Research Articles | Behavioral/Cognitive

Mnemonic but not contextual feedback signals defy dedifferentiation in the aging early visual cortex

1 **Mnemonic but not contextual feedback signals defy dedifferentiation in the**

2 **aging early visual cortex**

3 **Abbreviated Title: Dedifferentiation in feedback signals**

4

5 Isabelle Ehrlich[1*], Javier Ortiz-Tudela[12], Yi You Tan[1], Lars Muckli[3], Yee Lee Shing[145*]

6

7

8 [1]Department of Psychology, Goethe University Frankfurt, 60323 Frankfurt Am Main,
9 Germany.
10 [2]Mind, Brain, and Behavior Research Center, Department of Experimental Psychology,
11 University of Granada, Spain.
12 [3]School of Psychology and of Neuroscience, University of Glasgow, G12 8QB United
13 Kingdom.
14 [4]IDeA Center for Individual Development and Adaptive Education, 60323 Frankfurt am
15 Main, Germany.
16 [5]Brain Imaging Center, Goethe University Frankfurt, 60528 Frankfurt am Main, Germany.

17

18 ***Corresponding authors:**
19 Isabelle Ehrlich (ehrlich@psych.uni-frankfurt.de)
20 Yee Lee Shing (shing@psych.uni-frankfurt.de)

21

22 Number of pages: 42
23 Number of figures: 6
24

27 Introduction: 691
28 Discussion: 1618
29
42
43

44

45

Abstract

Perception is an intricate interplay between feedforward visual input and internally generated

feedback signals that comprise concurrent contextual and time-distant mnemonic (episodic

and semantic) information. Yet, an unresolved question is how the composition of feedback

signals changes across the lifespan and to what extent feedback signals undergo age-related

dedifferentiation, i.e., a decline in neural specificity. Previous research on this topic has

focused on feedforward perceptual representation and episodic memory reinstatement,

suggesting reduced fidelity of neural representations at the item and category levels. In this

fMRI study, we combined an occlusion paradigm that filters feedforward input to the visual

cortex and multivariate analysis techniques to investigate the information content in cortical

feedback, focusing on age-related differences in its composition. We further asked to what

extent differentiation in feedback signals (in the occluded region) is correlated to

differentiation in feedforward signals. Comparing younger (18 - 30 years) and older female

and male adults (65 - 75 years), we found that contextual but not mnemonic feedback was

prone to age-related dedifferentiation. Semantic feedback signals were even better

differentiated in older adults, highlighting the growing importance of generalized knowledge

across age. We also found that differentiation in feedforward signals was correlated with

differentiation in episodic but not semantic feedback signals. Our results provide evidence for

age-related adjustments in the composition of feedback signals and underscore the importance

of examining dedifferentiation in aging for both feedforward and feedback processing.

4

Significance Statement

Cognitive decline in aging is related to reduced neural specificity (dedifferentiation) in the brain, which has mainly been examined in feedforward processing. Using an occlusion paradigm, we tested whether there is dedifferentiation in contextual and mnemonic feedback signals internally generated in the early visual cortex to aid perception. Older adults' contextual but not mnemonic feedback signals suffered from dedifferentiation, with semantic mnemonic representations being even better differentiated in older age. Neural differentiation between feedforward and episodic feedback signals was positively correlated in both age groups. In sum, these results highlight the growing importance of semantic knowledge across the lifespan and imply that the impact of dedifferentiation on cognition highly depends on the nature of the recruited information.

5

Introduction

100 **Introduction**

101 Throughout the lifespan, our brain undergoes structural and functional changes. A notable

102 pattern emerges within the memory systems as we approach later stages of life: episodic

103 memory tends to decline, while semantic memory is mostly preserved (Shing et al., 2008;

104 Ofen and Shing, 2013; Lalla et al., 2022). At the same time, the notion of *dedifferentiation*

105 has emerged in the literature as an important factor contributing to age-related functional

106 changes in cognition. Age-related dedifferentiation refers to the finding that neural

107 representations become less distinct with advancing age and, therefore, less representative of

108 the evoking stimulus. Support for this view comes from non-human animal (Schmolesky et

109 al., 2000; Yang et al., 2008, 2009) and human neuroimaging studies, which showed that

110 neural selectivity for visual stimuli declines with age (Voss et al., 2008; Zheng et al., 2018;

111 Koen et al., 2019, 2020). The visual system has been widely used for studying neural

112 differentiation (Park et al., 2004; Payer et al., 2006; Carp et al., 2010, 2011a, 2011b). Its

113 hierarchical and retinotopic organization allows the mapping of the visual field onto brain

114 voxels, which enables nuanced control of the feedforward input reaching a given portion of

115 the visual cortex. In this study, we combined nuanced control with multivariate analysis

116 techniques to enable us to test the influence of internal models on the constellation and quality

117 of perceptual representations.

118   State-of-the-art models of perception recognize the brain's heavy reliance on internal

119 representations of the outside world that are formed early in life and updated throughout the

120 lifespan (Berkes et al., 2011; Larkum, 2013; Shin et al., 2021). The predictive processing

121 framework integrates this influence, postulating that feedback signals travel from higher-level

122 brain areas to the earliest sensory regions (Rao and Ballard, 1999; Friston, 2005; Clark, 2013).

123 Importantly, neural units and long-range connections transmitting internally generated

124 feedback signals are distinct from and proportionally more numerous than pathways

125 transmitting external feedforward visual input (Markov et al., 2014). As a result, feedback

6

126   signals can traverse the visual hierarchy and powerfully drive disambiguation of the percept at

127   early stages. Thus, exploring to what extent age-related dedifferentiation manifests in these

128   top-down directed perceptual processing streams can provide key insights into the interplay

129   between mnemonic and perceptual systems.

130   So far, several studies have investigated age-related dedifferentiation in feedback

131   signals mostly in the form of memory reinstatement (Bowman et al., 2019; Deng et al., 2021;

132   Katsumi et al., 2021; St-Laurent et al., 2011, 2014). The overall finding is that

133   dedifferentiation affects the older brains' integrity by acting on both feedforward sensory

134   input and internally generated representations of information. A recent study by Ortiz-Tudela

135   and colleagues (2023) showed that feedback signals carry information of different natures.

136   More concretely, their results showed that concurrent contextual and time-distant mnemonic

137   information coexist as feedback signals in primary and secondary visual cortices V1 and V2.

138   Concurrent contextual information refers to visual input that does not reach a given brain

139   region via feedforward but lateral connections. Time-distant mnemonic information describes

140   content drawn from stored knowledge acquired in the past. They found that mnemonic

141   episodic and semantic components explained different portions of the variance of the

142   multivariate neural pattern of feedback signals. Such compositional complexity of feedback

143   signals has not been considered in studies of age-related dedifferentiation so far.

144   In this study, we combined an occlusion paradigm with fMRI and multivariate pattern

145   analysis to examine: 1) if concurrent contextual and time-distant mnemonic information can

146   be decoded in feedback signals within V1 and V2 of older adults, as it was found in younger

147   adults; 2) if feedback signals in older adults are less differentiated; and 3) how the

148   relationship between feedforward and feedback signals is characterized across age. We

149   hypothesized to find contextual and mnemonic information in older adults' V1 and V2

150   feedback signals. Compared to contextual feedback, we expected mnemonic episodic, but not

151   semantic, feedback to be impacted by age-related dedifferentiation, as episodic memory

7

152 decline is a well-established aging phenomenon. Finally, we predicted a positive relationship

153 between feedforward and feedback signals in older compared to younger adults. To our

154 knowledge, this is the first study that examined the detailed interplay of feedforward and

155 feedback components in a cross-sectional lifespan sample.

156

157 **Materials and Methods**

158 **Reanalysis of published data and registration**

159   The current study is an extension of a previous study by Ortiz-Tudela et al. (2023),

160 which reported data from 30 younger participants. We collected additional data from younger

161 adults to match the sample size of older adults. All reported results for younger adults in this

162 study refer to the topped-up sample. We pre-registered the study prior to data collection on

163 the OSF platform. The preregistration is available at https://doi.org/10.17605/OSF.IO/X7B6Z,

164 and any deviations from it are indicated in the corresponding sections.

165

166 **Participants**

167   We conducted sensitivity and a priori power analyses using G*Power (Faul et al.,

168 2007) and validated the results using WebPower (version 0.6; Zhang & Yuan, 2018). Based

169 on the data of Ortiz-Tudela et al. (2023), we obtained a minimal statistically detectable effect

170 size of $f = .37$. The sample size calculation resulted in 80 participants, i.e., 40 participants per

171 age group to detect this effect with a power of .90 and an alpha of .05. For the younger adults'

172 sample, we reused 30 participants from the Ortiz-Tudela et al. (2023) study and recruited

173 additional 15 younger adults between 18 and 30 years of age via advertisements across the

174 campus of the Goethe University Frankfurt. We excluded three participants in the younger

175 adults' sample due to low training performance ($< 80\%$) on day one, one due to low retrieval

176 performance ($< 25\%$) in the post-scan phase on day two, three due to technical issues during

177 scanning, one because of excessive movement, and one participant who had diagnosed

8

aphantasia. Additionally, we recruited 46 healthy older adults between 65 and 74 years of age via E-Mail advertisements to attendees of the University study program for the third age and via invitation letters to residents within the required age range. We excluded two participants due to low training performance ($< 80\%$) on day one, another one due to low retrieval performance ($< 25\%$) in the post-scan phase on day two, two due to MRI incompatibility, one due to technical issues during scanning, and one participant due to no-show on day two. The final sample included 36 younger adults (23 female, M= 24.18 years, SD = 2.54) and 39 old adults (18 female, M = 69.28 years, SD = 2.99). Before participation, we screened all participants for MRI compatibility, visual capacity, and state of health via phone. We tested older adults additionally with a phone-compatible version of the Mini-Mental State Examination (Folstein et al., 1975) and invited them only if they correctly responded to 16 out of 18 questions. All participants gave written informed consent as approved by the Department for Psychology ethics committee at Goethe University Frankfurt (Protocol number: 2019-38). For their participation, participants received either course credits (only for psychology students) or monetary compensation (8€/h for behavioral tests and 10€/h for the fMRI session).

