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High tide or low tide

Reliving memories of emotional events

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Um. I came back from vacation, um, to Italy. Then I got back on the train. I really missed my boyfriend a lot. And then I arrived at his house. And he told me he just wanted to go for a walk, so I was fine with that. And then he wanted to talk about something, and I still didn't get it yet. So we walked along the canal in Utrecht, and then all of a sudden he started saying that he didn't feel it anymore. And that he felt it less than before. And that he wanted to change something or something. I don't remember exactly what he said. But I didn't get it the whole time. Then at some point it became clear that it was over for him. Then I begged him to try again, but he wouldn't. He felt nothing anymore. Then he started saying things like, "You really are a wonderful person." And this and that. And: "Maybe we can try again in five years." But I just sat there. I just couldn't believe what was happening. I was just thinking all the time, 'this isn't happening. This isn't happening, it isn't happening.' Yes, it wasn't until I realized it was happening that I cried and that was much later. And when I went home after the walk, he also tried to give me a hug. But I just completely froze. I let my hands hang at my sides. I just kept looking at the wall in front of me as he tried to hug me. Then I was on the street and I didn't know what to do with my life. All the time I just thought: 'what happened now, what, what is this? This just can't be true.'

Um. I was in Australia and I had lived on a, um, farm in the North for a very long time. And then we went south, and then we arrived at the island where we would stay and we arrived at um, the huts where we would sleep. And we saw the sea again in such a long time and it was so beautiful. The sun was just setting and the whole sky was pink. And we ran to the sea with all our clothes still on, and we took off our clothes and dived into the sea. And it was super shallow but the water was very nice and warm, and um, yes. The sky was all pink and it reflected so clearly on the water, pink and blue, and it was really beautiful. And I loved being there with people that I had come to know so well and who now felt like family. And it just felt like we were welcomed, um, on that island. That was a very nice experience.

Chapter 1

General Introduction

People have the remarkable ability to travel back in time and relive events that they experienced in the past. We don't need technology or tools except for our brain and body to re-experience the happiest and proudest moments of our lives or to feel the keen sting of lost love again. As the examples of memories throughout this dissertation illustrate, people can often remember past events in great detail. Thinking back on happy experiences might be a tremendous source of joy and confidence, while remembering negative moments of a past disappointment or failure might cause us to be more cautious or to try harder the next time. These are examples of emotional episodic memories, that is, memories of emotional events from our personal past. However, episodic memories do not only allow us to dwell in the past, they also bear valuable information that can guide our behaviour in the present and the future (Moulton & Kosslyn, 2009; Schacter, Addis, & Buckner, 2007). When memory processes become distorted, they can have a significant impact on mental health. For example, people with depressive symptoms have difficulties remembering positive events (Bower, 1981; Everaert, Vrijssen, Martin-Willett, van de Kraats, & Joormann, 2022; Matt, Vázquez, & Campbell, 1992) and they might remember their past excessively sombre, focusing on past pain and failures rather than on joy and success (Dalgleish & Werner-Seidler, 2014; Gotlib & Joormann, 2010). Such memory distortions may contribute to the onset and maintenance of mental disorders (Askelund, Schweizer, Goodyer, & van Harmelen, 2019; Hallford, Rusanov, Yeow, & Barry, 2021, 2022; Young, Drevets, Bodurka, & Preskorn, 2016). Given the assumed impact of emotional episodic memories on people's behaviour and mental health, this dissertation aims to provide insights into the emotional processes that are elicited when people remember past events, and how these processes are altered in people with depressive symptoms.

