Chapter 5.11 Content Reinstatement

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Please provide a concise abstract for the chapter (100–250 words).		

Episodic remembering is fundamentally related to the reinstatement of patterns of neural activity evoked during the initial encoding of memories. This chapter reviews the phenomenon of reinstatement, with a focus on reinstatement of content information ('what' is being remembered). It first reviews evidence for, and properties of, content reinstatement across different brain regions (sensory cortex, the hippocampus, fronto-parietal cortex). Next, it considers how reinstatement is related to objective and subjective behavioral measures of memory retrieval, including memory accuracy and memory vividness. Finally, it considers how memory reinstatement influences reinstated memories, separately considering reinstatement that occurs during deliberate retrieval, memory encoding, and during offline periods of rest or sleep.

Please suggest 5–10 keywords that can be used for describing the content of the chapter.

reinstatement, retrieval, reactivation, multivoxel pattern analysis, remembering, hippocampus, episodic memory

Introduction

"Brain-matter, we may imagine, is like a fluid jelly, in which impressions may be easily made, but are soon closed over again ... But it may occur here, just as in other gelatinous substances, that an impression will vibrate throughout the brain, and send waves into other parts of it. In cases of this sort, although the immediate impression may fade out quickly, it does modify the cerebral mass; for the paths it makes there may remain, and become so many avenues through which the impression may be reproduced if they ever get excited again."

- William James (1914)

What William James speculated, well over a century ago, is that experiences leave an impression on the brain, and that these impressions may become active again, or *reinstated*. James explicitly linked this neural reinstatement process to memory, long before tools or methodologies were in place to confirm this idea. In the time since James speculated on the physical basis of memory, there have been remarkable advances in methods for observing and recording the process whereby impressions left by sensory experiences are 'reproduced' during acts of remembering (Danker & Anderson, 2010; Rissman & Wagner, 2012). Although memory takes many forms, the present chapter primarily focuses on *episodic memory* and the reinstatement of the *content* of memories—that is, information about 'what' is being remembered. Reinstatement of contextual information ('where' or 'when' something occurred) is outside the scope of the chapter, but is considered elsewhere in this volume (see, for example, Chapter 5.12).

The first part of the chapter considers the specific brain regions in which content reinstatement has often been observed along with some properties of reinstatement in these regions. The second part of the chapter considers how neural measures of content reinstatement are related to objective and subjective behavioral measures of memory retrieval—to the phenomenology of remembering. The final part of the chapter considers the consequences of reinstatement, emphasizing that content reinstatement is not only a correlate of remembering but that reinstatement plays an active role in influencing future remembering.

The distributed nature of content reinstatement

Memory reinstatement is a distributed neural phenomenon in two senses. First, reinstatement has been observed across a wide variety of brain regions—from the hippocampus to sensory cortex to association cortex. Thus, the phenomenon of reinstatement is distributed across brain regions. Second, within each of these brain regions, memory reinstatement has frequently been measured as a *distributed pattern of neural activity* (K. A. Norman, Polyn, Detre, & Haxby, 2006; Rissman & Wagner, 2012). In particular, multivariate pattern analyses—which have surged in popularity in the past 10-15 years—allow for the identification of relatively fine-grained patterns of distributed activity (typically in fMRI or EEG) that are associated with specific categories of remembered stimuli (e.g., faces vs. scenes), specific stimuli from a category (e.g., a particular face) or even specific features of a remembered stimulus (e.g., color). Below, we consider properties of reinstatement across several brain regions (sensory cortex, frontoparietal cortex, the hippocampus) with many of the findings based on multivariate pattern analyses applied to functional data from these brain regions.

Sensory cortex

"I name the image of the sun, and that image is present in my memory. For I recall not the image of its image, but the image itself."

- St. Augustine (1909)

One of the most remarkable properties of memory is that it allows for the re-experiencing of sensations in the absence of the original physical stimulus that produced those sensations. As such, research on content reinstatement has largely focused on sensory cortical areas. That is, are the sensory cortical responses evoked during perceptual experience reinstated when that perceptual experience is remembered?

In humans, evidence for sensory reinstatement came from early neuroimaging studies which used memoranda from distinct sensory modalities. For example, in a seminal study (Wheeler, Petersen, & Buckner, 2000), participants first studied words paired with either pictures or sounds. During retrieval, participants were shown the words again and asked to recall the associated picture or sound. Recalling pictures was associated with activation in some of the same parts of visual cortex that were active during the encoding of pictures; likewise, recalling sounds was associated with activation in some of the same parts of auditory cortex that were active during the encoding of auditory cortex that were active during the encoding of sounds. In other words, memory retrieval was associated with modality-specific reinstatement. Similar examples of modality-specific reinstatement have been observed in motor, premotor, olfactory, and somatosensory regions (Goldberg, 2006; Gottfried, Smith, Rugg, & Dolan, 2004; Halpern, 1999; Nyberg, Habib, McIntosh, & Tulving, 2000; Nyberg et al., 2001; Wheeler & Buckner, 2003; Wheeler et al., 2000, 2006; Zatorre, Halpern, Perry, Meyer, & Evans, 1996).

Reinstatement has also been measured by comparing different classes of stimuli within a given modality. The most common example of this has been reinstatement of visual category information in ventral temporal cortex. For example, the fusiform face area and the parahippocampal place area are two regions of ventral temporal cortex that exhibit relatively selective responses to visual images of faces and scenes, respectively. Critically, this stimulus selectivity in high-level visual cortex is preserved (or reinstated) when images are retrieved from memory (Kuhl, Rissman, Chun, & Wagner, 2011; Liang & Preston, 2017; Mack & Preston, 2016; O'Craven & Kanwisher, 2000; Polyn, Natu, Cohen, & Norman, 2005; Ranganath, 2004; Schultz et al., 2019).

