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Contributions of representational distinctiveness and stability to memory performance and age differences

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ABSTRACT

Long-standing theories of cognitive aging suggest that memory decline is associated with age-related differences in the way information is neurally represented. Multivariate pattern similarity analyses enabled researchers to take a representational perspective on brain and cognition, and allowed them to study the properties of neural representations that support successful episodic memory. Two representational properties have been identified as crucial for memory performance, namely the *distinctiveness* and the *stability* of neural representations. Here, we review studies that used multivariate analysis tools for different neuroimaging techniques to clarify how these representational properties relate to memory performance across adulthood. While most evidence on age differences in neural representations involved stimulus category information, recent studies demonstrated that particularly item-level stability and specificity of activity patterns are linked to memory success and decline during aging. Overall, multivariate methods offer a versatile tool for our understanding of age differences in the neural representations underlying memory.

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Introduction

Cognitive performance, especially episodic memory, declines in old age (Nyberg et al., 2012). The neural dedifferentiation hypothesis of cognitive aging states that representations become less distinct in old age which accounts for age-related cognitive impairments (D. C. Park et al., 2004; Koen & Rugg, 2019; Koen et al., 2020). An influential model by Li et al. (2000, p. 2001) ascribes age differences in cognition to deficient neuromodulation that produces more variable activation to identical informational input, leading to reduced representational quality in old age. These predictions can be tested using multivariate neural pattern similarity analysis, comparing neural representations measured as the patterns of neural activity elicited during perception or imagination of stimuli (e.g., Carp, Park, Hebrank et al., 2011; Chadwick et al., 2010). Accordingly, aging researchers have recently started to explore whether episodic memory decline in old age is associated with age-related differences in the way information is represented in the brain. By comparing patterns of neural activation between various conditions, multivariate pattern similarity analyses enable a representational perspective on brain and cognition, and

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allow researchers to study the properties of neural representations that support successful episodic memory. High fidelity neural representation means that different information elicits distinct neural representations whereas identical information is represented by stable, similar neural patterns. Hence, two prominent representational properties have been identified as crucial for memory performance, namely the distinctiveness and the stability of neural representations (cf., Kobelt et al., 2021; Sommer et al., 2021b). Critically, the relation between distinctiveness and stability is essential for memory: Combining representational stability and distinctiveness, neural representational specificity is measured by the similarity of neural representations to themselves (stability) corrected for their similarity to other representations (distinctiveness) which expresses how precisely and uniquely a neural activation pattern corresponds to the information it represents (Hasinski & Sederberg, 2016; Kobelt et al., 2021; Sommer et al., 2021b; Zheng et al., 2018).

Here, we review studies that used multivariate analysis tools for different neuroimaging techniques to elucidate how representational distinctiveness, stability, and their interactions relate to memory performance across adulthood and specifically during aging. The review aims at helping researchers to navigate through the large body of evidence and to better understand age-related changes in neural representational properties that are associated with memory success and provide an overview of how multivariate methods can be used to tackle such questions.

Investigating Neural Representations with Multivariate Pattern Similarity Analysis

The brain encodes information in the spatial distribution, timing, and dynamics of its electrochemical signals (e.g., Cohen, 2011; Fries, 2015; Treves, 2007). Multivariate analysis approaches for functional magnetic resonance imaging (fMRI) and magneto-/electroencephalography (M/EEG) data enable neuroscientists to investigate the content and properties of neural representations. Neural representations are a key concept in cognitive neuroscience that link the physical world to the way it is mentally and neurally expressed (Bain, 1874; Churchland, 1986; Koch, 2004). In the (mass-) univariate standard fMRI approach, each voxel's hemodynamic response function is modeled and voxels are identified that show common activity changes and thus maximal activation in the condition(s) of interest (e.g., Friston et al., 1994). In contrast to that, multivariate pattern analysis considers multiple voxels at once (Pillet et al., 2020) and thus takes the full "landscape" pattern of high and low activations into account (Mur et al., 2009). From these patterns of activity, aspects of a person's current mental state can be "read out" using machine-learning classifiers (decoding models; e.g., Haynes & Rees, 2006; Mitchell et al., 2004; Rissman et al., 2010) and future, untrained activity patterns can be generatively predicted (encoding models; e.g., Kay et al., 2008; Mitchell et al., 2008; Van Gerven, 2016). Multivariate pattern analysis is more commonly adopted in fMRI analysis, but in recent years it has also gained traction for time-resolved brain recordings like M/EEG (Carlson et al., 2019; Fahrenfort et al., 2018; Jafarpour et al., 2013; Sommer et al., 2019, Sommer et al., 2021b). While multivariate fMRI analysis mainly focusses on how content is represented in spatial patterns of neural activity, M/EEG is more time-sensitive and therefore enables researchers to study the temporal, often oscillatory dynamics of neural

