

Aging, pattern separation, and categorical perception of faces<sup>☆</sup>Ariana Youm<sup>a,b,\*</sup>, Morris Moscovitch<sup>a,c,\*\*</sup><sup>a</sup> Department of Psychology, University of Toronto, Canada<sup>b</sup> Krembil Research Institute, University Health Network, Canada<sup>c</sup> Rotman Research Institute, Baycrest Hospital, Canada

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## ABSTRACT

Categorical perception (CP) is the phenomenon by which observers view linear changes that occur across a continuum as distinct categories. Although categorical perception is a perceptual phenomenon, it may be subserved by mnemonic processes such as pattern separation. To examine this hypothesis, following standard CP tasks, we assessed younger and older participants' abilities to identify and discriminate between members of pairs of famous or non-famous faces. We hypothesized that if CP is dependent upon neural pattern separation, which declines with aging, discrimination ability as indexed by CP would be compromised in older adults, as was found in our study. Since familiarity promotes pattern separation, CP should be enhanced for famous, as compared to non-famous faces, even in older adults. We found that all participants benefited from familiarity, but younger adults outperformed older adults overall. We next examined the effects of face inversion on CP for both famous and non-famous faces. If pattern separation, and CP, is determined solely by the similarity across physical features, then CP should be similar for upright and inverted faces since these features are perceptually invariant across orientation. If, however, pattern separation, and CP, depends on how stimuli are represented, then orientation may matter as upright and inverted faces are represented holistically or part-based, respectively. We found that inversion disrupted CP in younger adults whereas older adults performed similarly across both conditions, suggesting that face-representation is more part-based in older adults.

## 1. Aging, pattern separation, and categorical perception of faces

A rainbow is physically a continuous spectrum of wavelengths but is often perceived as discrete color bands. This is an example of a phenomenon called *categorical perception* (CP; Harnad, 1987). CP occurs when we perceive a continuum of physical, linear changes as not gradual, but rather, separable into discrete categories. Our perception is biased such that differences between categories are accentuated while the same differences within a category are more obscured (Harnad, 2006). Using the example of the rainbow, when there is a transition between two categories of colors (e.g., yellow to green), it is easy to recognize that there is a change. When, however, there is a transition within one color category (e.g., lime green to light green), it is more difficult to perceive the change, though the physical difference in wavelength may be identical in the two cases. As such, one feature that is indicative of CP is enhanced discrimination for between-category stimuli compared to within-category stimuli. In this study, we examine the

effects of aging, familiarity, and stimulus inversion on CP for faces with the hypothesis that pattern separation processes mediated by the hippocampus may contribute to CP.

Perceiving stimuli in a categorical fashion is useful because it allows us to simplify our experiences. This effect applies to several perceptual domains, including simple features such as colors (Bornstein and Korda, 1984), and to multidimensional features such as faces (Beale and Keil, 1995). It has been found, however, that CP diminishes with age (e.g. Kiffel et al., 2005; Bidelman et al., 2014; Lee et al., 2014). In an experimental setting, CP is typically tested by generating a continuum of equally spaced stimuli and administering identification and discrimination tasks to participants (Goldstone and Hendrickson, 2009). In the identification task, participants classify the stimuli according to their endpoint identities. This task allows for the computation of a category boundary, a point at which there is a relatively sharp change in the probability of participants classifying the stimuli as one endpoint identity to another. In the discrimination task, participants judge whether

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two stimuli are the same or different. Performance on the discrimination task is indicative of CP if there is enhanced discrimination for between-category stimuli compared to within-category stimuli. With diminished CP, however, older adults do not show this predicted advantage for stimuli that straddle the categorical boundary (Lee et al., 2014).

In our study, we were interested in investigating if mnemonic processes, namely pattern separation, contribute to categorical perception and its decline in aging. Pattern separation is the process whereby similar representations are orthogonalized and stored in a distinct, non-overlapping manner so that interference does not occur among them (Marr, 1971; O'Reilly and McClelland, 1994; Rolls, 2013). The hippocampus, which sits at the top of the visual processing system (Felleman and Van Essen, 1991), has been strongly implicated in pattern separation, and within it, crucial regions are the dentate gyrus (DG) and CA3 subfields (Bakker et al., 2008). In a process similar to one leading to CP, the DG/CA3 responds to incoming signals in a stepwise manner, such that small changes in input results in a marked change in representation (Yassa and Stark, 2011; Lacy et al., 2011).