While there are many examples of reinstatement in high-level visual cortical areas, one interesting question is whether reinstatement also occurs in earlier sensory regions. Early neuroimaging studies of mental imagery found that the act of imagining an image evokes activation in primary visual cortical areas (Kosslyn & Thompson, 2003), suggesting that reinstatement may extend into these early sensory regions. Indeed, more recent studies that have used multivoxel pattern analysis methods have confirmed that reinstatement of stimulus-specific information occurs even in early visual cortex. For example, in a study by Hindy and colleagues (Hindy, Ng, & Turk-Browne, 2016), participants first learned sequences of visual fractals and were then shown partial sequences (**Figure 1A**). These partial sequences triggered reinstatement of the sequence outcomes (i.e., the remembered fractals) in early visual cortex (V1-V2) (**Figure 1B**). Similarly, the remembered orientation of visual gratings can be successfully decoded from

early visual cortical areas (V1-V3) (Bang, Sasaki, Watanabe, & Rahnev, 2018; Bosch, Jehee, Fernandez, & Doeller, 2014). Thus, while somewhat more limited than evidence of reinstatement in high-level visual areas, there is compelling evidence that reinstatement occurs even in early visual cortical areas.

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Hippocampus

In rodent studies of reinstatement, the hippocampus has been a major focus of interest (see also Chapter 5.7). In large part, this reflects the prevalence of, and relative ease of recording from, place cells in the rodent hippocampus. Specifically, place cells that fire in specific sequences during spatial navigation will 'replay' the same firing sequences during periods of rest or sleep (Carr, Jadhav, & Frank, 2011; Z. Chen & Wilson, 2017; O'Neill, Pleydell-Bouverie, Dupret, & Csicsvari, 2010; Rasch & Born, 2013; Wilson & McNaughton, 1994). Although reinstatement of spatial contexts is outside the scope of the present chapter, the findings from rodent studies of spatial reinstatement reveal fundamental points that also apply to content reinstatement in human episodic memory: (1) reinstatement does occur in the hippocampus (Carr et al., 2011; O'Neill et al., 2010), and (2) the hippocampus coordinates or triggers reinstatement in neocortical areas (Ji & Wilson, 2007; Khodagholy, Gelinas, & Buzsáki, 2017; Siapas, Lubenov, & Wilson, 2005; Sirota & Buzsáki, 2005). We consider each of these points below.

In humans, evidence for reinstatement in the hippocampus is somewhat limited compared to evidence for reinstatement in sensory cortical areas. There are two likely reasons for this. First, place cells (which have been the focus in rodent studies) are less accessible to neuroimaging methods (fMRI, PET, or scalp EEG) that have commonly been used to study reinstatement in humans. That said, there is some evidence for reinstatement in the human hippocampus in the context of spatial navigation tasks (Brown et al., 2016; Miller et al., 2013). Second, whereas many studies of content reinstatement in humans have exploited visual category selectivity (e.g., faces vs. scenes) in ventral temporal cortex, the hippocampus exhibits little to no selectivity to visual categories (Huffman & Stark, 2014; LaRocque et al., 2013; Liang & Preston, 2017). Thus,

evidence for content reinstatement in the human hippocampus mostly comes from examples of stimulus-specific reinstatement (as opposed to reinstatement of broad categories of information). For example, in a study that used intracranial recordings in patients being monitored for epileptic activity, individual neurons within the hippocampus were identified that exhibited selectively to specific film clips and this selectivity was preserved (reinstated) during free recall of the movies (Gelbard-Sagiv, Mukamel, Harel, Malach, & Fried, 2008). Several other studies have reported content reinstatement in the human hippocampus, with a consistent finding being that the reinstatement effects are stimulus-specific (Chadwick, Hassabis, & Maguire, 2011; Chadwick, Hassabis, Weiskopf, & Maguire, 2010; Hindy et al., 2016; Mack & Preston, 2016; Schapiro, McDevitt, Rogers, Mednick, & Norman, 2018; Tompary, Duncan, & Davachi, 2016).

With respect to the role of the hippocampus in coordinating or triggering reinstatement in other brain regions, several fMRI studies have found that hippocampal activation during memory retrieval is correlated with reinstatement in neocortical areas (Bosch et al., 2014; Gordon, Rissman, Kiani, & Wagner, 2014; Mack & Preston, 2016; Staresina, Henson, Kriegeskorte, & Alink, 2012). While these observations suggest a potential causal role of the hippocampus in orchestrating cortical reinstatement, the poor temporal resolution of fMRI makes it difficult to establish whether hippocampal activation temporally precedes cortical reinstatement. However, intracranial EEG studies have provided critical insight into these temporal dynamics. In particular, both increases in hippocampal firing rate (Staresina et al., 2019) and hippocampal sharp-wave ripples (Y. Norman et al., 2019) have been shown to temporally precede cortical reinstatement (i.e., reinstatement outside the hippocampus). Indeed, the relative strength of hippocampal firing rate predicts the fidelity of cortical reinstatement (Staresina et al., 2019). Moreover, cortical oscillations during successful memory retrieval are temporally coupled to oscillations in the medial temporal lobes (Vaz, Inati, Brunel, & Zaghloul, 2019). Collectively, these findings are consistent with the idea that the hippocampus plays a critical role in guiding or orchestrating cortical reinstatement (Hindy et al., 2016).

Cortical reinstatement during memory retrieval has also been linked to hippocampal responses during memory *encoding*. For example, fMRI measures of hippocampal activation during encoding predict the strength of reinstatement at retrieval (Danker, Tompary, & Davachi, 2016). Similarly, the fidelity of ventral temporal stimulus representations during encoding is correlated not only with the fidelity of reinstatement during retrieval, but also with the strength of

hippocampal activation at encoding (Gordon et al., 2014). Intracranial measures from the human hippocampus also indicate that sharp-wave ripples (Y. Norman et al., 2019) and oscillatory power (Lohnas et al., 2018) in the hippocampus during memory encoding predict content reinstatement at retrieval. Thus, hippocampal responses during memory encoding are predictive of subsequent content reinstatement.

Frontoparietal cortex

Although there is a long history of neuroimaging studies implicating frontoparietal cortical regions in memory retrieval, the traditional view has been that these regions support memory retrieval in a content-general way (Buckner & Wheeler, 2001; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). For example, prefrontal regions are thought to support multiple general cognitive control processes which can benefit successful retrieval (Badre & Wagner, 2007; Buckner & Wheeler, 2001). Areas of lateral parietal cortex, on the other hand, regularly show increased activation during successful remembering (retrieval success effects), leading to ideas that lateral parietal cortex may serve as a mnemonic evidence accumulator (Wagner et al., 2005) or it may direct attention to memory representations in other brain regions (Cabeza et al., 2008). Critically, none of these perspectives argue that frontoparietal regions play a role in reinstatement of mnemonic content.