Stimuli and materials

The stimulus set consisted of the same cartoon image material as in the study from Ortiz-Tudela et al. (2023) and is available at https://github.com/ortiztud/feedbes. It comprised 16 indoor room images (e.g., bathroom, kitchen, electronic store) and four object images (i.e., bathtub, oven, bed, and TV). With this material, we created two sets of object-room category pairs. One set consisted of eight combinations with minimal semantic relation (e.g., "bed" in "bathroom"), providing the stimulus material for the episodic trials. The episodic nature of these combinations is given by the need to create new associative memories binding object and room context, which must be retrieved 24 hours later during the fMRI scan. The other set

9

204 consisted of eight combinations with maximal semantic relation (e.g., "oven" in "kitchen"),

205 providing the stimulus material for the semantic trials. Note that the same four objects were

206 used for episodic and semantic trials, but the rooms were unique for each trial type. This was

207 done to ensure comparability between the retrieved object content for episodic and semantic

208 trials and to equate the difficulty between the pairings as much as possible. Object-room

209 combinations and the assignment of room categories to either episodic or semantic trials were

210 counterbalanced across participants. Thereby, we preserved the required (in)congruent

211 relationships in the respective stimulus sets and ensured that every object would be presented

212 in every possible room and in episodic trials as well as semantic trials across the entire

213 sample. Importantly, the objects were always placed in the lower right corner of the room.

214 Depending on the task, they were either visible or hidden behind a white patch that occluded

215 the respective corner. Previous studies successfully used such an occlusion paradigm to

216 separate feedback signals from feedforward visual input (Smith and Muckli, 2010; Muckli et

217 al., 2015; Morgan et al., 2019). During the learning phase on day one, we presented the

218 stimuli on a 60 Hz monitor (resolution 1680 x 1050, full HD) approximately 60 cm from the

219 participant's head. Subjects responded using a standard QWERTY keyboard. In the scanner,

220 participants saw the stimuli on a 60 Hz monitor (resolution 1920 x 1080, full HD) via a coil-

221 mounted mirror with an approximate total distance of 162 cm to the participants' eye. The

222 size of the stimuli spanned 16.4° x 12.1° of visual angle.

223

224 **Procedure**

225 For younger adults, the procedure was identical to the original study (see Ortiz-Tudela

226 et al., 2023). All necessary adjustments to ensure that older adults could manage the task as

227 similarly as younger adults are specified in the corresponding sections. The procedure was

228 split into two sessions across two consecutive days.

229

Day one

The first session took place in a quiet testing room. Participants started the first session by answering a set of questionnaires, including the Vividness of Visual Imagery Questionnaire (Marks, 1973), the Spot-the-Word test (Baddeley et al., 1993), the Digit Symbol test, which is a subtest of the Wechsler Adult Intelligence Scale (Wechsler, 1981), and the Health Dynamics Inventory (Saunders and Wojcik, 2004). After that, they proceeded with the learning phase.

Learning phase

In the learning phase, the participant's task was to study and remember the episodic object-room pairs, i.e., combinations with minimal semantic relation (Figure 1A). Younger and older participants underwent five and nine learning cycles, respectively, in which the object-room pairs were presented for 10 s sequentially and repeated ten times. The number of additional learning cycles was piloted to make sure that old adults could reach the threshold of at least 80% accuracy in the final block in order to compensate for the known decline of episodic memory in older adults (Shing et al., 2008). We instructed participants to memorize the object-room combinations and as many details as possible, including the object's exact position in the lower right corner. At the end of each learning block, their memory of the object-room pairings and the object's position was tested. In a 4AFC format, we presented a previously studied room with a white occluder and the four available objects; participants selected one object by pressing a number key, ranging from 1 to 4, on the keyboard with their left hand. We tested the remembered position by presenting the same room with the correct but slightly displaced object and asked the participants to move the object to its original place by pressing the arrow key corresponding to the moving direction with their right hand. While younger adults pressed the keys independently within a 2-s time window, older adults indicated their choice verbally, and the experimenter pressed the keys on their behalf within a

256 4-s time window. We adjusted the procedure after observing in pilots that some older adults

257 struggled to coordinate choice and response in time.

258   After completing all learning cycles, we familiarized participants with the structure

259 and timing of the scanner task on day two. In this task, the episodic rooms with the occluder

260 were presented sequentially for four seconds each; participants were instructed to fixate on the

261 cross in the center of the screen and to reinstate and hold the room in mind, including the

262 learned object in its original position. After each trial, participants rated the vividness of the

263 retrieved object on a 4-point Likert scale. Younger adults entered their ratings via the

264 keyboard, and older adults responded verbally. Finally, all participants conducted another

265 learning block to refresh their memory for the object-room pairs. Unlike in the preregistration

266 announced, participants did not additionally draw the objects on a printed version of the

267 occluded rooms due to time limitations.

268

269 **Day two**

270   The second session took place at the Brain Imaging Center (Frankfurt am Main).

271

272 *Pre-scan phase*

273   Before entering the scanner, we introduced participants to the semantic object-room

274 pairings (Figure 1B), with all rooms being novel to the participants. The eight new room

275 images appeared one after another, always with the occluder, and participants had to name

276 one among the four studied objects with the best semantic fit. The experimenter gave

277 feedback on incorrect object choices. Unlike the episodic object-room pairings, the semantic

278 room images were never directly shown together with the objects to participants. Older adults

279 were exposed to the semantic rooms for two more rounds and received additional practice. In

280 this practice, we presented both episodic and semantic rooms with occluder in random order,

281 and participants had to indicate the correct associated object, which was, depending on the

12

room, semantically or episodically retrieved. We added this practice to ensure that older

adults would understand the alternating order of episodic and semantic trials in the occlusion

task during scanning and would retrieve the required object depending on the presented room.

Scanning phase

The reported structure of the scanning session was identical to the one in Ortiz-Tudela

et al. (2023). The scanning sequences were distributed across two blocks of approximately 50

minutes, with a ten-minute break in between these two blocks. The break allowed participants

to go to the bathroom and refresh themselves to prevent discomfort and unwanted

movements. In block one, participants performed two occlusion task runs, a structural scan

and a functional retinotopy run. In block two, participants performed two more occlusion task

runs, another structural scan, another functional retinotopy scan, and a sensory template run.

One additional functional scan and one additional anatomical scan were collected but not used

for this project, and thus, they are not discussed further.

Occlusion task. Each of the four occlusion task runs presented all episodic and semantic

rooms intermixed. We optimized the presentation order using the MATLAB toolbox easy-

optimize-x by Spunt (2016) to obtain the most efficient design for detecting activation

differences between episodic and semantic trials. A white patch occluded the lower right

corner of the rooms, and a fixation cross designed to minimize unwanted eye movements

(Thaler et al., 2013) on a small white square covered the foveal region. In each run, all 16

rooms were repeated six times with a presentation duration of 4 s and an inter-trial interval of

2 s. Each run lasted 576 s. While the room images flashed at a 5 Hz frequency, the white

patches and the fixation cross remained stable, helping the participants focus their gaze on the

center of the room. We asked participants not to move, to focus on the fixation cross, and to

retrieve the associated object as vividly as possible. When an episodic room (studied on day

13

one) was presented, they had to retrieve the object that was studied together with this room on

day one (i.e., episodic trial). When a semantic room (introduced on day two) was shown, the

object with the best semantic fit had to be retrieved (i.e., semantic trial). This procedure

ensured the comparability of episodic and semantic trials, with the main difference being the

mnemonic retrieval route accessed by the participants.

Sensory Template. In order to compare feedback with feedforward signals, we ran an

additional task in which we showed the 16 correct object-room pairings 12 times (without

occlusions) for 1.5 s with an inter-trial interval of 1 s. The run lasted 480 s. We optimized the

presentation order, as in the occlusion task runs, using easy-optimize-x (Spunt, 2016).

Participants fixated on the cross in the center of the screen and performed a 1-back task,

which served as a cover task to ensure attention was paid to the stimuli. Whenever they

detected image repetitions, they had to press a button with the index finger on an MRI-

compatible button box.

Functional Retinotopy and Target Area Mapping. We used standard stimulation

procedures to demarcate the early visual cortex (EVC) primary and secondary subfields V1

and V2. For eccentricity mapping, we showed flashing and expanding contrast-reversing

checkerboard rings (9 cycles, 56 seconds/ expansion). For polar angle mapping, we showed a

flashing and rotating contrast-reversing checkerboard wedge (eight clockwise rotations, 64

seconds/ rotation). Through target area mapping, we identified voxels that topographically

represented the lower right corner within areas V1 and V2. To this end, we used two different

checkerboard patterns. The first pattern spanned 1° of visual angle along the inner boundary

of the occluded lower right corner, and the other pattern covered the remaining inside of the

occluded region. Voxels that represented the boundary of the occluder were eventually

excluded from further analyses to prevent spillover from adjacent receptive fields and to have

14

334 a buffer for small misalignments across functional runs (Smith and Muckli, 2010). For further

335 details, see the identical procedure in Ortiz-Tudela et al. (2023).

336

Post-scan phase

338   After both scanning blocks, we asked participants to do one last retrieval task on a

339 laptop outside the scanner. Identical to the memory test for object-room pairings and object

340 position on day one, each occluded room was presented together with the four available

341 object options. The presentation order was sequential, with all rooms from the episodic set

342 showing first, followed by all semantic rooms. As on day one, younger adults pressed the

343 number and arrow keys themselves with their left hand and within 2s, and older adults

344 communicated their decision verbally to the experimenter, who pressed the keys on their

345 behalf within 4s.

346

MRI setup and data acquisition

348   We scanned participants with a 3.0 Tesla Siemens MAGNETOM Prisma scanner with

349 a 32-channel head coil system. 3D structural scans (MPRAGE sequence; resolution: 1 x 1 x 1

350 mm; iPAT factor: 2) were acquired in both blocks for anatomical reference. Echo-planar

351 imaging sequences (EPI; TE=38ms; TR = 800ms, resolution = 2 x 2 x 2 mm; MB factor = 8;

352 flip angle= 52°; field of view = 208 mm; 72 axial slices, phase encoding direction = AP) were

353 applied to measure the brains' blood oxygen level-dependent (BOLD) response. After the first

354 occlusion task run in each block, we acquired five extra volumes for each phase-encoding

355 direction to allow susceptibility distortion correction in EPI sequences.