activity and its role in representing information (cf., Sommer et al., 2021b). Thus, different brain recording techniques can be used to investigate different aspects of the multi-dimensional nature of neural information representation.

Representational similarity analysis (RSA) is an often used multivariate pattern analysis technique offering a tool to study representational properties by comparing patterns of neural activity between different conditions (Edelman, 1998; Kriegeskorte & Kievit, 2013; Kriegeskorte et al., 2008). RSA assesses the similarity (or dissimilarity, if preferred) between neural representations by, for example, correlations of the underlying activity patterns. Similarity and dissimilarity are inverses of each other that are convertible and can be used interchangeably, for example, if similarity is measured as correlation, dissimilarity is the correlation distance $1 - \text{correlation coefficient}$ (e.g., Kriegeskorte et al., 2008). Comparing the (dis-)similarity of several conditions, for instance, stimulus categories, can provide a (dis-)similarity structure that is often illustrated in a matrix of all pairwise comparisons (representational similarity matrix, RSM; or representational dissimilarity matrix, RDM). These matrices can characterize the information that a given region represents and distinguishes (Kriegeskorte et al., 2008). The representational (dis-)similarity structure in a certain region can then be compared to other regions, modalities, computational models, behavior, or between different individuals or species (i.e., second-order isomorphism; Edelman, 1998; Kriegeskorte et al., 2008; Shepard & Chipman, 1970; e.g., Cichy et al., 2014; Cohen et al., 2019). This comparison of RSMs/RDMs provides a common, modality-independent measuring unit that can be used to relate findings from different methods and disciplines.

Although function and content in the brain are not separable in the strict sense (Feldman, 2016; Tulving & Bower, 1974) and every measurement of brain activity always comprises both, the differences between classic univariate and multivariate analyses have been interpreted as focusing on different neurocognitive aspects, for example, on the involvement of a particular region in a function versus the representational content in that region (Chadwick et al., 2010; Mur et al., 2009). While the mere localization of functions to specific regions does not explain the underlying neural mechanisms, multivariate analysis approaches are thought to be more sensitive to the brain's functional organization and subtle changes in activity that allow for the investigation of how the brain may encode information (Haxby, 2012; Yang et al., 2012). This has led to remarkable findings with regard to representation of contents during, for example, the perception (e.g., Haxby et al., 2001; Vetter et al., 2014) and retrieval of information (e.g., Chadwick et al., 2010; Polyn et al., 2005; Schultz, 2010). However, findings in simulated fMRI data have demonstrated that different results from multivariate pattern analysis and univariate analysis do not allow conclusions about the dimensionality of the patterns of activity in which information is encoded (Davis et al., 2014a). Moreover, Davis et al. (2014a) showed that univariate fMRI analysis was sensitive to between-subject differences in mean activation levels while multivariate pattern analysis was sensitive to voxel-level variability within subjects but insensitive to between-subject variability in mean activation levels. Thus, univariate and multivariate analyses allow to focus on different aspects and levels of variability in brain activation but different results do not per se allow conclusions about certain traits (e.g., dimensionality) of the neural code. Overall, multivariate similarity analysis of brain activity data, e.g., from fMRI and M/EEG, is especially suited for investigating neural representations by

focusing on informational content in neural activation. Relating these measures with behavioral outcomes enables the investigation of the neural representations underlying cognitive abilities such as episodic memory and age differences therein.