Episodic memory: The holistic reliving of past events

The ability to remember specific personally experienced events is called episodic memory (Tulving, 2002). The remembered episodes usually involve multiple pieces of information on the content of the memory (the what: e.g., going swimming with specific people) and its spatiotemporal context (the where and when: e.g., on an Australian island on a summer evening in 2015). When thinking back on past events, the different pieces of information are assumed to automatically fall back into place and form a coherent mental picture, in contrast to an agglomeration of incohesive and isolated mental pictures. That is, remembering one detail of an episode usually elicits the remembrance of other details that belong to the episode, while preserving spatial, temporal, and other properties of the external world (Horner, Bisby, Bush, Lin, & Burgess, 2015; Tulving, 2002; Wilson, 2002). This simultaneous retrieval of various elements that comprise a past event is usually referred to as holistic reliving.

Next to holistic reliving, episodic recollection is characterized by an 'experiential flavour', which results from the subjective awareness of oneself in time (autonoetic consciousness; Gardiner, 2001; Tulving, 2002). When remembering a past event, it is supposed to feel as if one experiences it again. This experiential flavour closely intertwines episodic memory with mental imagery, which refers to the sensation of perception in the absence of an actual percept (often explained as "seeing with the mind's eye"; Andrade, May, Deeprose, Baugh, & Ganis, 2014; Moulton & Kosslyn, 2009; Pearson, Naselaris, Holmes, & Kosslyn, 2015). Mental imagery allows to draw on information from the past to

simulate experiences (Moulton & Kosslyn, 2009; Pearson et al., 2015). For example, when remembering how we went swimming during a sunset, we can again see the beautiful sky and its rose and blue-toned reflection in the water. We might also imagine the sensation of warm water on our skin or the smell of a fresh, salty sea breeze. While episodic recollection specifically refers to simulating and reliving past events, imagery can also be future-oriented and concern entirely fictive events. Therefore, episodic recollection is considered a special case of imagery that focuses on simulating a past event.

Understanding episodic recollection as mental imagery brings forth important notions. Since imagery is a constructive process that allows to employ and manipulate mnemonic information, episodic recollection should also be at least partially constructive. Consequently, remembering events does not necessarily have to veridically re-instate past experiences but can deviate from the original experience, in line with other contemporary theories on episodic memory (Schacter, 2012). Moreover, mental imagery is supposed to critically involve affective processes (Moulton & Kosslyn, 2009). When simulating past events, people might partially re-instate affective processes as part of the simulation. In line with this idea, imagery processing of fictitious or remembered events elicits stronger self-reported affective responses than processing similar information verbally (Mathews, Ridgeway, & Holmes, 2013; Nelis, Holmes, Palmieri, Bellelli, & Raes, 2015; O'Donnell, Di Simplicio, Brown, Holmes, & Burnett Heyes, 2018). The notion that imagery and episodic recollection involves affective processes might be crucial to understand the role of episodic memory in mental health and psychopathology.

The importance of affective responses when remembering past events

Affective processes are thought to be crucial for imagery and episodic memory (Ji, Burnett Heyes, MacLeod, & Holmes, 2016; Kensinger & Ford, 2020; Moulton & Kosslyn, 2009; Talmi, 2013). People can often remember emotional events in remarkable detail, but they rarely vividly remember neutral episodes of the past (Kensinger & Ford, 2020; Talmi, 2013). For example, we might remember the positive experience of swimming into the sunset in Australia our entire lives, but we will quickly forget an uneventful bus ride or what we had for lunch on a particular day. However, studies on episodic memories that consider affective processes usually investigate the effect of emotions on the encoding, consolidation, and subsequent retrieval of declarative components of episodic memory (Bower, 1981; Kensinger & Ford, 2020; LaBar & Cabeza, 2006; Matt et al., 1992). A lot less is known about the effects that episodic memories have on people's emotions.

