopaminergic medication. The lack of effects of dopaminergic medication in the patients with PD may be explained by dopamine overdosing brain areas involved in novelty processing and memory encoding, such as the hippocampus and medial temporal cortex in some patients. These areas interact more closely with the ventral striatum, that is not yet strongly

affected in the early stages of PD (Agid et al., 1993; Gotham, Brown, & Marsden, 1988; Kish et al., 1988; Swainson et al., 2000b), than with the dorsal striatum, that is already affected from the onset of the disease (Bunzeck, Guitart-Masip, Dolan, & Duzel, 2011; Houk, 2005; Macdonald & Monchi, 2011). However, other explanations for these results cannot be excluded. For example, other brain abnormalities or differences in recall strategy may explain the observed deficits in PD relative to healthy controls.

In **Chapter 7** only differences for recall and not for recognition memory were observed after exploration of a novel versus a familiar environment. Similarly, in **Chapter 8** patients with PD were only impaired on recall compared to healthy controls, while recognition memory was unaffected. Recall is believed to be dependent on the hippocampus (Yonelinas et al., 2002), whereas recognition is thought to rely mainly on the perirhinal cortex (Aggleton & Brown, 1999; Duzel, Vargha-Khadem, Heinze, & Mishkin, 2001; Fernandez, Klaver, Fell, Grunwald, & Elger, 2002; Wan, Aggleton, & Brown, 1999; Yonelinas et al., 2002). The findings in **Chapter 7** could be explained by novelty activating the hippocampus triggering dopamine release through the hippocampal-VTA loop, regulating the entry of new information into long-term memory, thereby subsequently improving recall, but not recognition (Chowdhury, Guitart-Masip, Bunzeck, Dolan, & Duzel, 2012; Duzel et al., 2010; Lisman & Grace, 2005; Rangel-Gomez, Hickey, van Amelsvoort, Bet, & Meeter, 2013). The findings in **Chapter 8**, of a Von Restorff effect, may be explained by the same mechanism; however, the findings of a null effect of dopaminergic medication in the patients with PD complicate the interpretation of the role of dopamine in this process. Moreover, it is currently unclear whether a novelty signal from the hippocampus activates the SN/VTA, or novelty activates the SN/VTA directly. Nor have its effects of enhanced long-term potentiation in the hippocampus ever been directly measured in humans. More research is required to investigate the role of dopamine and the hippocampal-VTA loop in enhancing memory in humans more directly.

Theoretical and practical implications

The brain is tuned towards novelty; however, how novelty is detected in the brain is still not well understood. A novelty signal in brain may be formed when no match is found in long-term memory. Such a process would involve the comparison of the current input to everything that is already stored. Since the first responses to novelty already occur in the milliseconds after its presentation, such an explicit comparison process is very unlikely to occur. Alternatively, a novelty signal may reflect the absence of habituation, either in the form of a learned suppression of the orienting response to information that has already been encountered repeatedly, or in that familiar information is more efficiently processed than novel information (i.e. priming; Ranganath & Rainer,

2003). When something is encountered for the first time the brain did not habituate to it yet, and may therefore respond more strongly.

This idea cannot explain, however, why a stimulus that is truly novel impacts cognition less strongly when it is not deviant, as was found in several studies in this dissertation. A way to explain these findings could be found in theoretical and computational models of the predictive coding framework (Friston, 2005; Mumford, 1992; Rao & Ballard, 1999). Core to these theories is the idea that the brain continually forms a model of the world on the basis of what is known from past experiences and the current context to predict which sensory input is likely to be encountered next. Whether the brain indeed continually forms and adjusts predictions of what sensory stimulation is likely to occur in the future and whether such predictions are implicit (unconscious) or explicit (conscious) is currently unclear. Novelty may prove to be an excellent concept to investigate the effects of expectations independently from priming and other forms of implicit learning, given that novel stimuli are the ultimate unexpected stimuli that cannot be predicted by definition.