Representational distinctiveness and stability are critical for episodic memory performance

Multivariate pattern similarity analysis for fMRI and M/EEG data can be leveraged to investigate how information is represented in the spatial, temporal, and spectral patterns of brain activity. Research has identified specific representational properties that are related to cognition, particularly episodic memory performance. These properties concern the relation of neural representations to each other, that is, how similar or distinct they are (*representational distinctiveness*), and how stable they are over time, that is, how precisely they are reactivated (*representational stability*).

Representational distinctiveness

It is currently debated how the relation of different representations to each other shapes memory, namely whether high similarity or distinctiveness of the representations in memory is beneficial for remembering their associated content (note that here, “distinctiveness” is synonymous with “dissimilarity” and thus the inverse of “similarity” between different representations). Network models of long-term memory assume that memory is organized in systems of nodes, i.e., memory representations, that are connected by their semantic or episodic relations (Anderson, 1983; Barnden et al., 2003; Raaijmakers & Shiffrin, 1992; Tulving & Donaldson, 1972). More similar representations that share a lot of features can be conceived as nodes that are closer to each other in this network, for example, representing items from the same object category (within-category similarity), whereas more distinct representations have a larger distance between each other, for example, representing items from different categories (between-category similarity; Kriegeskorte & Kievit, 2013). Theories of global matching postulate that the memory strength for a specific item arises from the similarity of its representation to the representations of all other encoded items (“global similarity,” Clark & Gronlund, 1996; Hintzman, 1984; Humphreys et al., 1989; Raaijmakers & Shiffrin, 1992; Xue, 2018). Specifically, the model proposes that retrieval is achieved by matching a presented item to all items in memory, and the amount of overlap scales with the sense of familiarity that the item creates. This familiarity is interpreted as evidence that the item corresponds to a past experience and, if exceeding a specific decision criterion, the participant will claim to remember the item (Clark & Gronlund, 1996; Hicks & Starns, 2006) which can be correct or incorrect (Arndt & Hirshman, 1998; Hintzman, 1988). In the framework of memory networks, item representations with high global similarity are located in the center of the multidimensional memory space with relatively short distances to other representations (Davis et al., 2014b). Thus, according to these theories, high global similarity is linked to high memory performance.

The similarity with which information is neurally represented can be examined using multivariate pattern similarity analyses. By comparing the distributed activity patterns elicited by different stimuli, Davis et al. (2014b) could show that higher global similarity of

fMRI patterns in the medial temporal lobe (MTL), including the hippocampus, was related to higher memory confidence in a recognition task as well as higher memory strength in a category learning task (see also, Visser et al., 2013). This provides neural evidence for the benefit of similar representations as postulated, for example, by global matching. Similar results in neocortical regions were obtained by Wagner et al. (2016) who demonstrated that representational similarity between encoded items (unique picture–location associations) was larger for long-lasting memories compared with weaker and not remembered items. Adding evidence for the benefit of similarity also in time-resolved representations, Lu et al. (2015) found that, at around 500 ms after stimulus onset, global EEG spatiotemporal pattern similarity was higher for later remembered than for not remembered items. In older adults, a similar association was found for EEG time–frequency patterns that showed higher global similarity for better remembered scene–word pairs (see also the next section; Sommer et al., 2019). In line with the prediction that global matching can also result in false recognition, the fMRI study by Ye et al. (2016) showed that the similarity of both old and new item representations during recognition and all other items during encoding was associated with whether the item would be regarded as old. Specifically, high representational similarity in parietal regions was linked to reports of item recognition (whether correct or not), whereas representational similarity in visual cortex was only linked to correct recognition, suggesting distinct global matching signals in different brain areas. In summary, these studies show that similarity between different representations during encoding (Davis et al., 2014b; Lu et al., 2015; Visser et al., 2013; Wagner et al., 2016) and between encoding and retrieval (Ye et al., 2016) can be beneficial for memory performance, confirming cognitive models and previous behavioral results (Hintzman, 1988; see above). However, consistent with the models, high global similarity can also promote incorrect recognition (Ye et al., 2016), indicating that there may be a drawback of high similarity.