Other accounts, however, have argued that lateral parietal cortex, in particular, may play a role in actively representing retrieved content (Vilberg & Rugg, 2012). Indeed, neuroimaging studies that have leveraged multivoxel pattern analyses have found that content reinstatement is surprisingly widespread, including in frontoparietal regions (Bird, Keidel, Ing, Horner, & Burgess, 2015; Buchsbaum, Lemire-Rodger, Fang, & Abdi, 2012; Jost et al., 2012; Khader, Burke, Bien, Ranganath, & Rösler, 2005; Polyn et al., 2005; St-Laurent, Abdi, & Buchsbaum, 2015).

The prevalence of reinstatement in frontoparietal regions raises the obvious question of how or whether frontoparietal reinstatement differs from reinstatement in sensory cortical areas. While this topic is still an active area of investigation, a few tentative conclusions can be drawn. First, reinstatement of event-specific information in frontoparietal regions is, at least in some cases, stronger than event-specific reinstatement in sensory cortical areas (Favila, Samide, Sweigart, & Kuhl, 2018; Kuhl & Chun, 2014; Xiao et al., 2017). In particular, event-specific reinstatement is highly robust within the angular gyrus (Kuhl & Chun, 2014; Lee, Samide, Richter, & Kuhl, 2019; **Figure 2**), which is the sub-region of lateral parietal cortex that has consistently been associated with successful memory recall (Wagner et al., 2005). Why might event-specific reinstatement be particularly strong within the angular gyrus? One possible explanation is that the angular gyrus integrates multiple event features (Favila et al., 2018; Tibon, Fuhrmann, Levy, Simons, & Henson, 2019; Shimamura, 2011), and these multi-feature representations contribute to event-specific patterns of activity.

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A second characteristic of reinstatement in frontoparietal regions is that it is relatively more sensitive to top-down goals than is reinstatement in ventral temporal regions (Favila et al., 2018; Kuhl, Johnson, & Chun, 2013). That is, content representations in frontoparietal are biased in favor of goal-relevant information. Interestingly, this bias varies across frontoparietal regions; for example, relatively stronger bias is observed in more dorsal regions—particularly in superior parietal regions (Favila et al., 2018; Kuhl et al., 2013). The role of top-down goals is considered in greater detail later in this chapter.

Finally, while reinstatement, by definition, refers to similarity between activity patterns during encoding vs. memory retrieval, at least some of the frontoparietal regions that show reinstatement exhibit a bias wherein content representations are stronger during retrieval than during perception (J. Chen et al., 2017; Favila et al., 2018; Xiao et al., 2017). This contrasts with sensory cortical areas, where representations are stronger during perception than during memory retrieval. Interestingly, recent evidence indicates that the rodent parietal cortex also more strongly represents *past* sensory experience than *current* sensory experience (Akrami, Kopec, Diamond, & Brody, 2018), suggesting that this may be a fundamental property of higher-level, frontoparietal regions.

The fact that frontoparietal regions show stronger representations during memory retrieval than perception is surprising in that it does not fit with the intuitive idea that reinstated information is a degraded or reconstructed version of perception—that retrieval can only *approximate* perception. However, these findings align well with evidence that many frontoparietal regions exhibit asymmetries in univariate BOLD responses during memory retrieval vs. memory encoding. Namely, regions within the default mode network (including, the angular gyrus) exhibit *increased* BOLD responses during successful memory retrieval, but *decreased* activity during successful memory encoding (Daselaar, 2009; H. Kim, Daselaar, & Cabeza, 2010; Lee, Chun, & Kuhl, 2016; Vannini et al., 2011). While there is, to date, no definitive account of why frontoparietal regions might show stronger representations during memory retrieval than during perception, it suggests a transformation in how information is represented during perception vs. retrieval (Favila et al., 2018; Xiao et al., 2017). Potentially, this transformation reflects a difference between external attention (perception) vs. internal attention (memory) (Chun & Johnson, 2011). Alternatively, retrieved memories may fundamentally differ from initial perceptual events in terms of the reliance on or prioritization of semantic, schematic, or conceptual information as opposed to perceptual or sensory representations (Bird et al., 2015; J. Chen et al., 2017; Linde-Domingo, Treder, Kerrén, & Wimber, 2019).

Relationship between reinstatement and retrieval

While it seems obvious that the reinstatement of neural activity patterns should be related to the experience of remembering, it is important to emphasize that reinstatement is a purely neural measure whereas remembering is a subjective experience. William James appreciated this point even before there were tools for measuring reinstatement:

"No memory is involved in the mere fact of recurrence."

- William James (1918)

What James meant by this was that reproducing the same neural response in the brain is not, on logical grounds, enough to explain memory, because memory—or at least declarative memory— also requires the conscious knowledge that this experience has been experienced before. Thus,

the distinction between reinstatement and memory retrieval is important. As detailed below, neural measures of content reinstatement are clearly related to behavioral aspects of memory retrieval, yet reinstatement can also occur in the absence of conscious awareness.

Reinstatement and retrieval success

The majority of studies reporting content reinstatement have focused on either cued recall (Bosch et al., 2014; Danker et al., 2016; Favila et al., 2018; Gordon et al., 2014; Kuhl & Chun, 2014; Kuhl et al., 2011; Mack & Preston, 2016; Staresina et al., 2012; Vaz et al., 2019; Wing, Ritchey, & Cabeza, 2015; Xiao et al., 2017) or free recall paradigms (J. Chen et al., 2017; Gelbard-Sagiv et al., 2008; Y. Norman et al., 2019; Polyn et al., 2005). In cued recall paradigms, a cue stimulus (e.g., a word) is paired with an associate (e.g., a picture) and during recall, only the cue stimulus is presented. In studies of cued recall there is, not surprisingly, a strong relationship between recall success and neural measures of reinstatement (Kuhl & Chun, 2014; Kuhl et al., 2011; Mack & Preston, 2016; Staresina et al., 2012; Wing et al., 2015). In free recall paradigms, participants study a set of stimuli (e.g., a set of pictures) and then recall those stimuli in the order they come to mind. As with cued recall, many studies have found that successful free recall is associated with neural measures of reinstatement (Gelbard-Sagiv et al., 2008; Y. Norman et al., 2019; Polyn et al., 2005). While these links between successful cued/free recall and reinstatement are important, they also raise an interesting follow-up question: what is the temporal relationship between reinstatement and successful retrieval?