Novelty is not only theoretically important; it also has relevance for many research topics within and beyond the fields of psychology and neuroscience. The brain's response to novelty is known to be altered especially in diseases in which dopamine has been implicated, such as attention deficit hyperactivity disorder (ADHD) and schizophrenia (Devrim-Ucok, Keskin-Ergen, & Ucok, 2006; Marzinzik et al., 2012; Stevens, Pearlson, & Kiehl, 2007; van Mourik, Oosterlaan, Heslenfeld, Konig, & Sergeant, 2007). A task that is often used to study the orienting response in clinical populations is the oddball paradigm, which has also been proposed to be a useful tool for diagnostic purposes (Bruder et al., 2001; Stevens et al., 2007). Notably the novelty P3 is often interpreted as the psychophysiological index of the brain's automatic allocation of attention to novelty. For example, in schizophrenia the novelty P3 to novel stimuli is often reduced, which is interpreted as a disturbance in the orienting response towards novelty (Cortinas et al., 2008; Devrim-Ucok et al., 2006). Results presented this dissertation suggest that this reduction does not only imply an impaired orienting response, but could also reflects a failure to form predictions of what will happen in the future. It has been argued previously, that schizophrenic patients have trouble anticipating upcoming events, and that it is this deficit that may underlie their misperceptions of the world, possibly, resulting in some of their psychotic symptoms (Ford & Mathalon, 2012; Frith, Blakemore, & Wolpert, 2000). Research directly testing the hypothesis that schizophrenic patients fail to form expectations and that this contributes to their psychotic symptoms is still lacking, however.

The visual oddball paradigm provides a good opportunity to investigate the brain's response to novelty, but findings are somewhat difficult to generalize: Does a reduced P3 reflect an impaired orienting response towards novelty, a failure to form expectations, or reduced distraction? Performance on this task is typically at ceiling, making it also difficult to determine the consequences for behavior. Here, we introduced new paradigms that allowed to investigate

novelty's effects on cognitive performance (such as in **Chapters 2-4**), and the effects of attention on novelty processing (as in **Chapter 5**).

Results presented in the current dissertation suggested that novelty processing is also altered in patients with Parkinson's disease: The psychophysiological response to novel items was reduced, and this reduction was accompanied by memory impairments, especially for those novel items. Linking the psychophysiological indices of novelty processing to behavioral measures provides a valuable addition the visual oddball paradigm, making the findings more generalizable.

Our findings that exposure to a novel environment can improve learning on an unrelated task may provide an interesting venue for promoting learning in situations where optimal memory performance is desired (e.g. in schools and universities). A change of scenery may prime learning in students. Furthermore, the findings that novelty receives less attention when presented in a context where it is expected, could also be of value when developing teaching strategies. For example, when a main text in a textbook is printed in a simple font, but the main conclusions are presented in a different way (different font or background), more attention may be allocated to the important points.

Previous findings already suggested that novelty processing changes with age (Maatta et al., 2005; Brinkman & Stauder, 2008; Wetzel & Schröger, 2007). Little is known, however, about how novelty affects other cognitive processes in children compared to adults. Our finding that novelty has different effects on cognitive performance in children and adults has important implications for developmental psychology. Learning is especially relevant for the developing brain, and the effects of exposure to novel versus familiar environments may be different in children, adults, and elderly.

Novelty's effects on cognition could potentially be used in every-day applications. For example, in a task with low attentional demands (driving a car by night on a deserted highway) presentation of a novel stimulus can potentially reorient attention back to the task (paying attention to the road, and prevent accidents). Car accidents caused by drowsy driving account for 1-30 % of preventable vehicle accidents (Volna & Sonka, 2006). Anti-sleep alarms do exist, but only act at the moment when the driver already falls asleep (when the eyes are closed for a substantial amount of time), while an alerting system using novelty could *prevent* sleepiness, for example by randomly presenting novel sounds at unpredicted times.

Concluding remarks

To conclude, novelty elicits a wide range of responses in the brain, influencing a variety of cognitive processes. It is central to learning, affects attention and perception, and influences our behavior. Future research is required to determine which theory explains the brain's responses to novelty best. Whatever will turn out to be the case, this dissertation has shown that novelty is a

concept that lies at the core of many cognitive processes, and deserves a central role in cognitive neuroscience.