Although representational similarity benefits memory, representations that are too similar may be prone to interference. Behavioral studies showed that items that are very different from other studied items (isolation paradigm) are better remembered than similar items (Hunt & Worthen, 2006; Smith, 2011), which may indicate that high representational distinctiveness rather than similarity benefits memory. Interference from similar memories can also trigger a repulsion of memory representations in the hippocampus, making overlapping representations more distinct, which is suggested by activation patterns in the hippocampus becoming less similar with learning (Chanales et al., 2017, Chanales et al., 2021; Favila et al., 2016). Critically, these changes were only observed in hippocampal and not cortical regions (Favila et al., 2016), suggesting how pattern similarity outside the hippocampus and distinctiveness in the hippocampus (via pattern separation) may jointly benefit memory (see also, Ye et al., 2016). In line with the presumed pattern separation processes in the hippocampus that form distinct representations of overlapping experiences (Chadwick et al., 2011; Kumaran & Maguire, 2006; Schlichting et al., 2015), LaRocque et al. (2013) found that encoding-related global (within-category) similarity in perirhinal and parahippocampal cortex was positively related to recognition memory, whereas the opposite relationship was observed in the hippocampus, where lower similarity was linked to better memory (see also, Wing et al., 2020). Seemingly at odds with the benefit of representational similarity, Kuhl et al. (2012) demonstrated that the better the BOLD response to a given encoding trial could be

classified as face or scene image, the higher was the probability that the corresponding item would be later remembered correctly. This suggests that more distinct face and scene representations were related to successful memory encoding. Confirming these decoding results as an indicator for representational distinctiveness, additional (correlation-based) pattern similarity analyses showed that between-category (faces/scenes) similarity was lower for remembered than not remembered items. However, at the same time, the representational similarity between items within the categories was higher for later remembered items, demonstrating that within-category similarity in temporal and prefrontal regions was beneficial for memory. That is, on the category-level, distinctiveness benefited memory, and on the item-level (within-categories), similarity benefited memory. These results highlight that the accurate representation of the similarity structure of presented information, for example, that related information is represented more similarly than unrelated information, reflects high-fidelity encoding and is thus linked to successful retrieval.

All in all, the relationship between different representations is a critical property to consider when investigating the formation of memories, which can be addressed with multivariate pattern similarity analyses. The discussed findings suggest that distinctiveness between representations of distinct information (e.g., different categories), but similarity between representations of related information (e.g., items of the same category), may often benefit memory. At the same time, highly similar inputs should be separable by the hippocampus, indicated by dissimilar patterns in the hippocampus being related to memory success. In conclusion, the current evidence suggests that it is not a categorical question about neural distinctiveness versus similarity. Instead, both, and particularly the right balance between them, are beneficial for memory. Whereas similarity is advantageous by giving rise to familiarity and thus recognition (global matching), it can also result in false recognition. Highly distinct representations may prevent false memories, but may also hamper correct recognition, if generalization or holistic retrieval (pattern completion) fail. Different brain regions contribute to balancing these opposing requirements of similar yet distinct neural representations, such as certain hippocampal subfields (dentate gyrus) that orthogonalize similar inputs and thus represent specifics (e.g., LaRocque et al., 2013; Wing et al., 2020) and other subfields (CA3) and neocortical areas that integrate related information (Grande et al., 2019; Keresztes et al., 2017; McClelland et al., 1995; Neunuebel & Knierim, 2014; Norman & O'Reilly, 2003; Schlichting et al., 2015; Wagner et al., 2016).