356

Behavioral data analysis

15

358   We conducted all behavioral analyses in R (version 4.0.3; R Core Team, 2020) and

359   used the results to explore the data and to identify participants performing below a threshold

360   of 80%.

361

362   **fMRI data analysis**

363   *Preprocessing*

364   Except for the retinotopic and target mapping runs, we preprocessed the fMRI data

365   using fMRIPREP 20.1.1 (Esteban et al., 2019, 2020). fMRIPREP's output provides a CC0-

366   licensed citation boilerplate that includes all preprocessing details. As requested by

367   fMRIPREP's authors, an unchanged copy is available in the corresponding OSF repository.

368   The preprocessing of retinotopic and target mapping runs was conducted in BrainVoyager

369   21.4 (Brain Innovation) for Linux and included slice time correction, 3D motion correction,

370   and temporal high-pass filtering at 0.01 Hz with linear detrending.

371

372   *ROI definitions*

373   We defined regions of interest as the subset of voxels in the left EVC for V1 and V2,

374   topographically representing the room images' lower right corner. In this corner, the object

375   was either presented as feedforward visual input (in the sensory template run) or covered (in

376   the occlusion task runs). Covering the corner removed any meaningful feedforward visual

377   stimulation because all the trials in the occlusion task included the same-sized white patch in

378   the identical position. We conducted all further analyses on this particular subset of voxels.

379   We created masks for early visual areas V1 and V2 using standard retinotopic mapping

380   procedures (see Retinotopic and Target mapping section) and manual delineation of the

381   subfields. The resulting masks were restricted exclusively to the voxels representing the

382   room's lower right corner using the target mapping run (see Ortiz-Tudela et al. (2023) for a

383   detailed procedure description).

384

Generalized linear model

386   We extracted single-trial beta estimates by applying a Least Squares Separate (LSS)

387 approach, where each trial is modeled as a separate regressor (Mumford et al., 2012;

388 Abdulrahman and Henson, 2016). For each of the four occlusion task runs, we computed 96

389 GLMs. A single GLM comprised one regressor for the onset of the current trial, 16 regressors

390 for the onsets of each room, six raw head motion regressors (three for displacement and three

391 for rotation), and three regressors for global, WM, and CSF intensities. For the sensory

392 template run, we conducted 192 GLMs with the same combination of regressor coefficients.

393 In our preregistration, we planned to include six additional nuisance regressors for volume-to-

394 volume eye motion measures in each spatial axis for each eye. We extracted the eye bulbs of

395 each participant using Eye State fMRI (Brodoehl et al., 2016) to compute directional vectors

396 for each eye along the anteroposterior axis in a three-dimensional space (x,y,z). However, in

397 our older adults sample, due to large head sizes, the EPI's field of view (208 mm) did not

398 always include a sufficient portion of the eye bulbs to calculate those directional vectors

399 reliably. Thus, to provide comparability of findings across age groups, we decided not to

400 include regressors for eye motion in either sample.

401

Multi-voxel pattern analysis

403   We applied multivariate pattern analysis (MVPA) to decode the different components

404 of feedback signals in nonstimulated voxels of V1 and V2 during the occlusion task. We used

405 binary linear support vector machine (SVM) classifiers with a 4-fold leave-one-run out cross-

406 validation procedure. We trained classifiers on three of four occlusion task runs (288 trials)

407 and tested on the remaining run (96 trials). We repeated this train-test procedure for all four

408 runs and averaged the resulting classification accuracies across folds. All classification

409 analyses were performed separately for episodic and semantic trials. Figure 2 illustrates the

410 classification schemes we adopted to decode the specific feedback components, i.e.,

411 contextual and mnemonic. Contextual refers to the visual information provided by the room

412 image surrounding the occluded region. This contextual information is fed through lateral

413 connections to the adjacent nonstimulated receptive fields, where it can be used to

414 disambiguate the percept and aid the retrieval of the associated object. To capture contextual

415 information in V1 and V2, we trained a classifier with and tested on "same object – different

416 room" combinations (i.e., the two class labels share the object but differ in the room) so that

417 only contextual feedback could provide the classifier with information to discriminate

418 between room and object. Mnemonic refers to the object information retrieved through an

419 episodic or semantic route and transmitted to nonstimulated receptive fields in V1 and V2.

420 We trained another classifier based on a cross-classification schema to decode mnemonic

421 information. The training set consisted of "different object – different room" combinations

422 (i.e., the two class labels neither share the object nor the room), in which the classifier learned

423 to discriminate between object and room using both feedback information types. A classifier

424 tested in this set could use either (or both) the object and the room to discriminate the classes.

425 However, when tested on a different subset of rooms that shared the same objects across

426 training and test sets, above-chance classification could be achieved only by relying on the

427 mnemonic object information. We chose this more conservative cross-classification schema

428 as it prevents using any learned room information and enables classification solely on object

429 information. Note that an alternative classification schema would be training a classifier with

430 and testing on "different object – same set of rooms" combinations. However, this

431 combination was not part of the experimental design and would lead to interference if a

432 particular room cues two different objects. We performed all decoding analyses with The

433 Decoding Toolbox (Hebart et al. (2015). We averaged classification estimates across

434 participants and tested for significance using a two-step bootstrapping approach (Stelzer et al.,

435 2013). An accuracy distribution was created for each participant by randomly permuting the

trial labels 100 times and calculating classification accuracies for each iteration. We drew a

random sample (with replacement) from each distribution and averaged across participants

1000 times, thus creating a null distribution of 1000 average accuracies. If classification

estimates were larger than 99.9% of the accuracies in the null distribution (p < .001), they

were considered significant. For age group comparisons, we used linear mixed effect models

(LMMs, lmer function in the *lme4* package; Bates et al., 2015) instead of ANOVAs, as

written in the preregistration, to control for additional variance attributed to participants. Age

group (older versus younger), trial type (episodic versus semantic), and ROI (V1 versus V2)

were included as predictors and random intercepts were specified per subject. For main effect

testing, we calculated type-II Wald F tests using the Anova function in the *car* package (Fox

and Weisberg, 2019) and type-III Wald F tests for interaction testing. Confidence intervals

were determined using the confint function from the *stats* package (R Core Team, 2020).

Representational similarity analysis

For each participant, we used single-trial beta estimates to compute Representational

Dissimilarity Matrices (RDMs) between every pair of individual trials (Kriegeskorte et al.,

2008). We calculated all RDMs using The Decoding Toolbox (Hebart et al., 2015). As

distance measures, we used the cross-validated Mahalanobis distance for the occlusion task

RDMs and Pearson r for the single-run sensory template RDMs.

Model correlations

To investigate to what extent contextual and mnemonic information is represented in

feedback signals within both ROIs, we created two model RDMs that reflected the ideal

correlation pattern for each feedback component (see Figure 3). Both model matrices were

equally sized as the individual neural RDMs, spanning 96x96 trials (48 episodic and semantic

trials, respectively). The contextual model had zero values for "same object – same room"

462 cells because we expected those combinations to have the lowest dis-similarity and maximal

463 values (i.e., ones) for the remaining high dissimilarity cells. The diagonal, containing only

464 zeros, was excluded from all analyses. In the mnemonic model, we expected the lowest

465 dissimilarity for "same object – different room" cells, therefore having zero values. "Different

466 object – different room" cells had maximal values representing the highest dissimilarity.

467 "Same object – same room" cells were removed as the low dissimilarity between the same

468 rooms would artificially reduce the final dissimilarity measure, which should be solely based

469 on the object. Both models were Spearman rank correlated with all individual RDMs.

470 Correlating the dissimilarity matrices results in correlation values that can range from zero to

471 one, with low values representing low similarity between the model and individual RDMs and

472 high values representing high similarity between the model and individual RDMs. The

473 correlation coefficients were Fisher-z transformed and compared against zero using Wilcoxon

474 signed-rank tests (wilcox.test function from *stats* package, R Core Team, 2020). As for

475 MVPA, we performed age comparisons using LMMs with random intercepts per participant,

476 and model (object versus room), trials (episodic versus semantic), and age (older versus

477 younger) as predictors.

478

479 *Differentiation index*

480   Similar to the procedure in Koen et al. (2019), we calculated Differentiation indices

481 (DIs) to obtain a measure for the specificity of neural responses. For the DI calculation, we

482 used the dissimilarity values from the individual neural RDMs and subtracted the average

483 within from the average between dissimilarities. *Within* dissimilarity refers to the pairwise

484 distance of trials that share the same object, for example, TV versus TV, whereas *between*

485 dissimilarity refers to the pairwise distance of trails comprising different objects, for example,

486 TV versus bathtub. Thus, well-preserved neural differentiation is represented by higher DIs

487 resulting from lower within and higher between dissimilarities. We computed DIs for each

20

488   participant, occlusion task trials (episodic or semantic), and ROI. We followed the same

489   procedure for the sensory template runs. DIs for the occlusion task are henceforth referred to

490   as feedback DIs, and DIs for the sensory template run as feedforward DIs. We contrasted the

491   resulting indices against zero with one-sided Wilcoxon tests and conducted age group

492   comparisons separately for feedforward and feedback DIs using LMMs with age (older versus

493   younger), trial type (episodic versus semantic), and ROI (V1 versus V2) as predictors and

494   random intercepts per subject.

495

496   *Correlation of feedforward and feedback differentiation indices*

497   We transformed all feedforward and feedback DIs into z-scores. Note that a single

498   feedforward DI was computed per participant and ROI as the 1-back task in the sensory

499   template run did not include a distinction between episodic and semantic trials. Outliers were

500   defined as DIs above or below 3.29 standard deviations (signaling the most extreme 0.1%)

501   from the mean and excluded from further analyses. For younger adults, we removed two

502   feedforward and two feedback outliers from DI data of ROI V2, and for older adults, we

503   excluded two feedforward and one feedback outlier from DI data of ROI V1. Finally, we

504   Spearman correlated (one-sided) the average feedforward DIs with episodic and semantic

505   feedback DIs separately for age groups and ROIs. All p-values were adjusted using the

506   Benjamini & Hochberg correction (Park et al., 2010).

507

508   **Results**

509   **Behavioral results**

510   *Training performance on day one*

511   Both age groups learned the object-room associations successfully across their designated

512   number of learning cycles, i.e., five for younger and nine for older adults, plus one refresher

513   cycle at the end of the session. All participants crossed the threshold of at least 80% learning

21

514   performance either in the last training or in the refresher cycle at the latest. Figure 4 shows the

515   learning progress of both age groups for object recognition and object position memory,

516   respectively.