Nederlandse Samenvatting

Wat is nieuw? De interactie tussen nieuwigheid en cognitie

Nieuwe stimuli (prikkels) kunnen zowel een beloning als een bedreiging betekenen. Daarom is het niet verwonderlijk dat mensen nieuwe informatie in de omgeving snel kunnen detecteren. Niet alleen de nieuwe informatie zelf is relevant, maar ook de omgeving waarin men deze nieuwe informatie tegenkomt. Vanuit een evolutionair oogpunt is het dan ook logisch dat nieuwigheid sterke effecten heeft op perceptie en gedrag. Wanneer men een nieuwe stimulus tegenkomt veroorzaakt dit een cascade van effecten in het brein. Hierbij worden belangrijke neurotransmittersystemen geactiveerd, waarbij een breed scala aan cognitieve processen beïnvloed wordt. Deze processen zijn het onderwerp van het onderzoek dat beschreven is in deze dissertatie. Er zijn twee factoren die bepalen op welke manier de waarneming van nieuwigheid effect heeft op cognitie. Ten eerste is de tijdschaal waarop het brein reageert op nieuwigheid van belang. Dit kan erg snel zijn, in de orde van milliseconden, maar de effecten kunnen ook uitspelen op een langzamere tijdschaal, in de orde van tientallen minuten. Consistent met de timing van de kortdurende en langdurende effecten van nieuwigheid in hersenprocessen, vinden ook de meetbare effecten op cognitie en gedrag plaats op verschillende tijdschalen. Ten tweede blijkt uit het onderzoek dat de verwerking van nieuwigheid minder automatisch verloopt dan eerder werd gedacht. We vonden dat verschillende aspecten van de nieuwe stimulus zelf, maar ook van de context invloed hebben op hoe nieuwigheid wordt verwerkt door het brein en daarmee wat de effecten zijn voor waarneming en actie.

In **Deel 1** van deze dissertatie zijn de effecten van nieuwigheid ('*novelty*') van stimuli op cognitie en gedrag onderzocht. In **Hoofdstuk 2** werd een studie beschreven waarin nieuwe stimuli de waarneming verbeterden. In twee experimenten moesten proefpersonen detecteren of een doelobject exact verticaal georiënteerd was of iets gedraaid. Elk doelobject werd voorafgegaan door een bekende of nieuwe stimulus, die het verschijnen van het doelobject aangaf. Wanneer proefpersonen een nieuwe stimulus zagen werd de waarneming voor daaropvolgende stimuli gevoeliger dan na het presenteren van een reeds bekende stimulus. Dit effect werd vooral duidelijk zichtbaar aan het einde van het experiment, wanneer de bekende stimulus al vaker herhaald was en dus bekender werd voor de proefpersonen, terwijl de nieuwe stimuli juist relatief nieuwer werden. Zowel de bekende als nieuwe stimuli waren fractal-figuren en weken dus in vorm relatief weinig van elkaar af. Dit is een belangrijk punt, omdat - zoals later gelezen kan worden - de effecten van nieuwigheid mede afhangen van in hoeverre de nieuwe en bekende stimuli van elkaar afwijken. Het

is reeds bekend dat ook emotionele stimuli dit soort effecten laten zien, doordat deze kortdurend aandacht kunnen versterken. Aangezien nieuwe stimuli dezelfde netwerken in het brein kunnen activeren als emotionele stimuli, is het mogelijk dat nieuwe stimuli eenzelfde effect op aandacht en perceptie te hebben als emotionele stimuli. Als nieuwe stimuli de amygdala activeren kunnen ze via verbindingen met de visuele cortex invloed hebben op de vroege verwerking van sensorische informatie.