Representational stability

The retention of representations over time and the potential to retrieve them constitute the ability of memory for past experiences. If an event is neurally represented by the activation pattern it elicited, then re-encountering or remembering aspects from that event should reactivate the corresponding pattern. The more precisely a representation can be reactivated the more accurately and confidently its content should be remembered (Xue, 2018). Thus, in addition to representational distinctiveness, high-fidelity neural representation furthermore implies that the representations are stable over time, indicated by accurate reactivation of the underlying neural activity patterns that benefit memory. We can distinguish between representational stability across repetitions, i.e.,

identical stimulus presentations, and stability between only partly overlapping stimulus presentations. Identical repetitions can, for example, occur as repeated learning/encoding or in the context of an encoding and subsequent recognition task in which the participant is asked to respond whether they remember the repeated stimulus (old/new recognition). In these studies, high stability may be due to high similarity in processing the percept as well as to reactivation of the previously formed memory trace. In contrast, partly overlapping stimulus presentations often involve repetition of parts of the original stimulus as cues to retrieve the full stimulus (cued recall). In these cases, stability depends mostly on reactivation or cortical reinstatement of the previously formed memory trace. In both cases, the stability of the representations is quantified by the similarity of the underlying neural activity patterns.

Accordingly, studies using multivariate analysis approaches on fMRI and EEG data have demonstrated that activation patterns of subsequently remembered items showed higher stability across repetitions compared to not remembered items (e.g., Kobelt et al., 2021). In three fMRI experiments, Xue et al. (2010) showed that greater pattern similarity across repeated encoding (of faces or words) was associated with better subsequent recognition and recall. This positive relationship between representational stability and subsequent memory was identified in many brain regions, including prefrontal, parietal, occipitotemporal, and MTL areas (see also, Visser et al., 2013). Reanalysis of parts of the data furthermore indicated that higher (univariate) frontoparietal activity may increase pattern similarity across the cortex, resulting in more consistent input to the MTL and thus improving memory encoding (Xue et al., 2013). In line with this, Lu et al. (2015) demonstrated that beyond the positive link between spatiotemporal EEG pattern stability (approximately 500 ms after stimulus onset) and subsequent memory, transcranial direct current stimulation (tDCS) of the left lateral prefrontal cortex enhanced both pattern stability over right frontal electrodes and memory performance. This finding indicates a causal role of frontal activity for representational stability and memory (Lu et al., 2015). To sum up, fMRI and EEG studies have shown that the stability of neural representations in cortical and subcortical areas, measured as pattern similarity of the underlying activity patterns, is supported by frontal activity and positively associated with memory outcomes.

In addition to stable neural representations during repeated encounters, it is a key element of multiple models of episodic memory (Alvarez & Squire, 1994; McClelland et al., 1995; Norman & O'Reilly, 2003; Rolls, 2000; Shastri, 2002) that the neurocognitive processes involved during event encoding are also involved when that event is retrieved (Damasio, 1989; Nyberg et al., 2000; Rugg et al., 2008). During memory retrieval, re-encountering stimuli or contexts related to the initial event can improve the access to the target memory and facilitate remembering through the reinstatement of memory representations (Danker & Anderson, 2010; Norman & O'Reilly, 2003). This reinstatement can be studied by measuring the encoding–retrieval similarity of the neural activity patterns. Accordingly, several studies using fMRI or MEG showed reinstatement of stimulus category information during successful retrieval (Jafarpour et al., 2014; Kuhl & Chun, 2014; Kuhl et al., 2011; Polyn et al., 2005). Furthermore, reinstatement of item information has been demonstrated in spatial fMRI representations (Ritchey et al., 2013; Staresina et al., 2012; Tompariy et al., 2016; Wing et al., 2015) and temporal/spectral EEG and iEEG representations (Kerrén et al., 2018; Michelmann et al., 2018; Yaffe et al., 2014; Zhang et al.,

2015). These findings show that neural activity patterns during retrieval reflect the reinstatement of the representations of encoding, which is supported by the hippocampus (e.g., Staresina et al., 2012), and positively related to memory outcomes. In contrast to the studies on stability during repeated encoding (see above), the majority of the studies on encoding–retrieval similarity did not show exact repetitions but showed cues to induce retrieval (exceptions: Ritchey et al., 2013; Zhang et al., 2015). Thus, stability of neural representations is not merely similarity in processing identical stimulus input but remains critical for memory success also in the absence of the full stimulus. However, the extent to which neural representations during retrieval resemble the initial representations from encoding may not fully explain memory retrieval processing. Recent evidence suggests that retrieved memory representations may be systematically transformed representations of the initial encoding representations and therefore not direct mirrors of encoded information (Xiao et al., 2017; for review, see, Favila et al., 2020). Future research should target the mechanisms, causes, and consequences of precise reinstatement yet systematic transformations in neural representations from perception to memory.