517

518   *Post-scan memory performance on day two*

519   After being scanned, we tested participants' memory for object-room associations and object

520   position to ensure they maintained the required retrieval performance during scanning. On

521   average, both age groups performed above 80 % in both trial types (episodic: $M_{younger}$ = .81,

522    $SD_{younger}$ = .16; M_{older} = .86, SD_{older} = .16; semantic: $M_{younger}$ = .84, $SD_{younger}$ = .15, M_{older} = .95,

523   SD_{older} = .07). Unpaired two-sided t-tests showed no differences across age groups in episodic

524   trials for either object memory ($t(68.49)$ = -1.43, p = .156) or object position ($M_{younger}$ = .77,

525    $SD_{younger}$ = .18, M_{older} = .78, SD_{older} = .21, $t(69.95)$ = -0.24, p = .805). The mean recognition

526   memory performance for objects from semantic trials was better for older compared to

527   younger participants ($t(43.77)$ = -3.61, p <.001).

528

529   **fMRI results**

530   The previous study with only younger adults (Ortiz-Tudela et al., 2023) showed that

531   contextual and mnemonic feedback signals contributed to the activation pattern in

532   nonstimulated voxels of the primary and secondary visual cortices V1 and V2. Interestingly,

533   the extent to which mnemonic feedback signals fed down to these early cortices depended

534   critically on the retrieval route. That is, only episodic mnemonic content was represented but

535   not semantic mnemonic content. This difference in content was revealed through RSA, which

536   was conducted after observing that the initial MVPA decoding approach was only sensitive to

537   contextual information and failed to capture mnemonic information.

538   Notably, the lifespan trajectories of episodic and semantic memory are different;

539   semantic memory remains relatively stable across age with later and less decline than episodic

540   memory (Li et al., 2004; Rönnlund et al., 2005). We, therefore, hypothesized that the

541   individual components of feedback would also change with age. More concretely, we

542   expected that the amount of episodic feedback would be reduced in older adults. Semantic

543   feedback, on the contrary, should be less affected by age-related changes as semantic memory

544   content tends to be relatively preserved in older age (Nyberg et al., 2003, 2012; Haitas et al.,

545   2021). Hence, we anticipated less or no decay in semantic feedback signals compared to

546   episodic feedback signals. For contextual feedback signals, we expected no substantial

547   differences between age groups because the contextual visual input was identical and

548   immediately available, and any visual impairment was corrected for all participants with

549   appropriate MRI-compatible glasses.

550

551   *Decoding contextual (and mnemonic) feedback signals*

552   Following the previous study by Ortiz-Tudela et al. (2023), we addressed our

553   hypothesis first with a classifier-based approach. We set up two classification schemes to

554   decode contextual and mnemonic information, respectively, from nonstimulated voxels of V1

555   and V2 (for details about classifier arrangements, see MVPA section). The first classifier

556   arrangement aimed at capturing contextual room information. In both age groups, the

557   classifier performed above chance level (.50) for both episodic and semantic trials in both

558   ROIs (younger adults: $V1_{epi}$ = .69, $V2_{epi}$ = .68, $V1_{sem}$ = .65, $V2_{sem}$ = .66; older adults: $V1_{epi}$ =

559   .58, $V2_{epi}$ = .58, $V1_{sem}$ = .58, $V2_{sem}$ = .58, all p's < .001; one-sided one-sample t-test). Linear

560   mixed model analysis revealed a significant main effect of age on contextual room

561   information, with classification accuracy in older adults being lower than in younger adults (β

562   = -0.077, 95% CI [-0.111, -0.043], t = -4.424, p < .001). These results replicate and extend

563   previous findings by showing that contextual information is a reliably traceable constituent of

564   feedback signals in nonstimulated voxels of early visual areas not only in younger but also in

565   older adults. Although we did not anticipate a significant age effect on contextual feedback,

23

566 the result is in line with some studies that found an age-related decrease in neural specificity

567 within feedback signals (St-Laurent et al., 2014; Trelle et al., 2019).

568   The second classifier arrangement aimed at capturing mnemonic object information.

569 The classifier did not perform above chance level (.50) in younger or older adults. Therefore,

570 we were unable to look further into age comparisons (younger adults: $V1_{epi} = .49$, $V2_{epi} = .47$,

571 $V1_{sem} = .49$, $V2_{sem} = .49$; older adults: $V1_{epi} = .51$, $V2_{epi} = .51$, $V1_{sem} = .50$, $V2_{sem} = .51$, all

572 p's> .05, one-sided one-sample t-test). This classification failure in older adults replicates the

573 previous study's finding with younger adults (Ortiz-Tudela et al., 2023). Nevertheless, this

574 null result does not rule out the possibility of mnemonic object information existence in

575 feedback signals. We reasoned that the classifier might have failed to decode object

576 information at test because it might have learned to classify primarily based on room

577 information and consequently could not generalize its' knowledge to a test set of new rooms.

578

579 *Coexistence of contextual and mnemonic feedback signals revealed by RSA*

580   Similar to the previous study, we addressed the null result for decoding mnemonic

581 information by using RSA, which enabled the identification of different sources of variance

582 within the same data (Ortiz-Tudela et al., 2023). We correlated individual RDMs from

583 episodic and semantic trials of both ROIs with two model RDMs that represent ideal

584 dissimilarity correlation patterns for room (contextual model) and object categories

585 (mnemonic model; see RSA section for further details about RDM model specifications).

586 Figures 5 A) and B) show the correlations with both model RDMs for younger and older

587 adults, respectively. Correlating the contextual room model with episodic RDMs resulted in a

588 moderate relationship for younger ($rho_{V1} = .31$, $rho_{V2} = .33$, both p's < .001) and a weaker

589 relationship for older participants ($rho_{V1} = .15$, $rho_{V2} = .20$, both p's < .001). We observed a

590 similar age pattern in the correlations between the contextual room model with semantic

591 RDMs: moderate for younger and weaker for older participants (younger: $rho_{V1} = .31$, $rho_{V2} = $

592 .30, both p's <.001; older: rho_{V1} = .14, rho_{V2} = .16, both p's < .001). Interestingly, correlating

593 the mnemonic model with episodic RDMs resulted in a low positive relationship for both age

594 groups (younger: rho_{V1} = .08, rho_{V2} = .11, both p's < .001; older: rho_{V1} = .06, rho_{V2} = .08, both

595 p's < .001), whereas correlating the mnemonic model with semantic RDMs resulted in

596 different relationships for the two age groups: In younger adults, a low negative relationship

597 emerged (rho_{V1} = -.03, p < .001, rho_{v2} = -.01, p = .009) but in older adults, the correlation

598 turned out positive (rho_{V1} = .01, p = .037, rho_{v2} = .02, p < .001).

599   Testing these observations formally, LMM analysis revealed a significant three-way

600 interaction between model, trial type, and age (β = -0.093, 95% CI [-0.183, -0.003], t = -

601 2.023, p = 0.043). We further investigated the interaction by running LMMs separately for the

602 two models. For the contextual model, only a main effect of age emerged (β = 0.153, 95% CI

603 [0.114, 0.191], t = 7.793, p < .001) but no significant interaction between age and trial type (β

604 = 0.006, 95% CI [-0.046, 0.059], t = 0.252, p = .800). In particular, older adults, compared to

605 younger adults, showed lower correlations between the contextual model with both episodic

606 and semantic RDMs. For the mnemonic model, we found a significant interaction between

607 age and trial type (β = -0.073, 95% CI [-0.103, -0.044], t = -4.859, p < .001), indicating that

608 the difference between younger and older age groups was larger in semantic trials (t(276) =

609 4.42, p < .001) than in episodic trials (t(276) = -2.37, p = .018), specifically because younger

610 adults showed lower correlation estimates in the negative direction, while older adults showed

611 higher, positive correlation estimates.

612   Taken together, these findings are in line with our classification results by showing

613 that 1) contextual information is present in feedback signals in both age groups, trial types,

614 and ROIs, and 2) the amount of contextual information is overall reduced in older adults early

615 visual areas V1 and V2, suggesting dedifferentiation of contextual feedback signals. In

616 contrast to our classification results and in line with the original study with younger adults

617 only, RSA revealed that mnemonic information exists in both younger and older adults'

25

618   primary and secondary cortices. Interestingly, episodic feedback was comparably well

619   reinstated in younger and older adults, whereas semantic feedback was more reliably

620   reinstated in older but not in younger participants. Even though these results are contrary to

621   our expectations, they lend support to previous research showing that older adults rely on

622   semantic knowledge more extensively, especially benefiting from it when learning new

623   information in line with their prior knowledge (Badham and Maylor, 2014; Mohanty et al.,

624   2016; Lalla et al., 2022).

625   In our preregistration, we included a variance partitioning approach to further explore

626   the unique contribution of different sources of information on activation patterns, particularly

627   the age differences therein. However, in observation of dedifferentiation, the reduced

628   contextual feedback results indicated a higher noise level in older adults' brains. Thus, the

629   amount of variance that could be explained is presumably lower in older adults and,

630   consequently, not comparable to the amount of variance available in younger adults.

631   Consequently, we did not pursue this analysis to prevent inappropriate interpretations when

632   comparing the amount of variance between age groups.

633

634   ***Dedifferentiation in mnemonic feedback signals and feedforward visual input***

635   So far, we have provided empirical evidence for the existence of contextual and

636   mnemonic feedback signals not only in younger but also in older adults. We further showed

637   that the composition of feedback signals changes over the lifespan. Compared to younger

638   adults, contextual feedback was reduced, episodic feedback was similar, and semantic

639   feedback was stronger in older adults. To further characterize dedifferentiation in mnemonic

640   feedback (i.e., specificity in object information), we calculated DIs for each trial type and

641   ROI. DIs were tested against zero and compared across age groups. Following previous

642   research on age-related episodic memory decline, we expected primarily episodic feedback to

643   suffer from age-related dedifferentiation; that is, older adults would have lower DIs in

644   episodic trials than younger adults.