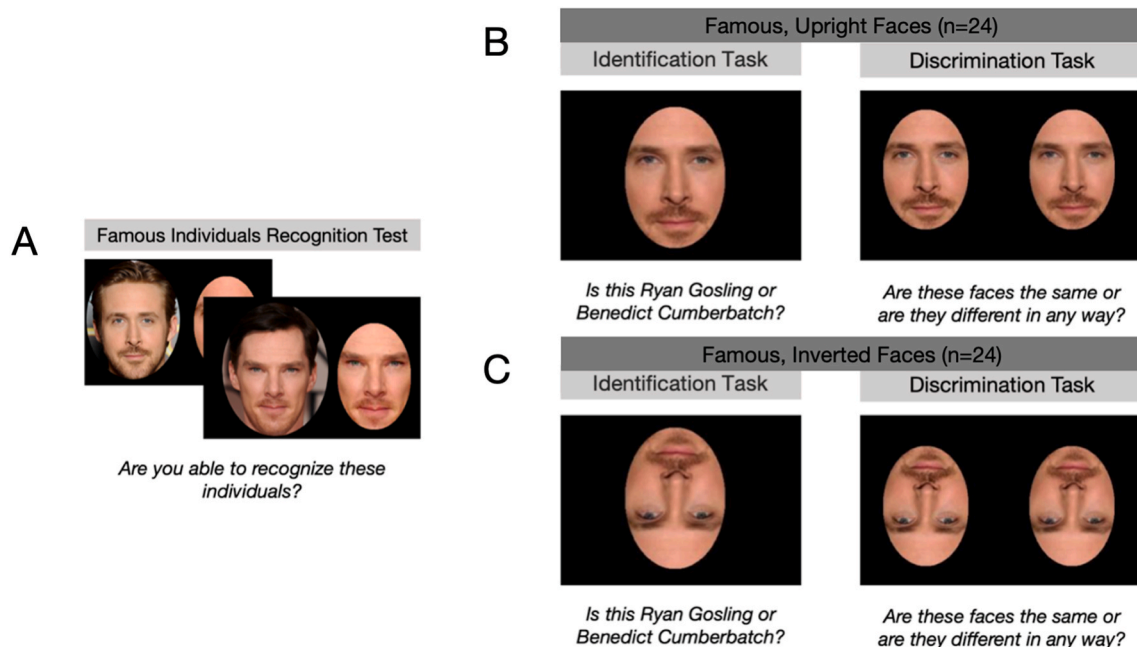
These same hippocampal regions have also been implicated in CP tasks. Using fMRI and multivariate pattern analysis, Bonnici et al. (2012) found that when participants viewed morphed scenes that spanned a continuum, like stimuli in a CP task, the patterns of activity coding highly similar stimuli of spatial scenes were most distinct in the hippocampus. Furthermore, an individual with highly selective bilateral ischemic lesions of the DG was found to exhibit significantly lower accuracy in discriminating high interference faces compared to control participants (Baker et al., 2021). These findings suggest that pattern separation mediated by the hippocampus may contribute to CP.

Like CP, pattern separation processes become compromised with age. For example, in a continuous recognition paradigm (Kirwan and Stark, 2007; Toner et al., 2009), it was reported that older adults with no neurological or psychiatric conditions were impaired on a pattern separation task for visual object memory. Similarly, high-resolution fMRI studies provide evidence that difficulty in distinguishing between similar representations in memory manifests with age (Yassa et al.,

2010). Taken together, the literature suggests that the pattern separation deficits that are found in older adults may be associated with the degeneration of the DG/CA3 network that also occurs with age.

Across a range of experimental paradigms, it has also been found that face recognition abilities decline with age. This decline is generally characterized by high false alarms to unfamiliar faces and is partially attributable to age-related impairments in cognitive function (Boutet et al., 2015; Fulton and Bartlett, 1991; Lamont et al., 2005; Norton et al., 2009). Importantly, previous research suggests that face recognition abilities depend more heavily on the hippocampus when tasks require relational binding and/or comparison (Olsen et al., 2015, 2016), as occurs when comparing faces seen from different viewpoints. As such, CP tasks may recruit hippocampal pattern separation to resolve the comparison between morphed faces, which have highly overlapping features and relations among them.

If hippocampal pattern separation contributes to CP, and if this function declines with age, then CP should be compromised in older, compared to younger, adults. We tested this hypothesis by examining CP for faces. Following Lee et al. (2014), we created the stimuli by linearly morphing two faces (i.e., 0% of Face 1 and 100% of Face 2, 10% of Face 1 and 90% of Face 2, and so on; see Fig. 1). With the morphed stimuli, we assessed CP with a standard identification task and a discrimination task. The identification task was a binary task, meaning that participants only had two options (i.e., Face 1 or Face 2) to categorize the morphed face that was presented to them. In the discrimination task, participants were required to determine whether two stimuli looked exactly the same as each other or if they were different in any way. For CP to occur, it is necessary that there is a non-linear transition in categorization of identity in the identification task, as determined by the category boundary and slope of the function at that boundary in addition to between-category separation and within-category compression in the discrimination task. Based on neural models of pattern separation and previous research, we hypothesized that we would find diminished CP in older adults compared to younger adults, as reflected by a reduced difference in discrimination accuracy at the boundaries between categories compared to within categories.



**Fig. 1.** Experiment procedure with exemplar stimuli of famous faces. All famous faces were of celebrities popular in North America. A) Prior to testing, all participants completed a Famous Individuals Recognition Test to select a set of famous faces with which they were most familiar. B) Participants were randomly assigned into two groups so that half the participants viewed faces that were in an upright orientation for the learning, identification, and discrimination tasks (Upright Condition). C) The other half viewed faces that were inverted by 180° (Inverted Condition). Within each condition, participants learned and were tested on 4 pairs of famous faces and 4 pairs of non-famous faces.