In summary, the above studies have shown that reliable neural reactivation in cortical and subcortical regions both during (repeated) encoding and, to a certain degree, during retrieval is positively related to the ability to remember the presented material. Thus, representational stability measured as the item-level similarity of neural activity patterns constitutes a representational property that benefits successful episodic memory.

Connecting representational stability and distinctiveness, the stability of neural patterns across repetitions can be compared to their similarity to other representations, which indicates the amount of stimulus-specific information. Hasinski and Sederberg (2016) related the stability of face representations to the representational similarity between different faces and revealed that only subsequently remembered faces showed larger stability than between-face similarity in the fusiform face area (FFA). This difference of within-item and between-item similarity is thus used as a measure of item specificity (see also, Kobelt et al., 2021; Sommer et al., 2021b; Xue et al., 2010; Zheng et al., 2018). The findings suggest that perceived information can be best remembered if eliciting stimulus-specific representations, that is, highly stable neural patterns and, in comparison, high distinctiveness between different representations. Given that most memory tasks require retrieving stimulus-specific information, it is plausible to assume that item specificity of neural representations is crucial for successful memory formation (Xue, 2018).

Together, the presented studies reveal that both the (dis)similarity between different representations (distinctiveness) and their similarity to themselves across repetitions and between encoding and retrieval (stability) reflect the fidelity of neural information representation and are important for memory performance. Thus, distinctiveness and stability are representational properties that provide crucial insights into the conditions under which experiences are successfully transformed into lasting memories and therefore may play an important role in the neurocognitive changes occurring during aging.

Age-related differences in neural representations

Aging is commonly associated with a loss in memory and other cognitive abilities. As the fidelity of information representation has been shown to be linked to memory success (see previous section), degraded quality of neural representational properties may explain age-related memory deficits. In line with the early idea that neural activity may become noisier in old age (Welford & Birren, 1965), an influential model by Li and colleagues suggested that cognitive aging was linked to deficient (mainly dopaminergic) neuromodulation, which increases neural noise and thus leads to less stable and less distinct neural representations (Li et al., 2000, Li et al., 2001; Li & Lindenberger, 2006; Li & Sikström, 2002). Accordingly, a prevalent hypothesis of cognitive aging states that neural representations become dedifferentiated with advancing age, with negative effects for cognitive abilities (neural dedifferentiation hypothesis; for recent reviews, see, Koen & Rugg, 2019; Koen et al., 2020).

First fMRI studies operationalized neural differentiation as how selectively regions in the ventral visual cortex (VVC) responded to their preferred stimulus categories, for example, FFA to face images and parahippocampal place area (PPA) to scene/house images. D. C. Park et al. (2004) showed that for young adults, the voxels that showed the largest BOLD response to stimuli from one category exhibited considerably less activity when stimuli from other categories were presented, but for older adults, the activation difference between these preferred and non-preferred categories was smaller. This provided evidence for age-related neural dedifferentiation in the form of reduced univariate regional selectivity and was replicated by a number of fMRI studies (e.g., Kobelt et al., 2021; Koen et al., 2019; Park et al., 2012; Pauley et al., 2021; Payer et al., 2006; Voss et al., 2008) that were also recently able to link this neural selectivity to memory performance (e.g., Kobelt et al., 2021; Koen et al., 2019).

By deploying multivariate analysis approaches, several further studies have also revealed reduced distinctiveness of the neural activation patterns elicited by different categories for older compared with younger adults (visual: Carp, Park, Polk et al., 2011; Kobelt et al., 2021; Koen et al., 2019; Park et al., 2010; Zheng et al., 2018; auditory: Lalwani et al., 2019). For example, Park et al. (2010) operationalized neural distinctiveness as how well a pattern classifier was able to differentiate between faces and houses based on the elicited BOLD patterns. Classification accuracy was lower in older adults compared to young adults, indicating age-related neural dedifferentiation. Other studies used the difference in similarity between representations of stimuli from the same and stimuli from different categories as an indicator of neural representational category specificity, which has been shown to be reduced in older adults (e.g., Carp, Park, Hebrank et al., 2011). To sum up, these findings provide evidence that neural representations are indeed less distinctive in old age, endorsing the neural dedifferentiation hypothesis.