645   Figures 5 C) and D) show feedback DIs for younger and older adults, respectively.

646   Feedback DIs for both age groups were significantly different from zero (younger adults:

647     $V1_{epi} = 25.34$, $z = 4.43$, $p < .001$; $V2_{epi} = 22.05$, $z = 5.64$, $p < .001$; $V1_{sem} = -3.87$, $z = -3.30$, p

648     $< .001$; $V2_{sem} = -3.69$, $z = -2.29$, $p = .010$; older adults: $V1_{epi} = 10.71$, $z = 5.70$, $p < .001$; $V2_{epi}$

649     $= 3.41$, $z = 6.09$, $p < .001$; $V1_{sem} = .50$, $z = 1.65$, $p = .049$; $V2_{sem} = 1.15$, $z = 2.74$, $p = .002$;

650   one-sided Wilcoxon test). LMM analyses resulted in a significant two-way interaction

651   between age and trial type ($\beta = -6.75466$, 95% CI [-10.521, -2.969], $t = -3.478$, $p < .001$). The

652   difference between age groups was higher in semantic trials ($t(284) = 3.21$, $p = .001$)

653   compared to episodic trials ($t(284) = -3.61$, $p < .001$), with younger adults having lower

654   semantic DIs than older adults. This finding is in line with the RSA model correlation results

655   suggesting that episodic feedback does not show compromise in neural specificity in older

656   age. Interestingly, semantic feedback signals even increased in DIs, such that the neural

657   specificity for this mnemonic content improves in older age. To complement those findings,

658   we explored neural differentiation within our ROIs when the objects were presented as

659   feedforward visual input during the sensory template run (i.e., episodic and semantic object-

660   room pairings were consecutively presented during scanning; for details, see Sensory

661   Template in the methods section). All feedforward DIs were different from zero (younger

662   adults: $V1_{epi} = .021$, $z = 6.08$; $V2_{epi} = .014$, $z = 5.64$; $V1_{sem} = .024$, $z = 6.23$; $V2_{sem} = .012$, $z =$

663   5.56; older adults: $V1_{epi} = .009$, $z = 5.25$; $V2_{epi} = .009$, $z = 5.65$; $V1_{sem} = .006$, $z = 4.10$; $V2_{sem}$

664     $= .005$, $z = 4.42$; all p's $< .001$, one-sided Wilcoxon test). Through LMM analysis, we

665   observed a significant main effect of age on neural differentiation ($\beta < .001$, 95% CI

666   [0.009338798, 0.027471357], $t = 3.936$, $p < .001$), meaning that feedforward DIs were lower

667   in older compared to younger adults. Therewith, we replicated previous research and

27

668　contributed additional evidence for age-related neural dedifferentiation at the item level in the

669　early visual areas V1 and V2.

670

671　*Relating feedforward and feedback components across age*

672　　　It has been suggested that dedifferentiation could result from a general age-related

673　deficient dopaminergic modulation (Li et al., 2001; Abdulrahman et al., 2017). If the

674　underlying mechanism for age-related dedifferentiation is general across brain areas and

675　pathways, feedforward and feedback signals might be impacted to a comparable extent. Based

676　on this assumption, we expected to find a positive relationship between neural specificity in

677　feedforward and individual feedback components as age increases. To this end, we correlated

678　the feedforward DIs with DIs for episodic and semantic feedback separately per age group

679　and ROI. The correlation between feedforward and semantic feedback DIs (see Figure 6)

680　neither resulted in a significant relationship in older (rho_{v1} = -.11, p = .736, rho_{v2} = .11, p =

681　.334) nor in younger adults (rho_{v1} = -.3, p = .179, rho_{v2} = -.05, p =.616). A different picture

682　emerged when we correlated feedforward with episodic feedback DIs. In older adults, we

683　observed a low positive relationship between feedforward and episodic feedback DIs in V1

684　and V2 (rho_{v1} = .34, p = .044, rho_{v2} = .35, p = .044), whereas, in younger adults, this positive

685　relationship appeared only in V1 (rho_{v1} = .41, p = .035, rho_{v2} = .18, p = .215). This pattern

686　supports the hypothesis that the putative mechanism of dedifferentiation (e.g., dopaminergic

687　modulation) impacts both feedforward and feedback signals but points out that this is only

688　true for a specific component of the feedback signal. Specifically, mnemonic content retrieved

689　through an episodic route was especially prone to age-related changes in the neural

690　mechanism that fosters dedifferentiation, while semantic content was spared. Furthermore,

691　this result implies that certain brain areas, such as V1, are more affected by dedifferentiation

692　than others.

693

28

Discussion

695   The present study examined age-related changes in the composition of feedback signals in the

696   early visual areas of younger and older adults. We combined an occlusion paradigm with

697   multivariate fMRI pattern analysis, allowing us to isolate and examine concurrent contextual

698   and time-distant mnemonic information in feedback signals in V1 and V2. As the first study

699   that scrutinized age-related differences in feedback signals, four main findings emerged.

700   First, concurrent contextual and time-distant mnemonic information coexist as

701   feedback signals in V1 and V2 of both younger and older adults. By this, we replicated

702   previous research that identified contextual (Smith and Muckli, 2010; Muckli et al., 2015) and

703   mnemonic (episodic or semantic) information in feedback signals (Ortiz-Tudela et al., 2023)

704   in younger adults' visual cortex occluded from feedforward visual input and extended this

705   finding to older adults. As occlusions are ubiquitous in everyday life, both young and

706   senescent visual systems must overcome the perceptual challenge of disambiguating uncertain

707   visual input. Feedback signals facilitate this process by carrying information from the

708   concurrent surroundings and internally retrieved time-distant memory representations to "fill

709   in the blank" in the case of occlusion.

710   Second, decoding accuracy of contextual feedback was reduced in older adults' V1

711   and V2. Lower correlations between a contextual feedback model and multivariate activation

712   patterns in older adults supported this finding. Reduced classification accuracy and

713   (dis)similarity measures have been previously interpreted to indicate age-related

714   dedifferentiation in neural representations (Abdulrahman et al., 2017; Trelle et al., 2019;

715   Folville et al., 2020). Our results showed that contextual feedback is prone to age-related

716   dedifferentiation. Common age-related changes in the neural circuitry within the visual cortex

717   could account for this reduction. For example, demyelination, reduced spine, and synapse

718   densities may lead to dendritic and axonal regressions, which may hamper the integrity of

719   neural signal that is transferred via lateral intracortical connections to adjacent receptive fields

(Smith and Muckli, 2010; Larkum, 2013; Danka Mohammed, 2021). However, the exact nature and impact of age-related decline in micro-structure integrity within early visual regions is not fully known and needs to be examined in future research. Additionally, an increased baseline noise level in older adults' EVC has been shown to compromise perceptual processing (Li et al., 2001; Tran et al., 2020). In line with this, we found feedforward DIs to be significantly lower in older adults, probably rendering the transmitted contextual feedback less representative of the original input. Future studies should consider including diffusion tensor imaging to obtain measures for the structural integrity of lateral neural connections to account for such changes (Voss et al., 2008).

Despite the compromised lateral transfer of contextual information, the representational quality of mnemonic feedback could nevertheless be preserved due to compensatory mechanisms (Park et al., 2001). For example, older adults have been shown to recruit more neural resources at low task demand levels as a compensatory strategy, improving neural distinctiveness (Reuter-Lorenz and Cappell, 2008; Carp et al., 2010). This observation may be important to consider with our third main finding: episodic feedback remained well differentiated across age groups, whereas semantic feedback was even better differentiated in older adults than in younger adults. The maintenance of episodic feedback signals was unexpected for several reasons. Age-related episodic memory decline is well established in the aging literature, as well as the notion that older adults tend to retrieve only the gist of a previously experienced episode; namely, contextual details are lost while the central aspects are preserved (Koutstaal and Schacter, 1997; Old and Naveh-Benjamin, 2008; Nyberg et al., 2012; Abadie et al., 2021). Interestingly, while there is evidence for reduced episodic memory reinstatement in the visual cortex (Zheng et al., 2018), some studies found neural reinstatement of episodic memory content as age-invariant (Wang et al., 2016; Thakral et al., 2017, 2019). According to the *Lifetime Experience Hypothesis* by Koen and Rugg (2019), the absence of age-related dedifferentiation could be explained by high familiarity

with the stimulus material in both age groups, attenuating differences in neural specificity of episodically retrieved feedback. Furthermore, our training procedure might have contributed to the well-differentiated episodic feedback, which was also mirrored by very high post-scan recognition memory performance for episodic object-room combinations. Older adults received four additional learning cycles for encoding the episodic set on day one. These additional cycles, together with the relatively small training set (eight object-room combinations), could have provided older adults the opportunity to compensate for any attentional or binding deficits during encoding and eventually diminished effects of dedifferentiation, leading to a comparable behavioral performance (for a similar pattern, see St-Laurent et al., 2014). Furthermore, we assume that due to our recruiting strategy through the university, the older adults were positively biased, characterized by youth-like memory integrity and distinctiveness of neural representations (Fandakova et al., 2015; Zhang et al., 2020; Katsumi et al., 2021). Taken together, our results show that episodic feedback is not compromised when performance level is matched between age groups.