In **Hoofdstuk 3** werden de effecten van verschillende soorten nieuwe stimuli op gedrag onderzocht. Complexe afwijkende visuele stimuli versnelden de reactie op een pieptoon wanneer die binnen 200 milliseconden na de visuele stimulus gepresenteerd werd. Facilitatie vond plaats onafhankelijk van of de visuele stimulus nieuw of herhaald was, maar vond niet plaats wanneer de afwijkende stimuli simpeler waren dan de niet-afwijkende stimuli. De faciliterende effecten werden dus niet veroorzaakt door de absolute nieuwigheid van een stimulus, maar eerder door een combinatie van afwijkendheid en complexiteit van de stimulus. Alleen wanneer een infrequente stimulus complexer was dan de context waarin deze voorkwam trad deze facilitatie op. Deze effecten op reactievermogen worden mogelijk gemedieerd door de locus coeruleus respons (een nucleus in de hersenstam die norepinefrine produceert). Deze respons in het brein piekt ook ongeveer na 200 milliseconden. In **Hoofdstuk 4** repliceerden we de bevinding dat nieuwe stimuli niet in facilitatie resulteren wanneer ze in een context voorkomen die even complex is als de stimuli zelf. Aan deze studie deden kinderen en volwassenen tussen 6 en 70 jaar mee. Volwassenen waren niet sneller of accurater wanneer ze nieuwe plaatjes zagen. Kinderen daarentegen reageerden wel sneller op een pieptoon door de nieuwe figuren, maar alleen wanneer zij van te voren een vrolijk in plaats van een neutraal filmpje hadden gezien. In het algemeen maakte een goed humeur de kinderen sneller, maar die effecten waren vooral zichtbaar voor de nieuwe en niet voor de bekende plaatjes. Een reden voor het sneller reageren kan liggen in het feit dat de kinderen die een positief filmpje gezien hadden ook een liberaler responscriterium hanteerden, dat wil zeggen, ze waren eerder geneigd aan te geven dat ze een piepje hadden gehoord, ook wanneer er geen piepje was gepresenteerd. Zo'n liberaal responscriterium komt overeen met een toename in arousal. Deze bevindingen suggereren dat de responsiviteit op nieuwigheid verandert met het ouder worden en dat humeur hier ook invloed op kan hebben.

In **Hoofdstuk 5** werd de respons van het brein op nieuwigheid gemeten, gebruikmakende van EEG. Wanneer men het EEG signaal middelt over alle metingen waarin een zelfde soort stimulus wordt aangeboden, ontstaat een signaal waarin over een tijdspanne van enkele honderden milliseconden verschillende pieken onderscheiden kunnen worden. Deze pieken noemt men event-related potentials (ERPs). Jarenlang onderzoek heeft veel van deze pieken (“ERP componenten”) kunnen linken aan verschillende cognitieve processen. Zo zijn er ook *componenten* die geassocieerd worden met nieuwigheid, zoals de *anterior N2* en de *novelty P3*. Deze componenten werden

gebruikt in **Hoofdstuk 5** om de effecten van stimulus context op de verwerking van nieuwigheid te onderzoeken. In twee experimenten werd de complexiteit van de stimulus context en de frequentie van het voorkomen van nieuwe stimuli gevarieerd. Er werden geen verschillen gevonden voor de vroege (snelle) verwerking van nieuwigheid, zoals geïndexeerd door *de anterior N2*. In tegenstelling, de latere verwerking, zoals geïndexeerd door de *novelty P3*, werd sterk beïnvloed door de stimulus context. Nieuwe stimuli eliciteerden alleen een *novelty P3* wanneer de stimuli zowel afwijkend als complex waren ten opzichte van de context waarin zij voorkwamen. De stimulus context speelt dus een bepalende rol in hoe nieuwigheidheid verwerkt wordt: Wanneer complexe of nieuwe stimuli frequent zijn, is de novelty P3 sterk gereduceerd. Een verklaring voor dit patroon van resultaten kan zijn dat de latere evaluatie van nieuwigheid, zoals geïndexeerd door de novelty P3, gevoelig is voor verwachtingen. Mogelijkerwijs genereren nieuwe stimuli alleen een novelty P3 wanneer complexe of nieuwe stimuli niet verwacht worden. Recente, nog niet gepubliceerde, resultaten uit ons lab laten zien dat de novelty P3 inderdaad gevoelig is voor verwachtingen: De novelty P3 was gereduceerd wanneer een nieuwe stimulus op een voorspelbare in plaats van een onvoorspelbare positie in een sequentie werd gepresenteerd.