We also hypothesized that since familiarity promotes pattern separation (Bein et al., 2020), CP could also be influenced by experience, such as familiarity due to exposure (Lee et al., 2014). We predicted that if the stimuli were familiar to the observer, such as faces of famous people that often appear in the media, the advantage of discriminating faces between-categories compared to within-categories would become more pronounced (Campanella et al., 2003), accentuating CP in younger adults, and perhaps improving CP even in older adults.

Lastly, we wanted to determine if differences in performance between younger and older adults in face identification and discrimination would be affected by face inversion, which disrupts CP (Valentine, 1988; Campanella et al., 2001; McKone et al., 2001), but theoretically should have little or no effect on pattern separation since the physical overlap among stimuli is the same whether they are inverted or upright. If age-related changes in pattern separation account for differences in performance between young and older adults, then inversion should have little effect on that relationship, even though CP is reduced. If, however, age-related differences in identification and discrimination are reduced with inversion, it would suggest either that pattern separation is not the sole determinant of CP or that how stimuli are represented places limits on whether pattern separation can be applied and be effective.

## 2. Method

### 2.1. Participants

In the current study we tested younger adults between the ages of 18–24 and older adults between the ages of 60–85. We recruited 48 younger adults ( $M = 19.07$ ,  $SD = 1.49$ ) from the Introduction to Psychology course and through individual recruitment from the University of Toronto. The sample was predominantly female (76.7%, 23.3% male) and Caucasian (37.21%, 34.88% East Asian, 23.26% South Asian, 2.33% Hispanic, and 2.33% Black). 48 older adults ( $M = 72.6$ ,  $SD = 7.06$ ) were recruited from the University of Toronto's Adult Volunteer Pool and through individual recruitment. The sample was also predominantly female (70%, 30% male) and Caucasian (90%, 5% East Asian and 5% South Asian). All participants were screened to ensure that they had normal or corrected-to-normal vision, no neurological or psychiatric disorders, and no history of concussions or any other head injuries. Older adults were also screened with the Montreal Cognitive Assessment (MoCA); a less stringent cutoff of 23 instead of 26 was used (Luis et al., 2009; Rosetti et al., 2011). Only participants with a MoCA score over 23 were eligible to participate in the study.

### 2.2. Materials

Stimuli in this study consisted of famous and non-famous faces. For the famous face stimuli, all of the pictures were of a neutral, frontal view of celebrities popular in North America such as Ryan Gosling. For the non-famous face stimuli, we used the same stimuli as ones used in a previous study (see Lee et al., 2014). All stimuli were organized into pairs such that each pair either had two famous faces or two non-famous faces.

Faces in a pair were matched in gender, picture quality (e.g. brightness, contrast level), general appearance (e.g. skin tone, eye color), and age. We used Adobe Photoshop CS3 to create a face mask to crop out an oval region of each person's face, where their hair and ears were excluded. The face mask enabled the consistent positioning of each person's face within the oval region, which minimized variations in facial structures across the face images. Following the template, each face was prepared to be similar in size and perspective before morphing. Each paired face was morphed using the program FaceMorpher Lite (<http://www.facemorpher.com/>), which matched all of the facial feature coordinates of one face to those of the other (e.g. right eye to right eye, nose to nose). For each pair of faces that were morphed together, resulting morph images differed by increments of 10% on a

continuum from 10% to 90%, with a 50% morph having an equal percentage of each of the two faces. All of the face stimuli were presented on a black background.

### 2.3. Procedure

Participants were randomly assigned to two groups so that half the participants viewed faces that were in an upright orientation for the learning, identification, and discrimination tasks (Upright Condition), and the other half viewed faces that were inverted by 180° (Inverted Condition).

#### 2.3.1. Face recognition test

Prior to actual testing, older adults completed the Cambridge Face Memory test (Duchaine and Nakayama, 2006). Past literature shows that even patients with temporal lobe excisions do not have problems recognizing famous faces (Viskontas et al., 2002). We conducted this test on the participants to confirm face recognition abilities in older adults to support the validity of our study; individuals who scored 60% or lower were flagged to likely have prosopagnosia or impaired face recognition and were excluded from the study.

#### 2.3.2. Famous Individuals Recognition Test

We followed the procedure developed in a previous study (Lee et al., 2014). Prior to testing, we administered a Famous Individuals Recognition Test, which allowed us to select famous faces known by the participant to serve as stimuli for the upcoming tasks. Here, we showed participants a series of faces for the upcoming tasks, which included an original picture of each famous individual with full hair as well as its cropped picture for the face mask. If participants could recognize all or most of the faces in a set by stating their first and last names (with a minimum score of 83.3%), they would be able to move on to the identification task. If they did not know two or more famous faces from the set, a different selection of famous faces was presented. Individuals who did not know two or more famous people from all sets were excluded from the study. In this way, the stimuli used were individualized for each participant, ensuring both younger and older participants were equated in their knowledge of the faces used in the experiment.

#### 2.3.3. Learning task

Two faces were presented side by side on the screen with their corresponding names. All non-famous faces were also assigned names. Each participant studied 4 pairs of famous faces and 4 pairs of non-famous faces. Participants were asked to study each pair for 2 min. Participants then went through a brief recognition test in which they had to identify each face within the pair. One face and two names were presented on the screen at a time, and the participant was instructed to press either the up or down arrow on the keyboard to categorize the face as either that of the name written above the face or that written below. Participants received feedback as to whether they were correct or incorrect after their response to each face. This recognition testing session only finished when the participant successfully learned each identity, determined by two correct responses in a row for each face-name pair.