In one of the earliest studies to use multivoxel pattern analyses to measure content reinstatement, Polyn and colleagues (Polyn et al., 2005; **Figure 3**) found that, during recall of images, the visual category of an image could be decoded from fMRI activity patterns several seconds *before* the image was recalled. Similarly, studies using intracranial electrophysiological recordings—which offer much better temporal resolution than fMRI—have clearly established that electrophysiological measures of content reinstatement precede successful free recall (Gelbard-Sagiv et al., 2008; Y. Norman et al., 2019). While these findings are consistent with the idea that reinstatement gives rise to retrieval—as opposed to reinstatement being a consequence of retrieval—it is important to acknowledge the possibility that, in free recall tasks, participants may covertly retrieve an item and 'hold it in mind' for a couple of seconds before reporting it.

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Evidence from cued recall and recognition tasks provides additional support for the idea that reinstatement precedes retrieval. Numerous EEG studies of episodic memory have demonstrated that electrophysiological measures of recollection onset at approximately 500 ms after a cue has been presented (e.g., Rugg & Curran, 2007), which raises the critical question of whether reinstatement occurs *earlier* than this 500 ms mark. Indeed, one EEG study found that during memory decisions, incidentally-encoded background visual information was reinstated between 100-300 ms after the onset of a retrieval cue (Wimber, Maaß, Staudigl, Richardson-Klavehn, & Hanslmayr, 2012). Other EEG and MEG studies have reported reinstatement of spatial location information within a range of 100-400 ms of cue onset (Sutterer, Foster, Serences, Vogel, & Awh, 2019; Waldhauser, Braun, & Hanslmayr, 2016) and reinstatement of category/task information at approximately 500 ms after cue onset (Jafarpour, Fuentemilla, Horner, Penny, & Duzel, 2014; J. D. Johnson, Price, & Leiker, 2015). Strikingly, disruption of early reinstatement effects, via transcranial magnetic stimulation, directly impairs successful remembering (Waldhauser et al., 2016). Thus, existing evidence strongly suggests that reinstatement precedes—and gives rise to—behavioral expressions of successful remembering.

In free recall and cued recall paradigms, to-be-retrieved stimuli are, by definition, not currently perceptually available. Thus, reinstatement involves reproducing a pattern of neural activity in the absence of the perceptual input that initially gave rise to this pattern of activity. In contrast, in recognition memory tasks, the same stimulus that was initially encoded is re-presented during memory retrieval. On the one hand, it would seem that reinstatement is not relevant in this case because there is 'no need' to reinstate the stimulus if the stimulus is currently perceptually available. On the other hand, to the extent that successful recognition is fundamentally related to recognizing that a current perceptual input matches a previous perceptual input, then successful recognition may be associated with relative increases in similarity between activity patterns evoked during initial encoding and later (attempted) recognition. Indeed, several studies have found that successful recognition is associated with greater item-specific similarity of neural activity patterns between encoding and retrieval (Koen & Rugg, 2016; Ritchey, Wing, LaBar, &

Cabeza, 2013; Staresina et al., 2016). In other words, a recognition memory probe is more likely to be endorsed as 'old' if it evokes a pattern of neural activity that matches the specific pattern of activity that was evoked when that stimulus was initially encoded. These results are at least consistent with the idea that reinstatement also occurs—and is beneficial—during recognition memory decisions. That said, these results can also be explained in terms of encoding specificity: that successful remembering is more likely to occur to the extent that similar operations are performed on stimuli during encoding and retrieval (Tulving & Thomson, 1973).

Successful recognition can also be facilitated by reinstatement of *non-item specific* information (see Chapter 5.6). For example, in one study, individual items were encoded in different incidental encoding tasks and reinstatement of the encoding task was observed during successful recognition memory decisions (J. D. Johnson, McDuff, Rugg, & Norman, 2009). Interestingly, this reinstatement of the encoding task occurred even when participants only described recognition probes as 'familiar'—that is, when participants did not report remembering any contextual details. This raises an interesting question: can reinstatement occur without conscious awareness? As described above, there is evidence that reinstatement temporally precedes episodic recollection and there is also evidence that reinstatement occurs incidentally—that is, without any explicit demand to retrieve or report the reinstated information (Jonker, Dimsdale-Zucker, Ritchey, Clarke, & Ranganath, 2018; Kuhl et al., 2013; Nyberg et al., 2000). But can reinstatement occur in contexts when retrieval is *unsuccessful*?

In an early EEG study (Gratton, Corballis, & Jain, 1997), participants incidentally encoded the location of visual stimuli on a screen and later performed a simple recognition memory test ('old' or 'new') on these stimuli. Critically, during the recognition memory test, all of the items were centrally presented, yet EEG responses exhibited lateralization, with greater responses in the hemisphere contralateral to the location at which stimuli *previously appeared*, reflecting a reinstatement of spatial location. Strikingly, when participants were explicitly asked (in a separate experiment) to recall the spatial location at which stimuli had been encoded, they were at chance. Another EEG study found highly similar results: that reinstatement of incidental visual background information occurred during recognition memory decisions even though explicit memory for this background information was at chance in a separate behavioral experiment (Wimber et al., 2012). Finally, and as described later in this chapter, reinstatement also occurs during sleep (Z. Chen & Wilson, 2017; Deuker et al., 2013; Rasch & Born, 2013; Schapiro et al.,

2018; Wilson & McNaughton, 1994), which is, of course, an example of reinstatement in the absence of (immediate) conscious awareness. Collectively, these findings support the idea that reinstatement is involved—and likely causally involved—in episodic remembering. Yet reinstatement may not, on its own, be a sufficient condition for conscious episodic remembering and/or reinstatement may be detectable in situations where evidence falls short of decision bounds.

Reinstatement and vividness

While the preceding section addresses the relationship between reinstatement and *objective measures* of successful memory retrieval, episodic memory also critically involves the *subjective sense* of 're-experiencing' an event (Barsalou, 2008; Tulving & Thomson, 1973). One of the ways in which the subjective experience of remembering has been characterized is through measures of memory vividness. Naturally, successful retrieval generally co-varies with memory vividness, but the subtle distinction between objective vs. subjective measures is important and can have implications for the underlying neural responses (Richter, Cooper, Bays, & Simons, 2016). For example, a memory can be accurately retrieved without being vividly remembered, and, conversely, a memory can be very vivid without being accurate.