Componential emotion theories (Frijda, Kuipers, & ter Schure, 1989; Scherer, 2009) provide a framework for investigating affective responses to memories and how these could affect behaviour. They describe emotions as an interaction of multiple elementary processes that include an elicitor, appraisals of this elicitor, motivational change or action tendencies, psychophysiological responses and motor expressions, and finally subjective feelings that emerge from a combination of the other components. That is, emotional processes critically involve a motivational component or action tendency that determines how people act and re-act in an everchanging environment. Emotional responses can change the propensity to act in multiple ways, relying on different properties of affective processes. First, positive and negative valence indicate whether something is desirable or undesirable and as a consequence whether we should approach or avoid the elicitor of the emotional

response (Elliot, Eder, & Harmon-Jones, 2013; Lang & Bradley, 2010; Tamir & Ford, 2012). Second, whereas categorical differences of emotional valence indicate the directionality of our actions (approach or avoid), the intensity of such emotions may index how important it is to adjust our behaviour. The more intense the emotions are that past episodes elicit, the more likely they might be to determine our decisions and behaviour in the future. Finally, emotional processes include peripheral psychophysiological responses such as changes in heart beat (Pace-Schott et al., 2019) or pupil dilation (Snowden et al., 2016; Vries, Duken, Dzialija, Kindt, & Ast, 2022) that mobilize resources and physically prepare the body to respond in challenging situations (Elliot et al., 2013; Lang & Bradley, 2010; Löw, Lang, Smith, & Bradley, 2008; K. Roelofs, 2017; van der Wel & van Steenbergen, 2018). Consequently, affective processes while reliving episodic memories, in particular psychophysiological responses, might be an important component of episodic recollection and could explain how memories affect people's behaviour and well-being in the present and the future.

Episodic memory distortions in depression

Based on the assumption that affective processes while reliving episodic memories are crucial for motivating behaviour, it is likely that biased affective responses to memories might play a key role in memory distortions in psychopathology (Barry, Hallford, & Takano, 2021; Dalgleish & Hitchcock, 2023). However, most research on memory distortions focused on alterations of the content of episodic memories (Barry et al., 2021, 2022) (Dalgleish & Werner-Seidler, 2014; Hallford et al., 2022; Hitchcock, Werner-Seidler, Blackwell, & Dalgleish, 2017). For instance, people who suffer from major depression are thought to experience an overgeneral memory bias, that is, they have difficulties accessing memories of specific personal events in detail (Barry et al., 2021; Williams et al., 2007). When they think back to the past, they recall generic facts about their lives (e.g., I was not happy in school) or repeated events (e.g., I always used to go for a walk with my dog in the afternoon) rather than vividly reliving specific past experiences. A different line of research suggests that people with depression experience a negativity bias. They have difficulties remembering positive information that is incongruent with their depressive state, but they can remember negative information with great ease (Bower, 1981; Everaert et al., 2022). Overgeneral memory and negativity bias theories both predict diminished positive memories, but they disagree on whether negative memories are diminished or enhanced in depression. Therefore, it will be important to investigate how exactly positive and negative memories are altered in people who suffer from depressive symptoms. Regardless of these outstanding questions, the severity of episodic memory distortions can predict the onset, duration, or remission from depression and are therefore likely to be a contributing factor in the aetiology and maintenance of depressive disorders (Askelund et al., 2019; Sumner, Griffith, & Mineka, 2010). Memory distortions also persist when people have recovered from a depressive episode, which indicates that they might be a risk factor for subsequent depressive episodes (Hallford et al., 2022; Young, Siegle, Bodurka, & Drevets, 2016).

Next to establishing alterations in the accessibility and content of positive and negative memories in depression, it is important to investigate the effect of such memories on affective processes. For example, some studies suggest that people with depressive symptoms do not feel positive when mentally reliving supposedly positive experiences and they cannot use memories to

repair negative moods (Joormann & Siemer, 2004; Joormann, Siemer, & Gotlib, 2007). These biases may have detrimental consequences beyond the moment when a memory is retrieved. Specifically, if positive memories do not elicit strong positive affect including psychophysiological responses, this may reduce people's motivation to seek out similar events in the future, ultimately leading to a lack of engagement in rewarding, and joyful experiences (Dimidjian, Martell, Addis, & Herman-Dunn, 2008; Millgram, Joormann, Huppert, Lampert, & Tamir, 2019; Pizzagalli, 2014). Likewise, overly intense negative memories may have detrimental consequences. Memories of being hurt might push one away from engaging in meaningful and beneficial relationships, and memories of failures can cause one to not try again. Given that most studies on memory distortions in depression focused on how patients retrieve specific episodic information without investigating affective processes, much remains unknown about how affective process during memory retrieval are distorted in depression.