#### 2.3.4. Identification task

Following training, participants were shown morphed faces of the two distinct identities in each pair. In each trial, one morphed face was randomly presented from a set of 9 morphed images that differed on a continuum from 10% to 90% of Face 1 in the set, by increments of 10%. Participants were asked to categorize the identity of each morphed face by pressing the up or down arrow keys, with each key being associated to a particular name. Participants had 4000 ms to respond in each trial, but all participants were instructed to respond as accurately and as quickly as possible. Participants viewed four famous face pairs and four novel face pairs in total. Each morph pair appeared five times per morph

step, resulting in 180 trials for famous faces and 180 trials for novel faces. Trial order was randomized within blocks and across participants, and the order of presentation of the blocks was also randomized.

2.3.5. Discrimination task

The stimuli used in this task were exactly the same as the ones used in the identification task. Participants had 2 min to study each pair of faces, but they did not undergo recognition testing. In the discrimination task, two morphed images were presented on the screen simultaneously, and participants were instructed to judge whether the two images on the screen looked identical or if they differed in any way. In the “different” pairs, the faces differed by a 20% difference (e.g. one had 10% of Face 2 vs. 30% of Face 2). In the “same” pairs, morphs were identical (e.g. 10% vs. 10%). “Same” pairs (10-10, 20-20, 30-30, 40-40, 50-50, 60-60, 70-70, 80-80, 90-90) appeared three times per pair and “different” trials (10-30, 20-40, 30-50, 40-60, 50-70, 60-80, 70-90) appeared five times per pair, resulting in a total of 248 trials for famous faces and 248 trials for non-famous faces. Participants were instructed to focus on images rather than identity of the morphs. Participants pressed either the left or right arrow key, indicating either a same or different response, respectively. The order of face pairs was randomized within blocks, and all trials were counterbalanced. All participants were instructed to respond as accurately but as quickly as possible.

2.4. Analysis

All analyses were based on a previous protocol (Lee et al., 2014). In the current study, however, we ran linear mixed models rather than a repeated measures ANOVA to account better for fixed and random effects, and to account for missing data.

3. Results

3.1. Identification

Following a previous protocol (Lee et al., 2014), we counted the number of trials each individual classified the morphed face as Face 2. To identify whether the participants properly learned all the identities of the faces, we analyzed the accuracy at the endpoint (original) face identities. Those who did not perform above chance ( $n = 3$ ) were excluded from further analyses, and were not replaced. All remaining participants performed above chance ( $p < 0.001$ ). There were no group differences except in the identification of upright, non-famous faces, in which younger adults performed significantly better than older adults ( $p = 0.001$ ). Multiple comparisons used Bonferroni  $t$  tests.

A sigmoid function was fitted to the identification responses of each participant to estimate the predicted category boundary ( $x_c$ ) and the slope at the boundary for the individual ( $k =$  slope of the tangent at  $x_c$ ) using custom routines coded in MATLAB (The Math Works, 2019; see Fig. 2). The sigmoid fit optimally depicted the perceptual distortion underlying categorical perception (CP; McKone et al., 2001).

A linear mixed-effects model was used to analyze these data because familiarity was nested within participants. Slope at the category boundary ( $k$ , or the derivative at  $x_c$ ) as well as category boundary ( $x_c$ ) was modeled as a function of age, orientation, familiarity, and the interaction between these variables, along with a random intercept. Both models were estimated with an unstructured covariance matrix using the lmer function from the lme4 package (Pinheiro et al. (2020)) in R 3.2.2 (R Core Team, 2015).

As shown in Fig. 3, younger adults had significantly higher slope values than older adults,  $\beta = 0.03$ ,  $SE = 0.01$ ,  $t(90) = 3.04$ ,  $p = 0.003$ ,  $R^2 = 0.09$ . All participants had higher slopes when classifying upright faces compared to inverted faces,  $\beta = 0.03$ ,  $SE = 0.01$ ,  $t(90) = 2.22$ ,  $p = 0.029$ ,  $R^2 = 0.05$ , and when classifying famous faces compared to non-