Several studies have linked content reinstatement with vivid remembering (Buchsbaum et al., 2012; Favila et al., 2018; Wheeler et al., 2000) with other studies more specifically showing that content reinstatement parametrically scales with subjective ratings of memory vividness (Kuhl & Chun, 2014; Lee et al., 2019; St-Laurent et al., 2015). Moreover, some of the same brain regions that are sensitive to subjective reports of memory vividness are also sensitive to the fidelity with which content is reinstated (St-Laurent et al., 2015), suggesting a close relationship between vividness and reinstatement.

In one study, univariate BOLD activation was found to increase in the angular gyrus during vivid remembering and multivoxel pattern analyses confirmed that reinstatement of item-level information was particularly robust within this vividness-related region of angular gyrus (Kuhl & Chun, 2014; **Figure 2**). Thus, the same brain region that showed an overall increase in activation when memories were subjectively vivid, exhibited highly detailed information about the content that was being retrieved. Another study directly compared category-level reinstatement (face vs.

scene images) with item-level reinstatement (which face, which scene) and, again found a strong relationship between item-level reinstatement in angular gyrus and vividness ratings (Lee et al., 2019). Interestingly, the relationship between item-level reinstatement and vividness was relatively stronger in angular gyrus than in ventral temporal cortex. In contrast, the relationship between *category-level reinstatement* and vividness was relatively stronger in ventral temporal cortex than angular gyrus. These findings suggest that different levels of reinstatement, across different brain regions, contribute to the subjective vividness of a memory.

Insight into the relationship between reinstatement and memory vividness also comes from studies of aging. Interestingly, despite the fact that older adults generally exhibit weaker memory and weaker reinstatement than younger adults, older adults' subjective ratings of vividness are often as high or higher than those of younger adults (Folville et al., 2019; M. K. Johnson, Kuhl, Mitchell, Ankudowich, & Durbin, 2015; St-Laurent et al., 2015). One possibility is that older and younger adults rely on qualitatively different forms of reinstatement when judging a memory's vividness; indeed, older adults' vividness ratings are relatively better predicted by reinstatement in prefrontal regions whereas younger adults' vividness ratings are relatively better predicted by reinstatement in posterior regions (M. K. Johnson et al., 2015). Older adults' combination of high subjective vividness ratings and low reinstatement in posterior regions has been interpreted as reflecting older adults' reduced use of specific episodic details when judging a memory's vividness (Folville et al., 2019).

Reinstatement as a function of competition and top-down goals

In many situations, reinstatement occurs via automatic, pattern completion processes triggered by environmental cues (reminders). But, top-down goals play a critical role in guiding memory retrieval and corresponding reinstatement (Badre & Wagner, 2007)—something that is particularly important when a given retrieval cue is associated with multiple memories (Anderson, 1983; Levy, 2002).

When a retrieval cue is associated with multiple memories (e.g., seeing a favorite restaurant may trigger memories of multiple celebrations at that restaurant), the efficiency with which a target memory is retrieved (e.g., last year's birthday dinner) is thought to be negatively related to activation of other, competing memories (e.g., a birthday dinner from two years ago) (Anderson,

1983). In behavioral studies, however, the activation of competing memories can only be inferred; neural measures of reinstatement, in contrast, provide a means for (more) directly observing the spread of activation across associated memories. Indeed, when retrieving a target memory, activation in content-sensitive cortical areas parametrically increases as a function of the number of other, competing memories associated with the target (Khader et al., 2005, 2007; Öztekin, 2011). Moreover, these competition-related increases in content-sensitive areas are associated with slower reaction times during retrieval (Öztekin, 2011), consistent with the idea that reinstatement of non-target memories carries a cost.

Other studies have used pattern classification methods to index the relative strength of target vs. competing memories that come from distinct visual categories (e.g., faces vs. scenes) and have found that when competition is present (i.e.., a cue is associated with multiple associates), the fidelity of reinstatement during target memory retrieval is lower (Kuhl, Bainbridge, & Chun, 2012; Kuhl et al., 2011). In fact, even when target memories are successfully retrieved, competing memories may nonetheless be reinstated (i.e., the competing memory can be decoded from neural activity patterns) (Kuhl et al., 2012). Moreover, stronger reinstatement of competing memories is associated with slower reaction times during memory retrieval, providing critical evidence that competitor reinstatement carries a cost (Kuhl et al., 2012). Thus, just as reinstatement of a target memory is positively associated with behavioral measures of retrieval success, reinstatement of a competing memory is related to behavioral measures of memory interference.

In situations where memory retrieval is competitive, cognitive control mechanisms are thought to play both a 'pre-retrieval' and 'post-retrieval' role, with pre-retrieval control biasing what information is reinstated and post-retrieval control allowing for selection among reinstated information (Badre & Wagner, 2007). In the aforementioned studies where the relative reinstatement strength of target vs. competing memories was directly compared (Kuhl et al., 2012, 2011), an important point is that reinstatement was, on average, clearly biased in the direction of target memories. This bias toward target memories suggests an influence of pre-retrieval control in filtering which memories are reinstated, though it is difficult, in the absence of temporal dynamics, to rule out the possibility that competing memories are initially reinstated as strongly as target memories and that the bias toward target memories only evolves over time through post-retrieval selection.

Other studies provide evidence consistent with the idea of post-retrieval selection among reinstated memories. In one study (Kuhl et al., 2013), participants encoded face and scene images that appeared either on the left- or right-hand side of a computer screen. During retrieval, participants were either asked to retrieve (and behaviorally report) the visual category of the retrieved image (face or scene) or the original spatial location of the retrieved image (left or right). In visual cortical areas, reinstatement of visual category information was highly robust but was completely insensitive to participants' top-down goals: visual category reinstatement was as strong when visual category information was relevant compared to when it was irrelevant (location trials). In contrast, reinstatement of visual category information in parietal cortex was markedly stronger when that information was relevant. This pattern of results suggests that reinstatement of visual category information in visual cortical areas was relatively automatic, regardless of top-down goals, but that parietal cortex played some role in filtering information according to task demands. These findings were conceptually replicated in a study by Favila et al. (2018) in which participants were cued to retrieve either the category of an object image (e.g., backpack, flower, etc.) or the color of the object image (e.g., red, green, etc.) (Figure 4A). Strikingly, visual cortical areas represented both feature dimensions (object category and color) equally strongly, regardless of top-down goals. A similar pattern was observed in ventral aspects of parietal cortex, including angular gyrus. In contrast, dorsal parietal regions exhibited stronger (and selective) representation of task-relevant feature information (Figure 4B-C).