In tegenstelling tot de *novelty P3* werd de vroege verwerking van nieuwigheid, zoals geïndexeerd door de *anterior N2*, niet beïnvloed door de complexiteit van de stimulus context. De vormkarakteristieken van de nieuwe stimuli zelf speelden daarentegen wel een belangrijke rol: Complexere stimuli eliciteerden een grotere *anterior N2* dan simpele stimuli. De *anterior N2* heeft men in verband gebracht met het detecteren van nieuwigheid in de omgeving, maar het zou dus ook mogelijk kunnen zijn dat de *anterior N2* simpelweg de perceptuele verwerking van de stimulus reflecteert, in plaats van een specifiek detectieproces.

In de experimenten van **Hoofdstuk 5** eliciteerden de nieuwe stimuli ook een zogenaamde *P3b* ERP component. Deze *P3b* wordt geassocieerd met het updaten van het werkgeheugen. Door gebruik te maken van principale componenten analyse (PCA), konden de *novelty P3* en *P3b*, ondanks dat ze overlappen in tijd, goed van elkaar onderscheiden worden. Dit bevestigde dat deze twee ERP componenten een ander proces in het brein reflecteren en door andere factoren beïnvloed worden**.** Een interessante bevinding was dat de *P3b* kleiner was wanneer de nieuwe stimuli frequent waren. Dit is consistent met het idee dat de P3b het updaten van verwachtingen reflecteert, aangezien nieuwe stimuli de verwachtingen minder schenden wanneer de kans op een nieuwe stimulus hoog in plaats van laag is. Deze bevindingen suggereren dat de *novelty P3* het schenden van verwachtingen reflecteert, terwijl de *P3b* het updaten van het werkgeheugen reflecteert.

In **Hoofdstuk 6** werd de rol van aandacht in het verwerken van nieuwigheid onderzocht, zoals gemeten door verschillende electrofysiologische responsen op nieuwigheid. In twee ERP experimenten werden de taakeisen gemanipuleerd terwijl dezelfde sequenties van stimuli

gepresenteerd werden. Proefpersonen zagen nieuwe, bekende en zogenaamde *oddball*-objecten terwijl zij ofwel een gemakkelijke of moeilijke werkgeheugentaak of een visuele oddball-taak deden. Bij deze dubbeltaak dienen de proefpersonen het aantal *oddball* stimuli te tellen. Wanneer aandacht in beslag genomen was door de moeilijke werkgeheugentaak, was d*e anterior N2* groter dan wanneer men een gemakkelijke werkgeheugentaak of de visuele oddball taak deed. Dit suggereert dat de vroege verwerking van de *taak-irrelevante* nieuwe stimuli onderdrukt werd, wanneer proefpersonen aandacht besteedden aan de visuele stimuli. Wanneer aandacht al in beslag genomen was door de moeilijke werkgeheugentaak was de onderdrukking van nieuwe informatie gereduceerd, wat resulteerde in sterkere vroege verwerking van de irrelevante nieuwe stimuli. De verdere verwerking van nieuwigheid was daarentegen gereduceerd, zoals gereflecteerd door een kleine novelty P3, wanneer proefpersonen in beslag werden genomen door de moeilijke werkgeheugentaak.

Eerder werd het aangenomen dat nieuwigheid reflexief (automatisch) de aandacht trekt. Samengevat laten de bevindingen in de huidige dissertatie zien dat de vroege verwerking van nieuwigheid inderdaad relatief onafhankelijk is van de (complexiteit van de) stimulus context waarin men de nieuwe stimuli tegenkomt, maar wel beïnvloed wordt door taakmoeilijkheid. De daaropvolgende evaluatie van nieuwigheid is daarentegen gereduceerd wanneer proefpersonen in beslag genomen zijn door een andere (gemakkelijke/moeilijke) taak en wanneer complexe of nieuwe stimuli verwacht kunnen worden. De bevindingen in deze studies suggereren dat zowel de taakeisen en stimulus context een cruciaal effect hebben op hoe nieuwigheid verwerkt wordt in het brein en wat de consequenties zijn voor gedrag en dat deze effecten dus niet geheel automatisch zijn.