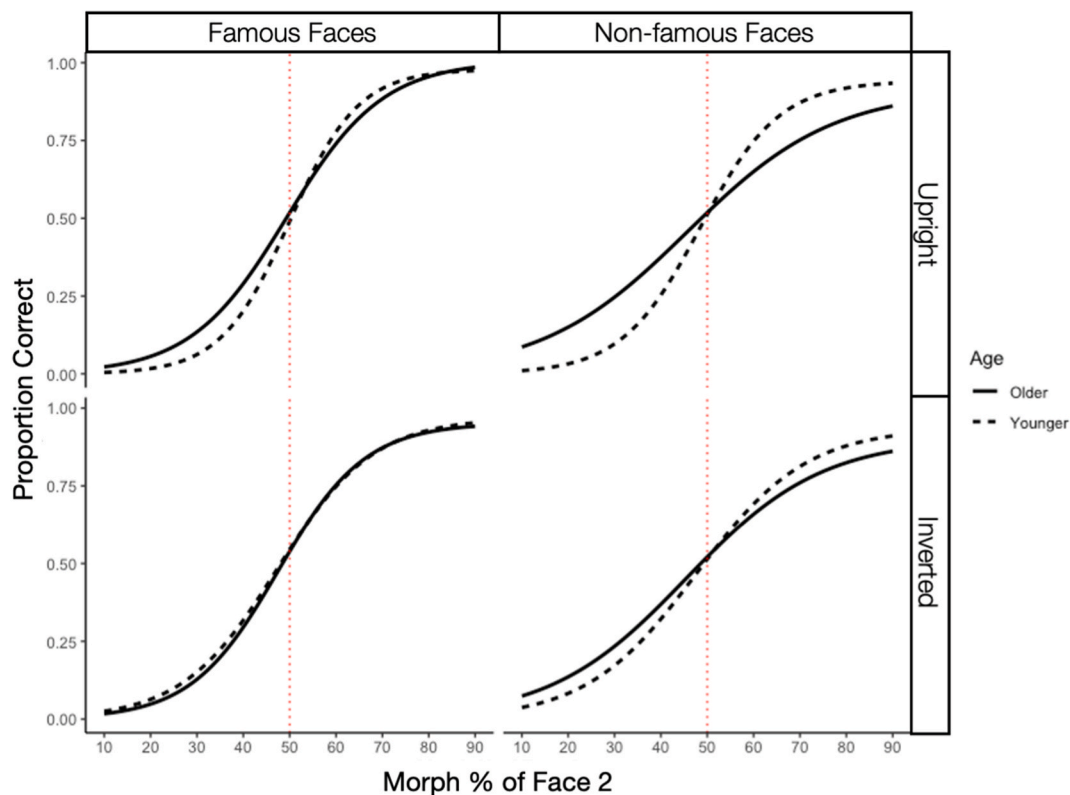


Fig. 2. Sigmoid fitting of identification responses. A sigmoid function was fitted to the identification responses of each participant to estimate the predicted category boundary and the slope at the boundary for the individual.

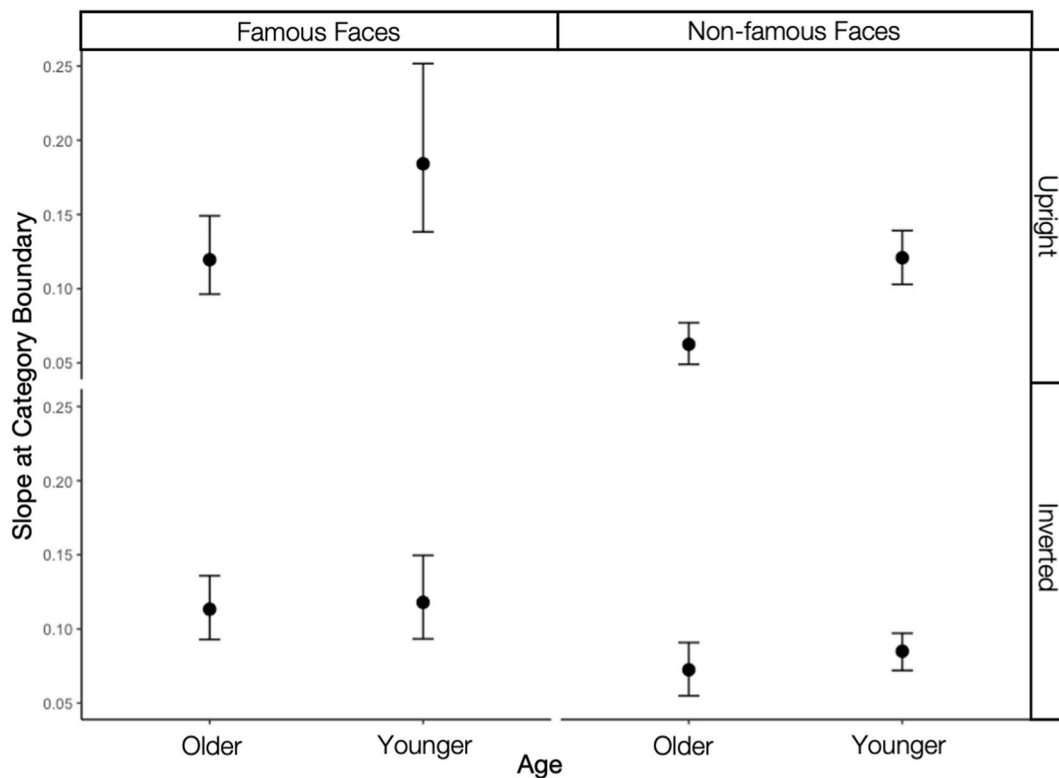


Fig. 3. Slope at the category boundary for famous and non-famous, upright and inverted faces, in older and younger adults.

famous faces,  $\beta = 0.05$ ,  $SE = 0.091$ ,  $t(90) = 4.98$ ,  $p < 0.001$ ,  $R^2 = 0.2$ . There was a significant interaction between age and orientation, in which the difference in slopes between younger and older adults was greater for upright faces than for inverted faces,  $\beta = 0.06$ ,  $SE = 0.03$ ,  $t$

(176) = 2.02  $p = 0.01$ ,  $R^2 = 0.02$ . There were no significant differences in category boundary,  $\beta = -5.89$ ,  $SE = 4.12$ ,  $t(90) = -1.43$ ,  $p = 0.154$ ,  $R^2 = 0.02$ .