In terms of semantic feedback, we expected no age difference or only slightly less differentiation in older compared to younger adults. Somewhat surprisingly, our results showed that semantic feedback was even better differentiated in older than younger adults. This finding supports studies suggesting that the semantic memory system remains relatively intact in older adults, even with improvements in some domains (Laumann Long and Shaw, 2000; Levine et al., 2002; Lalla et al., 2022). Interestingly, while most studies investigated dedifferentiation using episodic retrieval tasks, the only study that employed an additional semantic task did not find neural dedifferentiation, pointing to the preservation of generalized knowledge in older age (St-Laurent et al., 2011). Moreover, the ecological validity of our stimulus material, as well as the congruity between semantic object-room pairs, might have helped older adults at retrieval and thereby enhanced neural differentiation of semantic feedback (Badham and Maylor, 2014; Mohanty et al., 2016; Brod and Shing, 2019). Although

31

772   the semantic set was not as extensively trained as the episodic set, the semantic post-scan

773   retrieval performance was better in older adults than younger adults, which underlines the

774   growing impact of semantic knowledge over the lifespan and supports previously reported

775   relationship between higher neural differentiation and better memory retrieval (Katsumi et al.,

776   2021). Nevertheless, it should also be noted that the poorer post-scan memory performance of

777   younger adults for semantic trials could have been a by-product of the different response

778   formats between age groups. Younger adults entered their responses with their left hand

779   within 2 seconds time window, potentially leading to some premature response errors (note

780   that two errors would already result in a performance level of 75%). In contrast, older adults

781   verbally indicated the objects within 4 s, and the responses were entered by the experimenter.

782   In addition to the growing relevance of semantic memory, a decline in inhibitory

783   control might challenge older adults to suppress accessing semantic information, which

784   happens largely automatically (Karl Healey et al., 2013; Vachon et al., 2019). At the same

785   time, intensified recruitment of semantic knowledge could compensate for deterioration

786   elsewhere, such as feedforward perception and contextual feedback. Future research should

787   employ longitudinal study designs to track changes in feedback signals as they may emerge

788   gradually over the lifespan. To further scrutinize the sources and compensatory mechanisms

789   that may underlie age-related changes in feedback composition, connectivity analysis

790   techniques such as psychophysiological interaction analysis or deep neural networks could be

791   utilized (cf. Deng et al., 2021; Ortiz-Tudela et al., 2023).

792   Fourth, while differentiation of feedforward visual input was overall reduced in older

793   adults, the extent of differentiation was positively related to episodic feedback signals in both

794   older adults' V1 and V2 and younger adults' V1. That is, the retrieval of better-differentiated

795   information through an episodic route correlated with better differentiation of visual input in

796   early visual areas across age groups. This result partly met our hypothesis predicting a

797   positive relationship between neural differentiation in feedforward and feedback signals,

especially in older adults. Age-invariant relationships between neural selectivity at perception

and retrieval have been demonstrated before (Johnson et al., 2015; Hill et al., 2021; Katsumi

et al., 2021). In line with this research, our findings suggest that regardless of age, neural

specificity during feedforward processing is correlated with neural specificity of feedback.

We extend this postulation by demonstrating that this age-invariant relationship is only

present for information retrieved episodically but not semantically and that it holds even in

the absence of reduced neural differentiation of episodic feedback. The lack of relation

between feedforward and semantic feedback aligns well with Park et al. (2010), who showed

that neural specificity was associated with measures of fluid processing ability but not

crystallized knowledge. A possible interpretation is that as accumulated knowledge increases,

it is less dependent on the quality of neural differentiation in feedforward visual input. On the

contrary, episodic memory ability is more variable across the lifespan, and the integrity of

stored episodic content depends on the initial quality of neural differentiation at perception.

Hence, episodic memory is more prone to differences in neural selectivity regardless of age.

In sum, we demonstrated the coexistence of concurrent contextual and time-distant

mnemonic information in feedback signals in early visual areas V1 and V2 across age.

Furthermore, we showed that individual feedback components follow distinct trajectories

regarding neural dedifferentiation. Episodic feedback signals were comparably differentiated

across age, whereas semantic feedback signals showed better neural differentiation in older

adults than in younger adults, probably reflecting the lifelong accumulation of generalized

knowledge. Notably, while feedforward differentiation was reduced in older adults, it was

positively correlated with episodic feedback in both age groups. This suggests that measuring

dedifferentiation of internally generated signals depends on the nature of the retrieved

information. Our findings have important implications for the investigation of memory

reinstatement and aging, highlighting dissociations among different components of feedback

signals across the lifespan.

33

References

Abadie M, Gavard E, Guillaume F (2021) Verbatim and Gist Memory in Aging. Psychol Aging 36.

Abdulrahman H, Fletcher PC, Bullmore E, Morcom AM (2017) Dopamine and memory dedifferentiation in aging. Neuroimage 153:211–220.

Abdulrahman H, Henson RN (2016) Effect of trial-to-trial variability on optimal event-related fMRI design: Implications for Beta-series correlation and multi-voxel pattern analysis. Neuroimage 125:756–766.

Baddeley A, Emslie H, Nimmo-Smith I (1993) The Spot-the-Word test: A robust estimate of verbal intelligence based on lexical decision. British Journal of Clinical Psychology 32:55–65.

Badham SP, Maylor EA (2014) What you know can influence what you are going to know (especially for older adults). Psychon Bull Rev 22:141–146.

Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67.

Berkes P, Orbán G, Lengyel M, Fiser J (2011) Spontaneous cortical activity reveals hallmarks of an optimal internal model of the environment. Science (1979) 331:83–87.

Berron D, Neumann K, Maass A, Schütze H, Fliessbach K, Kiven V, Jessen F, Sauvage M, Kumaran D, Düzel E (2018) Age-related functional changes in domain-specific medial temporal lobe pathways. Neurobiol Aging 65:86–97.

Bowman CR, Chamberlain JD, Dennis NA (2019) Sensory representations supporting memory specificity: Age effects on behavioral and neural discriminability. Journal of Neuroscience 39:2265–2275.

Brod G, Shing YL (2019) A boon and a bane: Comparing the effects of prior knowledge on memory across the Lifespan. Dev Psychol 55:1326–1337.

Brodoehl S, Witte OW, Klingner CM (2016) Measuring eye states in functional MRI. BMC Neurosci 17:48.

Carp J, Gmeindl L, Reuter-Lorenz PA (2010) Age differences in the neural representation of working memory revealed by multi-voxel pattern analysis. Front Hum Neurosci 4:6978.

Carp J, Park J, Hebrank A, Park DC, Polk TA (2011a) Age-related neural dedifferentiation in the motor system. PLoS One 6:e29411.

Carp J, Park J, Polk TA, Park DC (2011b) Age differences in neural distinctiveness revealed by multi-voxel pattern analysis. Neuroimage 56:736–743.

Clark A (2013) Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behavioral and Brain Sciences 36:181–204.

Danka Mohammed CP (2021) Differential Circuit Mechanisms of Young and Aged Visual Cortex in the Mammalian Brain. NeuroSci 2:1–26.

863 Deng L, Davis SW, Monge ZA, Wing EA, Geib BR, Raghunandan A, Cabeza R (2021) Age-
864   related dedifferentiation and hyperdifferentiation of perceptual and mnemonic
865   representations. Neurobiol Aging 106:55–67.

866 Esteban O et al. (2020) Analysis of task-based functional MRI data preprocessed with
867   fMRIPrep. Nat Protoc 15:2186–2202.

868 Esteban O, Markiewicz CJ, Blair RW, Moodie CA, Isik AI, Erramuzpe A, Kent JD,
869   Goncalves M, DuPre E, Snyder M, Oya H, Ghosh SS, Wright J, Durnez J, Poldrack RA,
870   Gorgolewski KJ (2019) fMRIPrep: a robust preprocessing pipeline for functional MRI.
871   Nat Methods 16:111–116.

872 Fandakova Y, Lindenberger U, Shing YL (2015) Maintenance of youth-like processing
873   protects against false memory in later adulthood. Neurobiol Aging 36:933–941.

874 Faul F, Erdfelder E, Lang AG, Buchner A (2007) G*Power 3: A flexible statistical power
875   analysis program for the social, behavioral, and biomedical sciences. In: Behavior
876   Research Methods, pp 175–191. Psychonomic Society Inc.

877 Folstein MF, Folstein SE, McHugh PR (1975) "Mini-mental state". A practical method for
878   grading the cognitive state of patients for the clinician. J Psychiatr Res 12:189–198.

879 Folville A, Bahri MA, Delhaye E, Salmon E, D'Argembeau A, Bastin C (2020) Age-related
880   differences in the neural correlates of vivid remembering. Neuroimage 206:116336.

881 Fox J, Weisberg S (2019) Applied Regression 3E. Sage Publications.

882 Friston K (2005) A theory of cortical responses. Philos Trans R Soc Lond B Biol Sci
883   360:815–836.

884 Haitas N, Amiri M, Wilson M, Joanette Y, Steffener J (2021) Age-preserved semantic
885   memory and the CRUNCH effect manifested as differential semantic control networks:
886   An fMRI study. PLoS One 16.

887 Hebart MN, Görgen K, Haynes JD (2015) The decoding toolbox (TDT): A versatile software
888   package for multivariate analyses of functional imaging data. Front Neuroinform 8:88.

889 Hill PF, King DR, Rugg MD (2021) Age Differences in Retrieval-Related Reinstatement
890   Reflect Age-Related Dedifferentiation at Encoding. Cerebral Cortex 31:106–122.

891 Johnson MK, Kuhl BA, Mitchell KJ, Ankudowich E, Durbin KA (2015) Age-related
892   differences in the neural basis of the subjective vividness of memories: evidence from
893   multivoxel pattern classification. Cogn Affect Behav Neurosci 15:644–661.

894 Karl Healey M, Hasher L, Campbell KL (2013) The role of suppression in resolving
895   interference: Evidence for an age-related deficit. Psychol Aging 28:721–728.

896 Katsumi Y, Andreano JM, Barrett LF, Dickerson BC, Touroutoglou A (2021) Greater Neural
897   Differentiation in the Ventral Visual Cortex Is Associated with Youthful Memory in
898   Superaging. Cerebral Cortex 31:5275–5287.

899 Koen JD, Hauck N, Rugg MD (2019) The relationship between age, neural differentiation,
900   and memory performance. Journal of Neuroscience 39:149–162.

901 Koen JD, Rugg MD (2019) Neural Dedifferentiation in the Aging Brain. Trends Cogn Sci
902   23:547–559.

903 Koen JD, Srokova S, Rugg MD (2020) Age-related neural dedifferentiation and cognition.
904   Curr Opin Behav Sci 32:7–14.

905 Koutstaal W, Schacter DL (1997) Gist-based false recognition of pictures in older and
906   younger adults. J Mem Lang 37:555–583.