The malleability of emotional episodic memories

Even though memories allow us to relive past events, they are not always veridical replays of our personal history as if we recorded them with a camera. What people remember and how it makes them feel may differ depending on their current mood (Bower, 1981), on the situation they retrieve the memory in (Smith & Vela, 2001), on constructive imagery processes (Schacter, 2012; Schacter et al., 2012), or on the passage of time (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Robin & Moscovitch, 2017). Research with animals even suggests that the affective tone of memories can drastically and permanently change when the memory is retrieved in combination with new information (Grella et al., 2022; Haubrich et al., 2015; Redondo et al., 2014). For example, animals that avoided a certain context because they had learned that it predicted shocks, suddenly approached the same context if they learned that it was associated with a reward (food or a potential mate). Importantly, this change from avoidance to approach behaviour only occurred when the memory of the feared context was reactivated prior to new reward learning (either by artificially activating the memory engram through optogenetics or by placing the animal in the feared context; Haubrich et al., 2015; Redondo et al., 2014). Also research with human participants has shown that it is possible to change fear memories to a more benign level (Else, van Ast, & Kindt, 2018; Kindt, Soeter, & Vervliet, 2009; Sevenster, Beckers, & Kindt, 2013). However, evidence for changes of the affective tone of memories is mostly limited to relatively simple associative fear memories (e.g., learned associations between a picture and a mild electric shock). Therefore, it is not certain if the affective tone of more complex episodic memories can likewise change due to new learning. It is also not clear whether the possibility of affective change is limited to fear or can be extended to other emotions such as joy or sadness that play a role in mental disorders like depression.

If the affective tone of complex episodic memories was malleable, it would provide new avenues to understand the rise and possibly fall of emotional memory distortions in psychopathology. For example, on the trajectory towards depression, the reliving of past experiences in a negative mood might distort the episodes, making them excessively negative and vivid. This may ultimately change how one views their past, themselves, and the world in general. On the other hand, if harmful negative memories can become more positive, or if people learn to relive positive memories more vividly including strong affective responses, this might have positive effects on mental health.

Episodic memories in the lab: from neutral word lists to naturalistic emotional events

Even though theories of episodic memory emphasize the holistic and experiential nature of episodic memory, current approaches might not fully capture these core aspects of episodic recollection. For instance, holistic reliving is traditionally operationalized as the concurrent retrieval of a series of words or pictures, which facilitates a high degree of experimental control over the learned events but limits external validity (Bisby, Horner, Bush, & Burgess, 2018; Horner et al., 2015; Tulving & Thomson, 1973). While this approach allows for strong causal conclusions within specific study parameters, the events that people experience and remember in their lives are undoubtedly richer and more complex than a combination of words on a computer screen or a piece of paper. To reach a comprehensive understanding of the holistic re-experience of past episodes it will be necessary to complement highly controlled but reductionist approaches with studies of more naturalistic events.

Relatedly, current approaches to investigating episodic memories do not capture the affective responses that memories elicit because they mainly rely on neutral stimuli (R. T. Cohen & Kahana, 2022). Other studies use mildly emotional stimuli such as words with negative connotations, but these are unlikely to elicit affective responses that are comparable to complex emotional events like a wedding or a break-up (Danion, Kauffmann-Muller, Grangé, Zimmermann, & Greth, 1995; W. H. Liu, Wang, Zhao, Ning, & Chan, 2012). It will therefore also be important to investigate memories of intense positive and negative events while measuring affective processes. In other words, it is important to investigate emotional events as people experience them in their lives, rather than only investigating lab-based memories of relatively neutral combinations of words and pictures (Maguire, 2022).