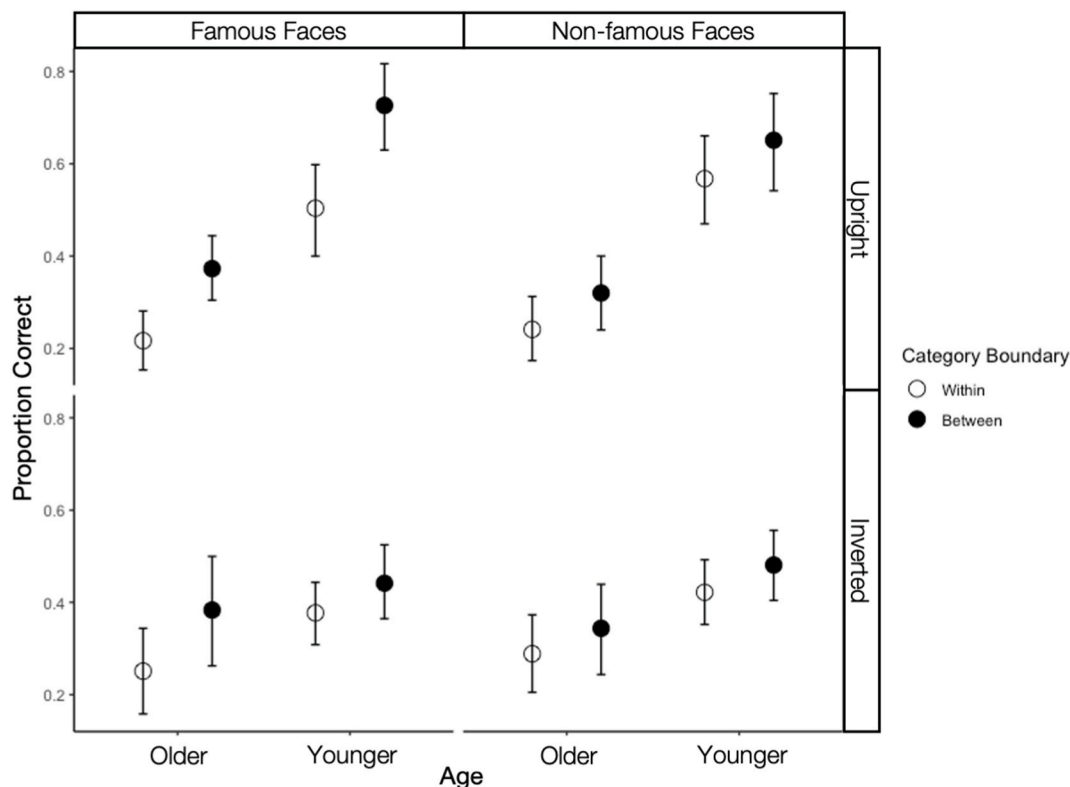


Fig. 4. Discrimination accuracy (proportion correct) within and between categories for upright and inverted faces in older and younger adults.

### 3.2. Discrimination

We calculated accuracy for different pairs only (e.g. 10% vs. 30% discrimination; Lee et al., 2014). We averaged accuracy scores for 10% vs. 30% trials and 70% vs. 90% trials to calculate the accuracy for within-category trials, and accuracy for 40% vs. 60% trials for between-category trials.

A mixed-effects model was used to analyze these data, because familiarity and category boundary were nested within participants. Discrimination accuracy was modeled as a function of age, orientation, familiarity, category boundary, and the interaction between these variables with a random intercept at the participant level. The model was estimated with an unstructured covariance matrix using the lmer function from the lme4 package (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2015) in R 3.2.2 (R Core Team, 2015). The ICC for the model suggested that discrimination accuracy was mildly clustered within participants,  $ICC = 0.14$ .

As shown in Fig. 4, younger participants had higher accuracy in discriminating morphed faces overall compared to older adults,  $\beta = 0.20$ ,  $SE = 0.04$ ,  $t(93) = 5.35$ ,  $p < 0.001$ ,  $R^2 = 0.23$ . This effect is partially explained by the fact that younger adults were better at discriminating upright faces,  $\beta = 0.15$ ,  $SE = 0.09$ ,  $t(140) = 1.68$ ,  $p = 0.05$ ,  $R^2 = 0.02$ , especially across the category boundary,  $\beta = 0.14$ ,  $SE = 0.07$ ,  $t(160) = 2.10$ ,  $p = 0.01$ ,  $R^2 = 0.03$ , compared to older adults. Overall, all participants were significantly better at discriminating

morphs of identities that crossed the category boundary (Between) as opposed to being within the same category (Within),  $\beta = 0.10$ ,  $SE = 0.01$ ,  $t(160) = 7.67$ ,  $p < 0.001$ ,  $R^2 = 0.39$ . Crucially, both younger and older participants were especially better at discriminating the identity of famous faces compared to non-famous faces in morphs that crossed this category boundary,  $\beta = 0.08$ ,  $SE = 0.02$ ,  $t(90) = 4.017$ ,  $p < 0.001$ ,  $R^2 = 0.15$ .