De positieve effecten van nieuwigheid op leren en geheugen

In **Deel 2** van deze dissertatie zijn langdurende effecten van nieuwigheid op leren en geheugen onderzocht. Om te leren hoe men gedrag kan optimaliseren zodat de beste resultaten behaald kunnen worden is het cruciaal om te leren welke specifieke condities leiden tot voordelige en welke tot nadelige uitkomsten. Aangezien nieuwe omgevingen bij definitie vele mogelijkheden tot leren verschaffen, zou het voordelig zijn wanneer leren bevorderd is wanneer men zich in een nieuwe omgeving bevind. Bevindingen van dierenstudies hebben laten zien dat het encoderen van nieuwe informatie inderdaad verbetert gedurende en nadat dieren een nieuwe in plaats van een bekende omgeving verkennen. Enkele studies hebben laten zien dat nieuwe stimuli ook tot een verbetering van het leervermogen kunnen leiden in mensen. In lijn met deze bevindingen, werden in de studie beschreven in **Hoofdstuk 7** geheugenverbeteringen gevonden op een ongerelateerde

woord-leertaak nadat proefpersonen actief een nieuwe versus een bekende virtuele omgeving verkend hadden. Alleen herinneringen ("recall"), waarvoor een proces nodig is wat afhankelijk is van de hippocampus, waren verbeterd, terwijl recognitie, een proces dat relatief onafhankelijk van de hippocampus kan plaatsvinden, niet verbeterd was. De leertaak vond ongeveer tien minuten na het exploreren van de virtuele omgeving plaats, wat suggereert dat de geheugenverbetering door nieuwigheid generaliseerbaar is en over een uitgestrekte periode in tijd kunnen plaatsvinden. Dit is een van de eerste studies die zulke over tijd uitgestrekte effecten van omgevingsnieuwigheid op geheugen in mensen laat zien.

Niet alleen nieuwigheid van de omgeving, maar ook de nieuwigheid van de te leren informatie zelf kan leren verbeteren. Geheugen is meestal beter voor worden die gepresenteerd werden in een nieuw en afwijkend in plaats van een standaard lettertype. Dit effect staat bekend als het Von Restorff, "isolation" of "distinctiveness" effect. In **Hoofdstuk 8** werd zo'n Von Restorff effect, met beter geheugen voor woorden gepresenteerd in nieuwe lettertypes, gevonden voor gezonde proefpersonen, maar niet voor patiënten met de ziekte van Parkinson. Met name wanneer proefpersonen woorden moesten herinneren in plaats van herkennen was het geheugen voor woorden gepresenteerd in nieuwe lettertypes slechter in de patiënten met de zieke van Parkinson. Dit effect ging gepaard een afname in de P3 voor woorden gepresenteerd in een nieuw versus standaard lettertype in pativnten met de ziekte van Parkinson in vergelijking met gezonde controleproefpersonen. Deze ERP component correleerde ook met succesvolle encodering in het geheugen. Dit zou kunnen duiden op een probleem met het encoderen van nieuwe woorden in de patiënten met Parkinson. De ziekte van Parkinson wordt gekarakteriseerd door een degeneratie van dopaminerge cellen in de substantia nigra (SN), wat resulteert in een gebrek aan dopamine in verscheidene regio's in het brein. De abnormaliteiten in leren en geheugen voor woorden gepresenteerd in nieuwe lettertypes in patiënten met de ziekte van Parkinson werden niet geremedieerd door dopaminerge medicatie. Het ontbreken van effecten van dopaminerge medicatie in de patiënten suggereert dat dopamine geen cruciale rol speelt bij het leren van nieuwe informatie, maar dit zou niet verklaren waarom de patiënten minder woorden herinnerden. Deze resultaten zouden verklaard kunnen worden door een zogenaamde overdosis aan dopamine in de hersengebieden geassocieerd met de verwerking van nieuwe informatie en het encoderen van nieuwe informatie in het geheugen, zoals de hippocampus en mediale temporale cortex. Deze hersengebieden interacteren sterker met het ventrale striatum – een gebied dat nog niet sterk geaffecteerd is in de vroege stadia van de ziekte van Parkinson – dan met het dorsale striatum, wat al geaffecteerd in vanaf het begin van de ziekte. Andere verklaringen kunnen echter niet uitgesloten worden. Bijvoorbeeld, andere abnormaliteiten in het brein of verschillen in de strategie gebruikt bij het herinneren zouden de geobserveerde tekortkomingen in leren en geheugen in patiënten in vergelijking met gezonde controleproefpersonen kunnen verklaren.