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The dissociation between ventral and dorsal parietal areas with respect to automatic vs. selective feature representations, respectively, is reminiscent of traditional accounts of attention which propose that ventral parietal areas support bottom-up attention while dorsal parietal areas support top-down attention (Corbetta & Shulman, 2002). Potentially, a similar bottom-up vs. top-down organization applies to parietal contributions to memory (Cabeza et al., 2008), or, more specifically, to differences in memory reinstatement across parietal regions.

Consequences of reinstatement

Thus far, we have focused on reinstatement as a neural correlate of concurrent memory retrieval. However, reinstatement is also a causal factor that can strengthen—or even weaken—reinstated memories. Critically, the consequence of reinstatement is a product of several factors, including *when* reinstatement occurs and the relationship between reinstated memories and ongoing cognition. Below, we separately consider the consequences of reinstatement that occurs during acts of memory retrieval, during the encoding of new memories, or during offline periods of rest or sleep.

Consequences of reinstatement during retrieval

A consistent and important behavioral finding is that retrieval practice strengthens memories, often to a greater degree than simply re-studying material—a phenomenon known as the "testing effect" (Roediger & Karpicke, 2006) (see also Chapter 11.1). While most fMRI studies of reinstatement during memory retrieval have focused on the relationship between reinstatement and concurrent memory retrieval, a few studies have also established relationships between retrieval-related reinstatement and *subsequent* remembering (Bird et al., 2015; Jonker et al., 2018; Karlsson Wirebring et al., 2015; Kuhl et al., 2013; Lee et al., 2019). For example, Bird and colleagues (2015) had participants study and then retrieve various video clips and memory for these videos was then tested a week later. Video clips that initially received retrieval practice were much better remembered a week later than video clips that did not receive retrieval practice, confirming a benefit of retrieval practice. Moreover, the fidelity of reinstatement of video-specific activity patterns during initial retrieval practice predicted the degree of this retrieval-related strengthening. Thus, the benefits of retrieval practice.

As discussed earlier in this chapter, reinstatement takes several forms (e.g., across multiple brain regions) and can occur at multiple levels (e.g., reinstatement of visual category information, item-specific information, or even different features of items). Likewise, while retrieval practice generally strengthens memories, it can also lead to slight distortions of memory (Bridge & Paller, 2012) or a shift toward reliance of semantic/schematic information (Bird et al., 2015). A study by

Lee and colleagues (2019) directly contrasted the consequences of category- vs. item-level reinstatement across parietal and visual cortical regions. In the study, participants first studied and then performed retrieval practice on various word-picture associations. Later, participants completed a recognition memory test during which participants saw images that were identical to studied images but also images that were *nearly* identical to studied images (similar lures). Although retrieval practice was, overall, beneficial to recognition memory, retrieval practice also increased the false alarm rate to similar lures (i.e., the probability that similar lures would be endorsed as 'old'). Strikingly, category- and item-level measures of reinstatement in parietal cortex, measured during retrieval practice, were oppositely related to these false alarms during the subsequent memory test: category-level reinstatement was associated with a relatively *greater* rate of false alarms whereas item-level reinstatement was associated with a relatively *lower* rate of false alarms. Thus, this study illustrates that different measures of reinstatement can predict subtly distinct consequences of retrieval practice (including the tendency for retrieval practice to increase false alarms to semantically-related information).

Another interesting way in which measures of reinstatement provide unique insight into the consequences of retrieval is that reinstatement can be measured for *non-target* information—that is, reinstatement of information that is, by definition, not behaviorally expressed. At least in some contexts, incidental reinstatement is associated with strengthening of non-target memories. For example, Jonker and colleagues (2018) found that retrieval of target memories elicited incidental reinstatement and strengthening of non-target memories that shared a similar encoding context. Notably, these benefits of retrieval practice were greater than the benefits of restudy, confirming that the benefit to incidental memories was induced by the act of retrieval. Similarly, Kuhl and colleagues (Kuhl et al., 2013) found that retrieving the spatial location at which an image appeared elicited incidental reinstatement of—and corresponding increases in subsequent memory for—the visual category to which the image belonged.

Although non-target memories may sometimes be incidentally reinstated with little cost to target retrieval (i.e., without interference), in other contexts there may be a competitive relationship between a target and non-target memory (Kuhl et al., 2012, 2011). In such cases, there is an adaptive advantage to limiting the reinstatement of the non-target memory. Indeed, when a memory cue is associated with competing associations, repeated retrieval of a target association

can suppress the reinstatement of the competing association (Wimber, Alink, Charest, Kriegeskorte, & Anderson, 2015; **Figure 5A-D**). Moreover, greater suppression of competitor reinstatement predicts subsequent forgetting of the competing memory (Wimber et al., 2015; **Figure 5E**). Interestingly, however, some degree of initial reinstatement of competing memories may be precisely what triggers the eventual suppression and forgetting of competing memories (Detre, Natarajan, Gershman, & Norman, 2013; Hulbert & Norman, 2015; Levy, 2002; Ritvo, Turk-Browne, & Norman, 2019).

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Together, these findings highlight that there are multiple, distinct consequences of reinstatement during retrieval, including the strengthening of target and closely related memories to the weakening of competing memories.

Consequences of reinstatement during encoding

While the vast majority of research on reinstatement has focused on reinstatement that occurs during memory retrieval, reinstatement can also occur during memory encoding. However, reinstatement during encoding falls into two very different categories

Consider, for example, encountering someone at the grocery store and being reminded of a past experience *with this same person*. This situation is quite distinct from encountering someone at the grocery store and being reminded of a past experience *with a different person* (e.g., someone very similar looking). In the former case, reinstating a prior experience could serve to strengthen the memory representation of that person. Indeed, several studies have found that when encountering a stimulus for a second or third time, greater neural pattern similarity between the original encoding event and the current encoding event is associated with better long-term memory for that stimulus (Ward, Chun, & Kuhl, 2013; Xue et al., 2010, 2013). In other words, these findings suggest that reinstating the original encoding representation helps to strengthen the memory.