907 Kriegeskorte N, Mur M, Bandettini P (2008) Representational similarity analysis - connecting
908   the branches of systems neuroscience. Front Syst Neurosci 2:4.

909 Lalla A, Tarder-Stoll H, Hasher L, Duncan K (2022) Aging Shifts the Relative Contributions
910   of Episodic and Semantic Memory to Decision-Making. Psychol Aging 37:667–680.

911 Larkum M (2013) A cellular mechanism for cortical associations: An organizing principle for
912   the cerebral cortex. Trends Neurosci 36:141–151.

913 Laumann Long L, Shaw RJ (2000) Adult age differences in vocabulary acquisition. Educ
914   Gerontol 26:651–664.

915 Levine B, Svoboda E, Hay JF, Winocur G, Moscovitch M (2002) Aging and autobiographical
916   memory: Dissociating episodic from semantic retrieval. Psychol Aging 17:677–689.

917 Li SC, Lindenberger U, Hommel B, Aschersleben G, Prinz W, Baltes PB (2004)
918   Transformations in the Couplings Among Intellectual Abilities and Constituent
919   Cognitive Processes Across the Life Span. Psychol Sci 15:155–163.

920 Li SC, Lindenberger U, Sikström S (2001) Aging cognition: From neuromodulation to
921   representation. Trends Cogn Sci 5:479–486.

922 Markov NT, Vezoli J, Chameau P, Falchier A, Quilodran R, Huissoud C, Lamy C, Misery P,
923   Giroud P, Ullman S, Barone P, Dehay C, Knoblauch K, Kennedy H (2014) Anatomy of
924   hierarchy: Feedforward and feedback pathways in macaque visual cortex. Journal of
925   Comparative Neurology 522:225–259.

926 Marks DF (1973) Vividness of visual imagery Questionnaire. Journal of Mental Imagery
927   64:17–24.

928 Mohanty PP, Naveh-Benjamin M, Ratneshwar S (2016) Beneficial effects of semantic
929   memory support on older adults' episodic memory: Differential patterns of support of
930   item and associative information. Psychol Aging 31:25–36.

931 Morgan AT, Petro LS, Muckli L (2019) Scene representations conveyed by cortical feedback
932   to early visual cortex can be described by line drawings. Journal of Neuroscience
933   39:9410–9423.

934 Muckli L, De Martino F, Vizioli L, Petro LS, Smith FW, Ugurbil K, Goebel R, Yacoub E
935   (2015) Contextual Feedback to Superficial Layers of V1. Current Biology 25:2690–
936   2695.

937 Mumford JA, Turner BO, Ashby FG, Poldrack RA (2012) Deconvolving BOLD activation in
938   event-related designs for multivoxel pattern classification analyses. Neuroimage
939   59:2636–2643.

940 Nyberg L, Lövdén M, Riklund K, Lindenberger U, Bäckman L (2012) Memory aging and
941   brain maintenance. Trends Cogn Sci 16:292–305.

942 Nyberg L, Rönnlund M, Dixon RA, Maitland SB, Bäckman L, Wahlin Å, Nilsson LG (2003)
943   Selective adult age differences in an age-invariant multifactor model of declarative
944   memory. Psychol Aging 18:149–160.

945 Ofen N, Shing YL (2013) From perception to memory: Changes in memory systems across
946   the lifespan. Neurosci Biobehav Rev 37:2258–2267.

947 Old SR, Naveh-Benjamin M (2008) Differential Effects of Age on Item and Associative
948   Measures of Memory: A Meta-Analysis. Psychol Aging 23:104–118.

949 Ortiz-Tudela J, Bergmann J, Bennett M, Ehrlich I, Muckli L, Shing YL (2023) Concurrent
950   contextual and time-distant mnemonic information co-exist as feedback in the human
951   visual cortex. Neuroimage 265:119778.

952 Park DC, Polk TA, Mikels JA, Taylor SF, Marshuetz C (2001) Cerebral aging: integration of
953   brain and behavioral models of cognitive function. Dialogues Clin Neurosci 3:151–165.

954 Park DC, Polk TA, Park R, Minear M, Savage A, Smith MR (2004) Aging reduces neural
955   specialization in ventral visual cortex. Proc Natl Acad Sci U S A 101:13091–13095.

956 Park J, Carp J, Hebrank A, Park DC, Polk TA (2010) Neural specificity predicts fluid
957   processing ability in older adults. Journal of Neuroscience 30:9253–9259.

958 Payer D, Marshuetz C, Sutton B, Hebrank A, Welsh RC, Park DC (2006) Decreased neural
959   specialization in old adults on a working memory task. Neuroreport 17:487–491.

960 Rao RPN, Ballard DH (1999) Predictive coding in the visual cortex: a functional
961   interpretation of some extra-classical receptive-field effects. Nat Neurosci 2:79–87.

962 Reuter-Lorenz PA, Cappell KA (2008) Neurocognitive aging and the compensation
963   hypothesis. Curr Dir Psychol Sci 17:177–182.

964 Rönnlund M, Nyberg L, Bäckman L, Nilsson LG (2005) Stability, growth, and decline in
965   adult life span development of declarative memory: Cross-sectional and longitudinal data
966   from a population-based study. Psychol Aging 20:3–18.

967 Saunders SM, Wojcik J V. (2004) The reliability and validity of a brief self-report
968   questionnaire to screen for mental health problems: The health dynamics inventory. J
969   Clin Psychol Med Settings 11:233–241.

970 Schmolesky MT, Wang Y, Pu M, Leventhal AG (2000) Degradation of stimulus selectivity of
971   visual cortical cells in senescent rhesus monkeys. Nat Neurosci 3:384–390.

972 Shin JN, Doron G, Larkum ME (2021) Neocortical Layer 1 - The Memory Layer? Science
973   374:538.

974 Shing YL, Werkle-Bergner M, Li SC, Lindenberger U (2008) Associative and Strategic
975   Components of Episodic Memory: A Life-Span Dissociation. J Exp Psychol Gen
976   137:495–513.

977 Smith FW, Muckli L (2010) Nonstimulated early visual areas carry information about
978   surrounding context. Proc Natl Acad Sci U S A 107:20099–20103.

979   Spunt B (2016) Easy-Optimize-X: Formal Release For Archiving On Zenodo.

980   Stelzer J, Chen Y, Turner R (2013) Statistical inference and multiple testing correction in
981   classification-based multi-voxel pattern analysis (MVPA): Random permutations and
982   cluster size control. Neuroimage 65:69–82.

983   St-Laurent M, Abdi H, Bondad A, Buchsbaum BR (2014) Memory reactivation in healthy
984   aging: Evidence of stimulus-specific dedifferentiation. Journal of Neuroscience
985   34:4175–4186.

986   St-Laurent M, Abdi H, Burianová H, Grady CL (2011) Influence of aging on the neural
987   correlates of autobiographical, episodic, and semantic memory retrieval. J Cogn
988   Neurosci 23:4150–4163.

989   Thakral PP, Wang TH, Rugg MD (2017) Decoding the content of recollection within the core
990   recollection network and beyond. Cortex 91:101–113.

991   Thakral PP, Wang TH, Rugg MD (2019) Effects of age on across-participant variability of
992   cortical reinstatement effects. Neuroimage 191:162–175.

993   Thaler L, Schütz AC, Goodale MA, Gegenfurtner KR (2013) What is the best fixation target?
994   The effect of target shape on stability of fixational eye movements. Vision Res 76:31–
995   42.

996   Tran TT, Rolle CE, Gazzaley A, Voytek B (2020) Linked sources of neural noise contribute
997   to age-related cognitive decline. J Cogn Neurosci 32:1813–1822.

998   Trelle AN, Henson RN, Simons JS (2019) Neural evidence for age-related differences in
999   representational quality and strategic retrieval processes. Neurobiol Aging 84:50–60.

1000   Vachon F, Marsh JE, Labonté K (2019) The Automaticity of Semantic Processing Revisited:
1001   Auditory Distraction by a Categorical Deviation. J Exp Psychol Gen.

1002   Voss MW, Erickson KI, Chaddock L, Prakash RS, Colcombe SJ, Morris KS, Doerksen S, Hu
1003   L, McAuley E, Kramer AF (2008) Dedifferentiation in the visual cortex: An fMRI
1004   investigation of individual differences in older adults. Brain Res 1244:121–131.

1005   Wang TH, Johnson JD, De Chastelaine M, Donley BE, Rugg MD (2016) The Effects of Age
1006   on the Neural Correlates of Recollection Success, Recollection-Related Cortical
1007   Reinstatement, and Post-Retrieval Monitoring. Cerebral Cortex 26:1698–1714.

1008   Wechsler D (1981) Wechsler Adult Intelligence Scale—Fourth Edition.

1009   Yang Y, Liang Z, Li G, Wang Y, Zhou Y (2009) Aging affects response variability of V1 and
1010   MT neurons in rhesus monkeys. Brain Res 1274:21–27.

1011   Yang Y, Liang Z, Li G, Wang Y, Zhou Y, Leventhal AG (2008) Aging affects contrast
1012   response functions and adaptation of middle temporal visual area neurons in rhesus
1013   monkeys. Neuroscience 156:748–757.

1014   Zhang J, Andreano JM, Dickerson BC, Touroutoglou A, Barrett LF (2020) Stronger
1015   Functional Connectivity in the Default Mode and Salience Networks Is Associated with
1016   Youthful Memory in Superaging. Cerebral Cortex 30:72–84.

1017 Zhang Z, Yuan K-H (2018) Practical Statistical Power Analysis Using Webpower and R
1018   (Eds). Granger, IN: ISDSA Press.

1019 Zheng L, Gao Z, Xiao X, Ye Z, Chen C, Xue G (2018) Reduced Fidelity of Neural
1020   Representation Underlies Episodic Memory Decline in Normal Aging. Cerebral Cortex
1021   28:2283–2296.

1022

1023

1024

1025

1026

1027

1028

1029

1030

1031   **Figure Legends**

1032   **Figure 1.** Schematic overview of training and test phases across days. A) During day one

1033   training, participants studied room-object combinations with minimal semantic relation, i.e.,

1034   the episodic set. The target objects were always placed in the lower right corner of the room

1035   image. After each training cycle, we tested object memory with a 4AFC format, followed by

1036   memory for the objects' original position. B) On day two, participants were introduced to the

1037   semantic set consisting of new room images and verbally indicated the object with maximal

1038   semantic relation to the room. During scanning, the occlusion task showed rooms from both

1039   episodic and semantic sets with a white occluder hiding the area of the target object.