Given that bodily responses indicate motivational value and are closely linked to action tendencies, research would particularly benefit from incorporating psychophysiological measures when investigating affective processes during episodic memory retrieval. Research on arousing fear and trauma memories already indicates that memories can elicit affective psychophysiological responses that can prepare or motivate behaviour, for example changes in skin conductance, heart rate or pupil dilation (Leuchs, Schneider, & Spoomaker, 2019; Pole, 2007; Vries et al., 2022). However, these findings cannot readily be translated to other types of memories, for example of joyous or sad events. First, fear and trauma memories are mainly characterized by high levels of arousal, which is not necessarily the case for sad or happy memories. Relatively little attention has been dedicated to affective processes beyond arousal in memory research and memory valence was often disregarded as less important (Bowen, Kark, & Kensinger, 2018; Talmi, 2013). Second, fear and trauma memories can be qualitatively different to emotional episodic memories in terms of the psychobiological processes involved (Ehlers & Clark, 2000; for a different account, see: David C. Rubin, Berntsen, & Bohni, 2008). For instance, fear memories usually represent a preparatory function in the face of an anticipated threat, which is unlikely to be the case when someone remembers a happy or sad episode (Fanselow, 1994; Kreibitz, Wilhelm, Roth, & Gross, 2011).

Since positive and negative episodes can be characterized by other affective properties than arousal, psychophysiological indices that are being used in fear memory research are not suited to quantify the affective impact of negative and positive episodic memories (e.g., skin conductance and

heart rate). However, facial expressions of emotions do allow to quantify the valence of emotional experiences. People typically smile when they experience positive affect and they frown when they experience negative affect (Larsen, Norris, & Cacioppo, 2003). These smiling responses depend on facial muscles, the activity of which can be measured with facial electromyography (fEMG). Crucially, stronger smiling and frowning responses correspond to stronger positive and negative affect, respectively (Larsen et al., 2003). Therefore, facial expressions can be investigated as an indicator of the affective value of complex positive and negative experiences, regardless of arousal. Indeed, early work on mental imagery found that imagining positive and negative events elicited smiling and frowning responses, respectively (Schwartz, Fair, Mandel, Salt, & Klerman, 1976; Schwartz, Fair, Salt, Mandel, & Klerman, 1976). Facial expressions might also be a particularly valuable readout of affect because they are supposedly closely linked to action tendencies and can therefore provide insights into the motivational value of remembered episodes (Adams, Ambady, Macrae, & Kleck, 2006; Frijda & Tcherkassof, 1997; Kroczeck, Lingnau, Schwind, Wolff, & Mühlberger, 2021).

While it is of course also important to consider subjective feelings of individuals when they relive memories, investigating psychophysiological responses as a complementary read-out of affective processes bears several advantages over only measuring self-reported emotions. Firstly, self-reports are prone to experimental biases such as demand effects, especially when experimental manipulations are not easily concealed (Sharpe & Whelton, 2016). Psychophysiological measures are more automatic and objective measures of affect and therefore less prone to experimental biases (Kreibig, Wilhelm, Roth, & Gross, 2007; Ray, McRae, Ochsner, & Gross, 2010). Secondly, psychophysiological measures provide more direct insights into basic affective and motivational processes, because self-reports rely on higher order cognitive processes that can be influenced by factors that are not directly related to the initial, basic affective response. For example, when depressed participants remember a positive event, the memory might initially elicit a normal positive affective response. However, when they are asked how the memory makes them feel, they might reflect on the memory and take their current self-image of being a depressed person into account, ultimately reporting that the memory does not make them feel positive because they do not consider themselves a happy person (Joormann & Siemer, 2004; Joormann et al., 2007). Finally, psychophysiological measures allow to quantify affective responses without interfering with memory retrieval. While facial electromyography can be measured continuously during the encoding and retrieval of episodes, self-reports require the conscious reflection and labelling of emotions, which would interrupt retrieval processes (or self-reports must be given after retrieval, rendering them susceptible to biases in retrospection). In sum, psychophysiological indices of affect allow to directly measure relatively automatic affective responses and provide important complementary information to self-reported emotions.