With respect to the second case (reinstatement of memory for a stimulus that is *different* from the current, to-be-encoded stimulus), here the consequence is less obvious. Will reinstating this past experience strengthen or weaken that memory? How might this experience influence memory for the *relationship* between the reinstated content and the current, to-be-encoded experience? As it turns out, the outcomes of such non-target reinstatements can be variable.

At least in some cases, reinstatement of older memories during the encoding of new (different) memories can strengthen the reinstated memories, despite the mismatch between reinstatement and encoding (Koen & Rugg, 2016; Kuhl, Shah, DuBrow, & Wagner, 2010). In other cases, however, reinstatement of older memories during the encoding of new experiences can actively weaken the reinstated memory. For example, Kim and colleagues (Kim, Lewis-Peacock, Norman, & Turk-Browne, 2014) used a paradigm in which participants viewed sequences of face and scene images. After repeatedly studying various sequences, violations were introduced where an expected stimulus was replaced by a new stimulus. Pattern classification methods were used to index the strength with which original sequences were reinstated on these violation trials. Critically stronger reinstatement on the violation trials (i.e., a greater prediction error) was associated with *weaker* subsequent memory for the reinstated stimulus. Several other studies have reported conceptually similar results linking non-target reinstatement strength (during the processing or encoding of other stimuli) to behavioral or neural measures of memory weakening (G. Kim, Norman, & Turk-Browne, 2017; Long & Kuhl, 2018; Poppenk & Norman, 2014).

Finally, there is also evidence that reinstatement of older memories during new learning can influence how older and newer memories are *organized*. For example, in a seminal study, Shohamy and Wagner (2008) demonstrated that during the encoding of overlapping associations, activation in the hippocampus predicts the subsequent ability to *integrate* across overlapping associations. Putatively, this relationship reflects the fact that the hippocampus *reinstated* overlapping (older) memories during the encoding of newer memories, allowing for the formation of integrated representations. This idea was more directly established in a study by Zeithamova and colleagues (2012) which used pattern classification analyses to directly index reinstatement of overlapping memories during new encoding. In the study, participants first learned an association between a pair of pictures (A-B) and then learned an association between a new, overlapping pair (B-C) (**Figure 6A-B**). Critically, reinstatement of the prior event (A) during encoding of the new pair (B-C) predicted performance on a subsequent inference task

which tested 'memory' for associations which were never directly studied (A-C) (**Figure 6C-D**). Subsequent experiments have provided additional evidence linking reinstatement during new encoding to subsequent behavioral measures of memory integration (Chanales, Dudukovic, Richter, & Kuhl, 2019; Richter, Chanales, & Kuhl, 2016; Wimmer & Shohamy, 2012).

----- Insert Figure 6 About Here -----

The preceding findings raise an important question: Why does reinstatement of older memories during new encoding sometimes lead to strengthening of the reinstated memory, other times lead to weakening of the reinstated memory, and yet other times promote the integration of older and newer memories? While a definitive account of these dynamics has yet to be achieved—and full consideration of this point is beyond the scope of the current chapter—at least several important factors have been identified. These factors include the similarity between older (reinstated) and to-be-encoded memories (Long & Kuhl, 2018; Schapiro, Kustner, & Turk-Browne, 2012), the temporal proximity of older memories and new encoding (Zeithamova & Preston, 2017), the strength with which older memories are reinstated (G. Kim et al., 2014; Ritvo et al., 2019), and also the state of the memory system during new encoding (Chanales et al., 2019; Duncan, Sadanand, & Davachi, 2012; Richter, Chanales, et al., 2016).

Offline reinstatement

Above, we consider the consequences of reinstatement that occurs either during memory retrieval or memory encoding. A final—and important—context in which reinstatement can influence subsequent remembering is when reinstatement occurs during offline periods of rest or sleep. However, because separate chapters in this volume are specifically dedicated to the topics of sleep (see Chapter 6.9) and memory consolidation (see Chapters 6.7 and 6.8), we only briefly consider the consequences of offline reinstatement here.

An important question to start with is: Can offline memory reinstatement be measured? In rodents, there are numerous, highly influential examples of reinstatement of sequences of place cell activities during sleep (Skaggs & McNaughton, 1996; Wilson & McNaughton, 1994). In

human episodic memory, however, methods for measuring offline reinstatement have only recently become widespread. In particular, a number of EEG and fMRI studies have used multivariate pattern analysis methods to index or decode spontaneous reinstatement of memories during sleep or rest (Bang et al., 2018; Deuker et al., 2013; Schapiro et al., 2018; Schönauer et al., 2017; Schreiner, Doeller, Jensen, Rasch, & Staudigl, 2018; Staresina, Alink, Kriegeskorte, & Henson, 2013). These studies generally use a similar approach: identify a pattern of neural activity evoked during perception or the encoding of a memory and then test for the reinstatement of that neural activity pattern during offline rest or sleep. Critically, a number of studies have found a positive relationship between offline reinstatement and subsequent memory—that is, greater evidence for offline reinstatement is associated with better subsequent memory for the reinstated information (Deuker et al., 2013; Gruber, Ritchey, Wang, Doss, & Ranganath, 2016; Schapiro et al., 2018; Schlichting & Preston, 2014; Schönauer et al., 2017; Shanahan, Gjorgieva, Paller, Kahnt, & Gottfried, 2018; Staresina et al., 2013; Tambini & Davachi, 2013; Tambini, Ketz, & Davachi, 2010). Offline reinstatement has even been associated with better subsequent encoding of new information that overlaps with (previously) reinstated information (Schlichting & Preston, 2014).

Thus far, we have considered offline reinstatement as a single phenomenon, ignoring the distinction between reinstatement that occurs during wakeful periods of rest vs. sleep (or even during different stages of sleep). While beyond the scope of the present chapter, there is at least some evidence that reinstatement during wakefulness may be less, or differentially, beneficial than reinstatement during sleep (Diekelmann, Büchel, Born, & Rasch, 2011; Oudiette, Antony, Creery, & Paller, 2013). Similarly, reinstatement during sleep may be particularly beneficial when it occurs during slow-wave sleep (Rasch, Buchel, Gais, & Born, 2007; Schönauer et al., 2017).