In **Hoofdstuk 7** werden alleen verschillen in herinnering, maar niet voor recognitie (herkenning) gevonden, nadat proefpersonen een nieuwe versus een bekende omgeving verkend hadden. Idem dito herinnerden patiënten met de ziekte van Parkinson in **Hoofdstuk 8** alleen minder woorden dan de gezonde controleproefpersonen, terwijl het herkenningsvermogen niet aangetast was. Bewuste herinneringen zijn afhankelijk van de hippocampus, terwijl van recognitie gedacht wordt dat het vooral afhankelijk is van de perirhinale cortex. De bevindingen in **Hoofdstuk 7** zouden verklaard kunnen worden doordat omgevingsnieuwigheid de hippocampus activeert, waarbij dopamine vrijkomt door de wederkerige verbinding tussen de hippocampus en substantia nigra/ventral tegmental area (SN/VTA; een regio in het middenbrein waar zich veel dopaminerge cellen bevinden), zodat de binnenkomst van nieuwe informatie in het langetermijngeheugen gereguleerd wordt en de latere herinnering, maar niet de latere recognitie verbeterd wordt. De bevindingen in **Hoofdstuk 8** van een Von Restorff effect zouden verklaard kunnen worden door eenzelfde mechanisme. Een gebrek van een effect door dopaminerge medicatie in de patiënten met de ziekte van Parkinson maakt het echter moeilijk om de exacte rol van dopamine in dit proces te interpreteren. Bovendien is het momenteel onduidelijk of er een nieuwigheidssignaal van de hippocampus de SN/VTA activeert of dat nieuwigheid de SN/VTA direct activeert. Ook zijn er nog nooit directe effecten van long-term potentiation, een proces geassocieerd met het vormen van herinneringen, in de hippocampus van mensen gemeten. Meer onderzoek is nodig om de rol van dopamine en de verbinding tussen de hippocampus en SN/VTA in het verbeteren van geheugen in mensen rechtstreekser te onderzoeken.

Slotbeschouwing

Ter conclusie, nieuwigheid wekt een groot aantal responsen op in het brein, waarbij een variëteit aan cognitieve processen beïnvloed wordt. Nieuwigheid ligt ten grondslag aan leren, affecteert aandacht, en perceptie en beïnvloed gedrag. De resultaten beschreven in deze disseratie hebben laten zien dat nieuwigheid een concept is wat dicht bij de kern van veel cognitieve processen ligt en daarom een centrale rol in de cognitieve neurowetenschap verdient.

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Author Publications

Schomaker, J., Meeter, M. (in preparation). The benefits of the new: Short- and long-lasting effects on brain and cognition.

Schomaker, J., Berendse, H.W., Foncke, E.M.J., van der Werf, Y.D., van den Heuvel, O.A., Theeuwes, J., & Meeter, M. (2014). Novelty processing and memory formation in Parkinson's disease**.** *Neuropsychologia, 62,* 124-136*.*

Schomaker, J., van Bronkhorst, M.L.V., & Meeter, M. (2014). Exploring a novel environment improves motivation and promotes recall of words. *Frontiers in Psychology, 5,* 918.

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Schomaker, J., & Talsma, D. (2009). The relationship between response times and the strength of top-down attentional control: *An ERP study. Journal of European Psychology Students 1*(1).