The observed age differences in neural representational properties provide evidence to assume a link between degraded neural representations and the commonly reported behavioral findings in the aging literature, such as impaired general cognitive capabilities (Park et al., 2010), the declining ability to remember event-specific details (Bowman et al., 2019; Greene & Naveh-Benjamin, 2020; Koutstaal & Schacter, 1997), and the tendency to over-generalize and thus the proneness to false memories, especially regarding highly similar information (Fandakova et al., 2013, Fandakova et al., 2020; Schacter et al., 1997;

Sommer et al., 2021a; Toner et al., 2009). The fMRI study by Park et al. (2010) showed that neural category specificity (classification accuracy) in older adults was associated with fluid processing abilities (but not crystallized knowledge). More recently, Koen et al. (2019) identified a direct link between neural category specificity (within-category minus between-category similarity during scene and object encoding) and recognition performance for the same stimuli for both young and older adults in PPA (see also, Katsumi et al., 2021, but compare Kobelt et al., 2021, who did not find any association between category specificity and memory performance). Furthermore, St-Laurent et al. (2014) investigated the similarity between representations of individual short video clips during perception and mental replay. The BOLD patterns elicited by the different videos were more similar to each other in older adults than in young adults. This age-related increase in similarity was larger during recall than during direct perception. Although older adults freely recalled fewer details about the clips, these performance differences were rather linked to the stable reinstatement of the representations than to their distinctiveness (see below). The same observation of higher similarity among different neural representations during encoding in older adults compared to young adults was also made in an EEG study by Sommer et al. (2019). In the study, participants used an imagery strategy to learn associations of unrelated scenes and words that were later tested in cued recall tasks. Older adults' cued memory recall performance actually benefitted from their increased global similarity in EEG time–frequency patterns during learning, which is in line with the global matching theory (see above). In contrast, young adults' performance benefitted from more distinct neural representations, which was related to their stronger reliance on the imagery strategy that involved forming distinct mental images of the scene–word pairs. These results suggest a shift in encoding strategies from young to older adulthood that is reflected in the relationship of neural representational similarity and memory performance. In summary, the discussed studies are in line with the observations from the general memory literature that high representational distinctiveness is beneficial for memorizing the respective material (Kuhl et al., 2012) and reduced distinctiveness may explain worse cognitive performance in older adults.

In addition to neural distinctiveness, the stability across repetitions and the reinstatement of neural representations during memory retrieval have been demonstrated to be important for memory success. Zheng et al. (2018) compared item stability across repeated encoding between younger and older adults and found that, independent of their distinctiveness from other representations, the stability of item representations in the visual cortex was reduced in older adults. This was furthermore associated with lower memory performance compared with young adults. Crucially, item stability was an important contributor to memory performance as indicated by subsequent memory effects (Paller & Wagner, 2002). Adding evidence to the importance of representational stability, also Kobelt et al. (2021) demonstrated reduced neural stability in older adults, which was associated with recognition performance. St-Laurent et al. (2014) furthermore identified less stable cortical reinstatement of item representations during mental replay of short video clips in older adults compared with young adults. Older adults freely recalled fewer details about the videos, which was linked to their less precise neural reactivation (see also Deng et al., 2021; Folville et al., 2019). To sum up, in line with the predictions by Li and colleagues, there is accumulating evidence that age differences in the stability of representations across encoding repetitions and retrieval are a critical

factor contributing to age-related memory decline (see also, Abdulrahman et al., 2017; Thakral et al., 2017; Wang et al., 2016, for findings on age differences in category or task context reinstatement). This reduced neural stability may lead to reduced neural distinctiveness; however, their direct interrelationship has rarely been investigated (Hill et al., 2021; Kobelt et al., 2021; St-Laurent et al., 2014).