Although evidence for positive relationships between offline reinstatement and subsequent memory are certainly consistent with the idea that offline reinstatement plays a causal role in strengthening memories, an alternative possibility is that memories which are more strongly encoded are more likely to be reinstated during offline periods and also more likely to be subsequently remembered. By this alternative account, offline reinstatement is a reflection of differences in memory strength as opposed to a cause of these differences. Interestingly, and in contrast to this alternative account, Schapiro et al. (2018) found that *weaker memories* are more

likely to be reinstated during offline periods, consistent with the idea that the weaker memories had a greater 'need' for strengthening. More directly, however, several studies have developed paradigms to actively cue specific memories during offline rest/sleep. Behaviorally, these studies have shown that memory cues during these offline periods enhance subsequent memory (Rasch et al., 2007; Rudoy, Voss, Westerberg, & Paller, 2009), establishing the critical point that offline cuing enhances memory. Moreover, neuroimaging studies have identified neural signals of memory reinstatement directly evoked by offline cues (Alm, Ngo, & Olson, 2019; Rasch et al., 2007). Collectively, these studies make a strong case that offline reinstatement causally influences subsequent memory.

Summary and Conclusions

As reviewed above, the phenomenon of content reinstatement is intimately related to episodic memory. Reinstatement is closely related to—and putatively gives rise to—objective and subjective expressions of memory retrieval. Moreover, reinstatement that occurs during memory retrieval, during memory encoding, or even during offline periods of rest and sleep, can powerfully shape future remembering by strengthening, reorganizing or sometimes weakening reinstated memories.

A point of emphasis in this chapter is that memory reinstatement is a highly distributed phenomenon, occurring across multiple brain regions—from sensory cortical areas to the hippocampus to frontoparietal regions. The properties and qualities of reinstatement across these brain regions has provided insight into how these regions support memory. Yet reinstatement, by definition, refers to a *match* between the brain regions, or the spatial activity patterns within these brain regions, activated during encoding and retrieval. As such, a focus on reinstatement—at least in the strict sense—necessarily ignores the ways in which representations during memory retrieval *differ* from representations during encoding (J. Chen et al., 2017; Favila et al., 2018; Xiao et al., 2017). Thus, one of the areas where future progress will be made is in understanding how representations of encoded content are *transformed* into representations of remembered content.

Figures



Figure 1. Design and findings from Hindy et al. (2016). (A) Participants learned sequences between a cue (fractal) an action (button press) and outcome (another fractal). On Cue + Action trials, the outcomes were withheld, whereas on Outcome trials only the outcomes were shown. (B) Pattern classifiers were trained on fMRI activity patterns during the Outcome trials and were then tested on the Cue + Action trials to test for reinstatement of the outcome. In early visual cortical areas (V1, V2), the outcome could be reliably decoded (chance = 50%) on the Cue + Action trials, indicating that the outcomes were reinstated in these early visual areas.



Figure 2. Findings from Kuhl and Chun (2014). (A) Region of angular gyrus (ANG) for which univariate activation increased during vivid memory retrieval. (B) Participants first learned word-image associations (images were either faces or scenes). During cued recall, words were presented and participants recalled corresponding images. Pattern classifiers applied to ANG activity patterns during cued recall trials were able to reliably classify the visual category of successfully recalled images (chance accuracy = 50%). (C) ANG activity patterns during cued recall trials also supported classification of successfully-recalled specific images (which face, which scene). Together, these findings indicate that the same region of angular gyrus that is involved in vivid remembering exhibits category- and item-specific content reinstatement.



Figure 3. Findings from Polyn et al. (2005). Participants studied lists of visual images from three visual categories (faces, locations, objects) and then freely recalled the images. Multivoxel pattern classifiers were trained to discriminate between the three visual categories of images and the classifiers were then tested on (applied to) free recall data. Reinstatement of visual category information systematically preceded behavioral recall of images. The data shown reflect the strength of evidence for each visual category (blue = face evidence, red = location evidence, green = object evidence) as a function of time (scans). Circles represent individual recall events. Data are from a single, representative participant.



Figure 4. Design and findings from Favila et al. (2018). (**A**) Participants learned associations between words and object images. The object images were organized along two dimensions: object category and color. (**B**) Lateral parietal regions of interest. (**C**) During cued recall, participants were provided a cue word and recalled the corresponding object image. However, on half of the cued recall trials, participants were explicitly asked to recall the color of the image and on the other half of trials participants were asked to recall the object category of the image. Multivoxel pattern analyses were used to measure the strength of feature information (color or object category) as a function of relevance (relevant, irrelevant). In dorsal lateral parietal areas, relevant feature information was stronger than irrelevant feature information; in ventral lateral parietal areas, the strength of feature information did not vary according to relevance.



Figure 5. Design and findings from Wimber et al. (2015). (A) Participants learned competing associations wherein the same word was paired with two difference images. (B) During competitive retrieval, one of the images served as the retrieval target and the other image served as the competitor. (C) Reinstatement was measured within high level visual cortical areas (ventral temporal cortex). (D) During competitive retrieval, pattern similarity with the competitor (reinstatement) was expressed relative to other memories from the same visual category. Across repeated target retrieval attempts, there was a suppression of the specific activity pattern associated with the competitor memory. (E) Between-participants, there was a correlation between competitor reinstatement and subsequent forgetting of the competitor: lower reinstatement of the competitor-specific activation pattern was associated with greater forgetting.



Figure 6. Design and findings from Zeithamova et al. (2012). (A) Participants learned various image-image associations. Some of these associations contained common images, creating overlapping associations (AB, BC). (B) After AB, BC associations had been repeatedly studied, it was hypothesized that re-encoding an AB association would reinstate the overlapping C image and, thereby, lead to integration of images that were never directly studied together (AC). (C) Multivoxel pattern analysis of fMRI activity patterns was used to measure reinstatement of C images during AB encoding trials and as a function of AB repetition. For AB, BC associations where the A and B images were objects and the C image was a scene, reinstatement of scene-related information increased as a function of learning. (D) Across participants, stronger reinstatement of C images during AB study was associated with better performance on an inference test that required linking A and C images which were only indirectly associated (via the common B image). Thus, reinstatement of overlapping images during encoding facilitated subsequent integration.

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