1040   Participants were asked to focus on the cross in the center of the screen and to reinstate and

1041   hold the entire room in mind, including the associated object, with as much detail as possible.

1042

1043   **Figure 2.** Classification setup. All trials used for decoding analyses stem from the occlusion

1044   task performed in the scanner on day two. Note that the objects were never shown during the

1045   actual task (shown here only for illustration purposes). We performed decoding on voxels in

1046   V1 and V2 that represented the occluded lower right corner. A) To decode contextual

1047   information, we provided the classifier with a training set of different rooms associated with

1048   the same objects (solid box). Based on this arrangement, the classifier could use only the

1049   contextual room information in feedback signals to distinguish trials of the upper stack from

1050   trials of the lower stack. The test set (dashed box) comprised the same object-room

1051   combinations from a separate run from the training set. B) To decode mnemonic information,

1052   the classifier was trained with two trial sets of different rooms associated with different

1053   objects (solid box). Here the classifier could use contextual and mnemonic feedback to learn

1054   to distinguish the upper from the lower stack. When tested on a set of new rooms that shared

1055   the same object (dashed box), only the mnemonic feedback that was consistent (across

1056   training and test sets) could provide sufficient information to discriminate between them.

1057   **Figure 3.** Model RDMs. Two model RDMs representing an ideal neural response pattern

1058   were created and correlated with the neural RDM of a participant. For illustration purposes,

1059   reduced model matrices spanning 24x24 trials instead of 96x96 trials are plotted. Cells

1060   represent four object-room pairings (TV-Room A, TV-Room B, Bed-Room A, Bed-Room B)

1061   containing either zeros (= lowest possible dis-similarity) or ones (= highest possible dis-

1062   similarity). In the left panel mnemonic model, "same object – different room" cells are

1063   colored in red, indicating zeros since retrieving the same object should ideally result in the

1064   lowest possible dissimilar neural signal. "Different object – different room" cells are colored

1065   in blue, indicating ones since retrieving different objects should ideally result in the highest

1066   possible dissimilar neural signal. "Same object – same room" cells are colored in white and

1067   were removed from the correlation analysis to prevent the coefficient from being artificially

1068   lowered through room similarity. In the right panel contextual model, "same object – same

1069   room" cells are colored in red, indicating zeros since perceiving the same room images should

1070   ideally result in the lowest possible dissimilar neural signal. "Same object – different room"

41

cells are colored in blue, indicating ones since perceiving different rooms should ideally result

in the highest possible dissimilar neural signal. The diagonal cells are colored in white and

were removed from the correlation analysis to prevent the coefficient from being artificially

lowered through overall similarity.

Figure 4. Memory performance across learning cycles on day one. The proportion of correct

responses for object recognition (upper panel) and position memory (lower panel) across five

learning cycles for younger (left panel) and nine learning cycles for older adults (right panel),

plus one refresher cycle at the end of the session, respectively. The dashed red line indicates

the threshold of 80% that had to be crossed, either in the last or the refresher cycle of the

object recognition task, to be included for fMRI analysis.

Figure 5. Model correlations and feedback differentiation indices. The upper panel shows

Spearman correlations (z scores) for A) younger and B) older participants between individual

RDMs and two model RDMs representing ideal dissimilarity correlation patterns for context

(contextual model) and object categories (mnemonic model), respectively. Correlations are

separately shown for episodic and semantic trials in ROIs V1 and V2. The lower panel shows

differentiation indices separately for episodic and semantic mnemonic feedback for C)

younger and D) older participants in both ROIs V1 and V2. The dashed vertical line indicates

zero.

Figure 6. Relationship between visual feedforward and mnemonic feedback DIs. Spearman

correlations between average feedforward DIs and episodic and semantic feedback DIs are

plotted for younger (left panel) and older adults (right panel) and separately for ROIs V1 (top)

and V2 (bottom). Darker colors and solid lines represent episodic feedback DIs, and lighter

colors and dashed lines represent semantic feedback DIs. Shaded ribbons represent the 95%
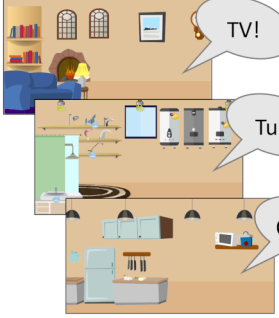
1097   confidence intervals. Average feedforward DIs were positively related to episodic feedback

1098   DIs in younger adults' V1 and older adults' V1 and V2.

A) Day 1

1. Training	2. Test

Episodic Set

Object?

Position?

B) Day 2

1. Training	2. Scanning

Semantic Set

TV!

Tub!

Oven!

Occlusion Task
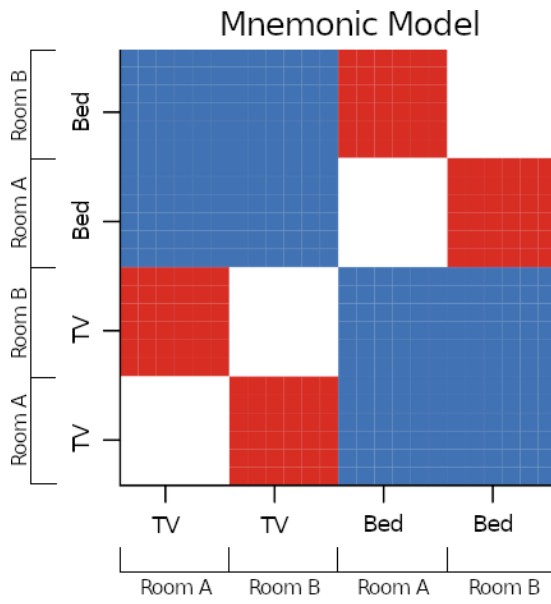
Episodic trial

Semantic trial

Episodic trial
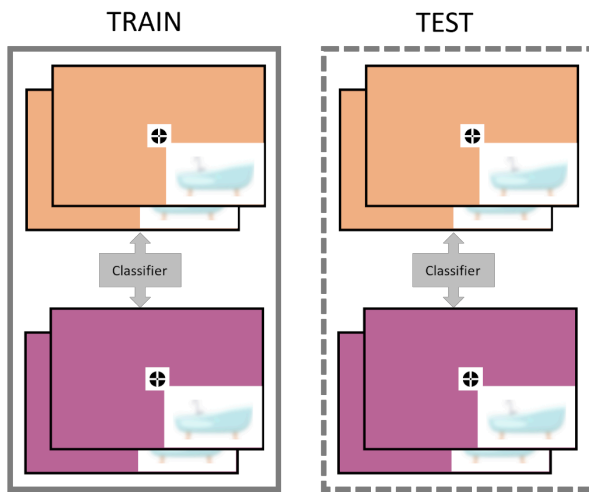
A) Contextual

TRAIN

TEST

Classifier

Classifier

B) Mnemonic

TRAIN

TEST

Classifier

Classifier
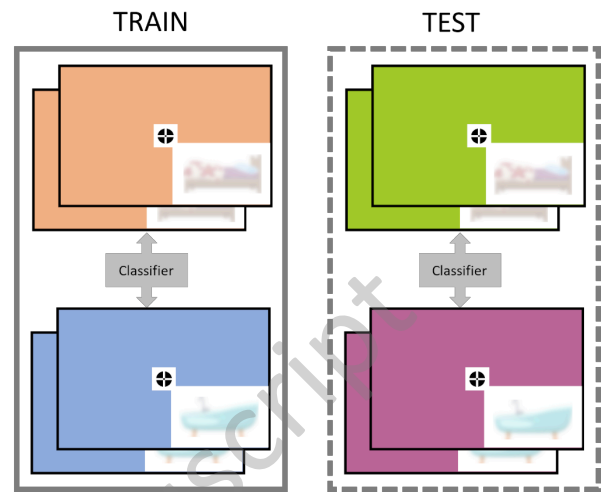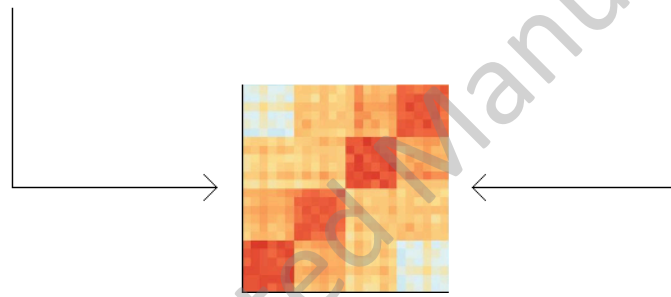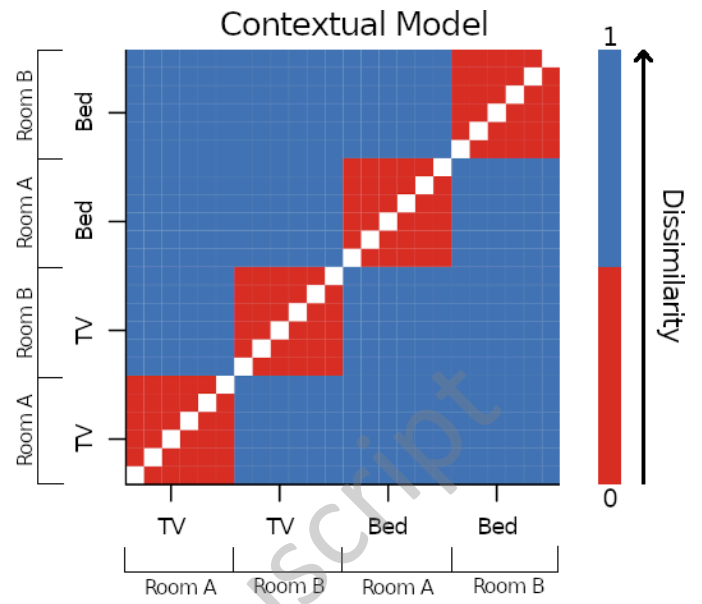
A) Young Adults   B) Old Adults