There was also a significant interaction between age and orientation (see Fig. 5). We found that while younger adults had higher accuracy than older adults in either orientation, younger adults were significantly more accurate in discriminating upright faces compared to inverted faces. By contrast, older adults did not differ in their ability to discriminate between upright and inverted faces,  $t(86) = 0.68$ ,  $p = 0.50$ .

### 4. Discussion

To investigate the relationship between categorical perception and pattern separation, we had younger and older participants study upright and inverted, familiar famous and novel non-famous faces using a standard categorical perception paradigm (Lee et al., 2014). As the ability to pattern separate becomes impaired with age (Toner et al., 2009; Yassa et al., 2010, 2011; Yassa et al., 2011a,b; Stark et al., 2015), we predicted that older adults would show poorer discrimination, and thus poorer CP, compared to younger adults. Our results with upright faces replicated those obtained by Lee et al. (2014). As hypothesized,

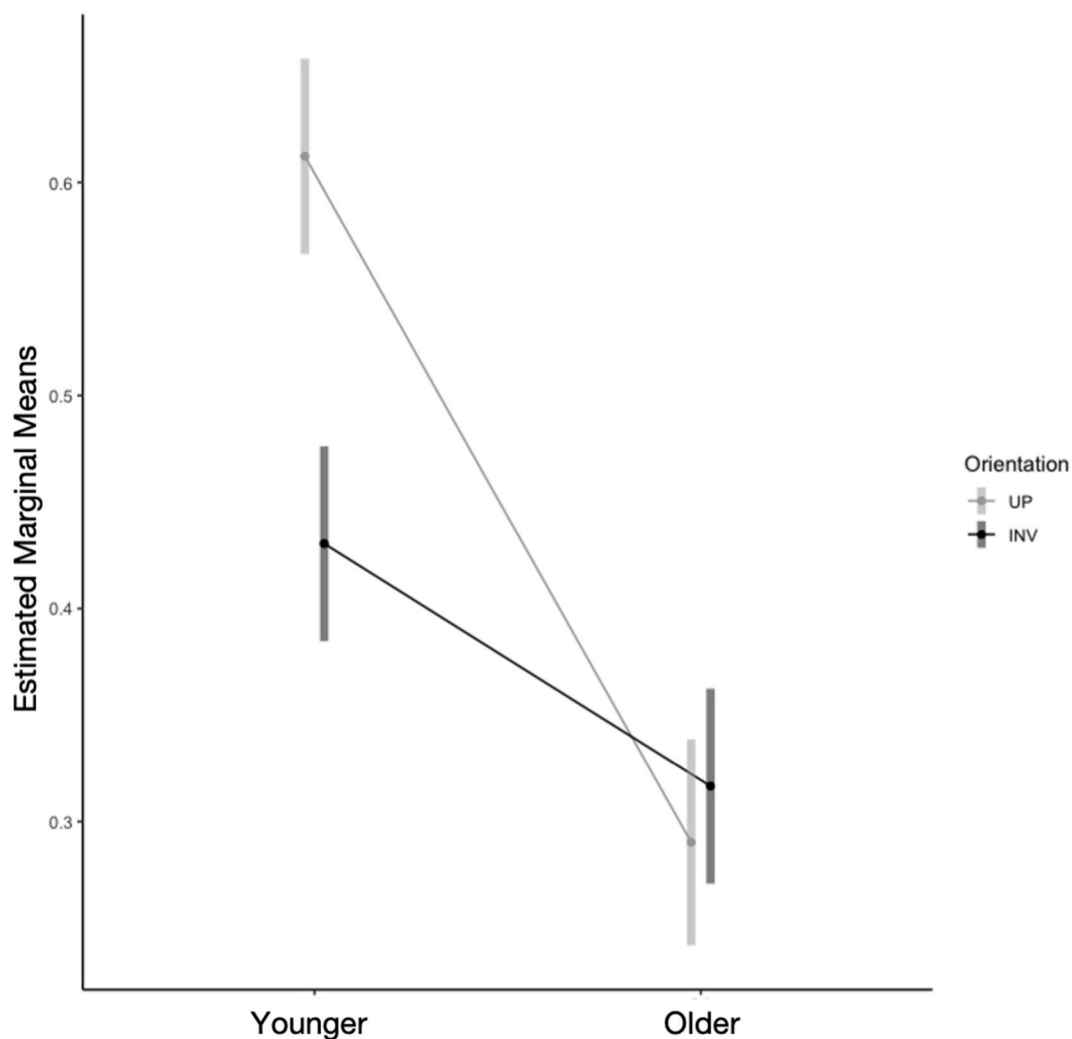


Fig. 5. Estimated marginal means (mean discrimination accuracy adjusted for any other variables in the model) for younger and older adults in the Upright and Inverted conditions.

although all groups exhibited enhanced discrimination for between-group categories compared to within-group categories, showing evidence for CP, older adults performed significantly worse compared to younger adults: their identification slopes were lower and they had more difficulty discriminating within category, compared to between category, exemplars.