The difference of stability and between-item similarity is a measure of item-level specificity (e.g., Hasinski & Sederberg, 2016). That is, high item specificity depends on high representational stability as well as high representational distinctiveness, both of which are associated with memory performance (see previous section). Zheng et al. (2018) showed that the level of item specificity of the BOLD representations in visual cortex was related to memory performance, while evidence regarding age differences were less clear (Koen & Rugg, 2019). In contrast, Kobelt et al. (2021) found reduced item specificity in occipital cortices of older adults compared to young adults that was related to recognition performance beyond category specificity. In summary, the discussed findings indicate that beyond category-level distinctiveness also single items are represented less distinctively in old age (see also, Trelle et al., 2019). These results are in line with the model by Li and colleagues about age-related cognitive decline (e.g., Li et al., 2001) and the underlying neural representational changes, namely that increased variability in neural responses would lead to less stable and in turn less distinct neural representations (Li et al., 2001).

In addition to category and item representations, age-related reduced neural distinctiveness has been shown between different tasks (Carp et al., 2010; St-Laurent et al., 2011) and in other modalities including the motor (Carp, Park, Hebrank et al., 2011; Cassady et al., 2020), sensorimotor (Cassady et al., 2019), somatosensory (Cassady et al., 2020), and auditory system (Erb et al., 2020; Lalwani et al., 2019; Erb et al., 2020; Lalwani et al., 2019). A recent preprint furthermore showed positive correlations between category specificity across different domains, i.e., in visual, auditory, and motor cortices (Simmonite & Polk, 2021), indicating that there may be a shared mechanism across brain regions inducing less specific activation patterns in older adults (see also below).

All in all, the representational properties distinctiveness and stability have been shown to be subject to age-related differences, that are linked to memory performance differences. This provides further evidence that the precision with which information is encoded in neural activation patterns shapes how detailed the information can be retrieved. The quality of neural representations appears to change across the adult lifespan, explaining memory deficits in both healthy and possibly pathological aging (Maass et al., 2019). Especially the item specificity of neural representations has shown to be critical for memory performance across the adult lifespan and furthermore addresses the relationship between distinctiveness and stability to each other.

Furthermore, investigating the neuromodulatory basis of altered neural representations across adulthood is currently a great matter of interest. In addition to the model by Li and colleagues (see above) that connected reduced neural distinctiveness mainly to deficient dopaminergic modulation, age-associated reduction in single-neuron selectivity of non-human animals has also been linked to a decline in inhibitory neurotransmission by gamma-aminobutyric acid (GABA; Ding et al., 2017; Hua et al., 2008; Leventhal et al., 2003). This relationship has also been demonstrated in humans (Cassady et al., 2019; Chamberlain et al., 2021; Lalwani et al., 2019): Measuring neural

distinctiveness with fMRI and GABA levels with magnetic resonance spectroscopy (MRS), it was found, for example, that individual differences in the neural distinctiveness of faces versus houses (Chamberlain et al., 2019) and music versus speech (Lalwani et al., 2019) were related to individual differences in GABA levels in older adults, suggesting a contribution of GABA in age-related neural dedifferentiation. Other studies showed that GABA concentrations were positively related to cognitive performance and thus reduced GABA levels in old age were linked to cognitive deficits (Hermans et al., 2018; Porges et al., 2017; Simmonite et al., 2019). These findings establish the key role of proficient neuromodulation for high-fidelity (i.e., stable and distinct) neural representations and cognitive performance and prepare for future research using multivariate analysis approaches for illuminating how age-related deficits in neuromodulation are related to altered neural representations in old age.

Conclusion

Multivariate pattern similarity analysis methods are a versatile tool that enable neuroscientists to study the neural representations underlying episodic memory performance and how they differ across adulthood. In particular, the distinctiveness, stability, and specificity of neural activation patterns have been identified as important predictors of memory success that differ between younger and older adults. This allows critical insights into the neural basis of cognitive decline in old age, for instance, by testing the predictions of the neural dedifferentiation hypothesis. Future studies should furthermore examine the longitudinal development of these representational properties across the lifespan to gain an understanding of the neural and cognitive changes occurring during aging.

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