Aim and outline of the dissertation

This dissertation investigates affective responses to emotional episodic memories upon their retrieval, how these responses are altered in people with mental health problems, and how the affective tone of memories might be malleable and therefore a target for the prevention and treatment of psychopathology. Current theories on emotional episodic memories provide a relatively

coherent picture of what reliving emotional events might entail, and how episodic memories affect people's behaviour and mental health. However, there is also some inconsistency across theories (particularly regarding memory distortions in depression) and many theoretical claims still lack empirical support. Together with my supervisors and collaborators, I therefore developed novel paradigms to investigate memories of naturalistic emotional events like the ones that people experience in real-life. In all paradigms, we used fEMG as an index of automatic affective responses during memory retrieval. Thereby, we hope to shed new light on the vivid, holistic, and emotional reliving of episodic memories. To strengthen the empirical grounding of current theories on episodic memory and imagery, we aimed to adhere to the best scientific practices that are currently available, which includes but is not limited to open science practices such as replication of results with new data, preregistration, and open data (Munafò et al., 2017; Nosek et al., 2019).

In **Chapter 2**, we investigated whether remembering naturalistic emotional experiences such as sad or happy events re-elicits corresponding affective psychophysiological responses. We developed a naturalistic paradigm that mirrors real-life experiences to capture the holistic and experiential nature of episodic memories. Specifically, participants viewed positive, negative, and neutral movie scenes, and relived these scenes on a subsequent day as vividly as possible. While participants viewed and remembered emotional scenes, we measured facial expressions of positive and negative affect. Chapter 2 also provided a foundation for subsequent studies (including Chapter 3 and 4) by introducing a naturalistic paradigm that embraces the complex nature of episodic memories and by validating fEMG as a psychophysiological measure of memory emotionality.

Chapter 3 evaluates evidence for prominent theories that describe memory distortions in depression. Specifically, overgeneral memory and negativity bias theories agree that people with depressive symptoms retrieve positive memories with reduced episodic detail and blunted affective reactions, but disagree whether they retrieve diminished or enhanced negative memories. We asked dysphoric and non-dysphoric participants to relive positive, negative, and neutral personal memories, and assessed the amount of episodic detail that they retrieved as well as the affective responses that were elicited by positive and negative memories (measured with fEMG and self-reported feelings). By resolving theoretical discrepancies regarding key memory distortions, Chapter 3 contributes to the ongoing development of therapeutics that aim at alleviating the burden of depression by treating memory distortions.

In **Chapter 4**, we investigated whether neutral episodic memories can become emotional due to memory updating processes in a three-day paradigm. On Day 1, participants viewed neutral movie scenes. On Day 2, they remembered each episode before they viewed a new emotional scene from the same movie. On Day 3, participants again remembered the episodes from Day 1. We tested whether the initially neutral Day 1 memory retroactively acquired a positive or negative affective tone with fEMG and self-reported feelings. If memories can become more negative due to updating processes, this may explain how excessively negative memories arise in mental disorders. Conversely, if memories can become more positive, they may provide a valuable target for interventions to improve mental health.

Finally, **Chapter 5** summarizes findings from the empirical studies and discusses considerations in the context of evidence derived from the three experiments. Specifically, I will reflect on the role of

psychophysiological expressions of affect when reliving emotional episodic memories, and why such expressions might deviate from subjective feelings. I will also emphasize the importance of positive episodes in mental health and psychopathology. Finally, I will discuss some considerations regarding implementing open science practices in experimental research and future avenues for research on emotional episodic memories.