We then tested the hypothesis that CP would be greater for famous faces compared to novel ones, as prior knowledge promotes mechanisms that mitigate interference by enhancing pattern separation. [Bein, Reggev and Maril \(2020\)](#) found that prior knowledge led to greater separation of underlying neural face representations in the hippocampus by looking at the multivoxel activity patterns of famous-novel pairs before and after learning. In addition, familiar faces are conceptually richer than unfamiliar faces ([Schwartz and Yovel, 2019](#)) and this, too, may enhance pattern separation. Both age groups benefited equally from the effect of familiarity when discriminating faces that crossed the category boundary. This familiarity benefit may have been influenced by stimulus effects such as face distinctiveness, although it is highly unlikely. This result suggests that although pattern separation may be compromised in older adults, it is operating at a sufficient level to benefit from familiarity.

Our findings on inversion indicate that the obverse can also occur. While an inverted face is identical to an upright face in terms of stimulus complexity and quality, it disrupts the familiar pattern of facial features as faces are normally only seen upright ([Valentine, 1988](#)). Inversion leads to diminished holistic processing of faces, forcing most participants to rely on part-based processing ([McKone et al., 2001](#); [Valentine, 1988](#)). To the extent that inversion leads to diminished CP, it may be the case that it does so by decreasing pattern separation, possibly because such processes operate more effectively on holistic than part-based representations.

Together, our results suggest there may be a two-stage process in CP. The first operates at the level of the perceptual system that distinguishes upright, holistic representations from part-based ones. Pattern separation processes then operate effectively on the upright, holistic representations, but not on inverted representations. For inverted stimuli, pattern separation cannot gain a purchase as performance is very low overall. This interpretation is supported by examining the effects of fame, in which a similar pattern is observed: fame benefits performance disproportionately in the upright condition, but hardly at all in the inverted condition.

These interpretations are supported by performance in the discrimination task. According to the strongest account of CP, if individuals solely use their categorizations to determine whether two stimuli are identical, the probabilities from the category identification task can completely predict discrimination performance, although this relation is rarely found in empirical results ([Pisoni and Tash, 1974](#); [Goldstone and Hendrickson, 2009](#)). When comparing obtained to prediction discrimination values (see Supplementary), obtained discrimination values were lower than predicted ones for all conditions and participants, except in younger adults when they viewed upright faces. Predicted discrimination values are derived from the participants' abilities to classify facial identities. This means that for older adults, and for all participants in the inverted condition, their actual discrimination performance was consistently worse than when discrimination was predicted solely on their ability to classify identities. That older adults also performed similarly even when discriminating between upright faces suggests that they may have relied more on part-based, than holistic, processes under these conditions, and only young adults primarily used configural/holistic processes to discriminate between upright faces. Face identification, however, lends itself better to holistic processes even in the case of older adults ([Konar et al., 2013](#); [Meinhardt-Injac et al., 2014](#)). Future work should investigate the role of holistic face processing in resolving mnemonic interference.

As we noted, evidence suggests that the hippocampus is critical for binding face-name associations ([Olsen et al., 2012](#)) and for relating

different viewpoints of a face with one another ([Olsen et al., 2015](#)). Likewise, comparison of highly, perceptually similar faces (i.e. morphed faces to endpoint identities) requires fine, mnemonic discrimination, which is thought to be subserved by hippocampal pattern separation ([Chang et al. \(2015\)](#)). Our results with inversion suggest that there are limits to what pattern separation can achieve: a minimum level of discriminability must be achieved before pattern separation can be effective.

In sum, our results suggest that binding and comparison functions of the hippocampus affect how we perceive and identify faces. Reduced CP in older adults, we suggest, may be mediated by hippocampal pattern separation deficits with aging, which may also contribute to age-related decline in face recognition.

## 5. Conclusion

Recent research shows that damage to the dentate gyrus, a region of the hippocampus implicated in pattern separation, compromises categorical perception of faces ([Baker et al., 2021](#)). Our results provide added support to this notion in two ways. First, older adults whose pattern separation processes are compromised ([Yassa et al., 2011a,b](#)) also show diminished categorical perception. Second, familiarity, which enhances pattern separation ([Bein et al., 2020](#)), also increases CP. Third, CP is better preserved in older adults when dealing with identification, which relies on memory, more than in discrimination, which does not, again pointing to pattern separation as a possible mechanism as its full effect is designed to orthogonalize memory representations. Last, when performance falls below a certain level, as it does for inverted faces, or when the representation is indeterminate, pattern separation has minimal effect, and CP is greatly diminished or absent. Although other mechanisms may account for diminished CP in older adults (see [Lee et al., 2014](#)), our findings suggest that pattern separation is a viable candidate whose contribution should be investigated in future research. If it proves to be correct, it would add to the growing list of non-mnemonic functions to which the hippocampus contributes and highlight the interaction between memory and perception ([Moscovitch et al., 2016](#)).

### Open practices statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request. This experiment was not preregistered.

### Credit Author Statement

Ariana Youm: Conceptualization, Formal analysis, Investigation, Project administration, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. Morris Moscovitch: Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2021.107999>.

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