Altered orbitofrontal cortex neural variability underlies idiosyncratic experiences during aging

Gargi Majumdar[1], Fahd Yazin[1,#], Arpan Banerjee[1*], Dipanjan Roy[1,2*]

1   Cognitive Brain Dynamics Lab, National Brain Research Centre, NH-8, Manesar, Gurugram, 122052, India.

2   Center for Brain Science and Applications (CBSA), School of AIDE, Indian Institute of Technology, Jodhpur 342030, India.

Present address: The University of Edinburgh 57 George Square Edinburgh EH8 9JU

Corresponding authors: Arpan Banerjee, Dipanjan Roy

Email: arpan@nbrc.ac.in (Dr Arpan Banerjee); droy@iitj.ac.in (Dr Dipanjan Roy)

Abstract

Moment-to-moment neural variability plays a crucial role in learning and behavioral flexibility. This variability has been linked to age-associated differences in task performances and resting-state activity. However, its directional effects – whether increased or decreased neural variability is beneficial – remain context-dependent and unclear. Here, we demonstrate that changes to cortical neural variability during naturalistic experience serve as a readout of changes to region-specific computations, distinct from resting-state variability and mean neural activity. During the affective experience, older adults exhibited a bi-directional neural variability shift within the medial and lateral orbitofrontal cortex. By employing a Bayesian learning model, we revealed that this corresponded to heightened uncertainty in the computational estimates of evolving valence in older adults. This was reflected in frequent state switching in neural response and temporally distorted representations within the lOFC in older adults, compared to stable, coherent representations in the young. Crucially, these representational changes mirrored the arousal responses of the two groups. These results advance our understanding of how neural variability might carry unique information in aging, particularly to their changing and possibly idiosyncratic affective experiences.

Significance Statement

With an increase in average lifespan, older individuals will be required to take greater responsibility for their physical and emotional wellbeing. However, the nature and neural

underpinnings of age-associated emotional changes still remain a paradox. Without a well-

grounded theoretical principle, the neurocognitive theories that ensued to explain these alterations

have yielded significant inconsistencies especially in relation to emotion processing under

naturalistic real-world scenarios. Combining evidence from large-scale behavioral and

neuroimaging data on both simple and naturalistic emotional tasks, we demonstrated that these

idiosyncratic emotional responses with aging, stems from their suboptimal computation of

uncertainty during hierarchical inference, manifested as increased neural variability and distorted

latent state representations in lateral orbitofrontal cortex. Together, our findings illustrate that age-

associated emotional changes can be unified under a singular framework of misestimation of

uncertainty, within a Bayesian brain purview, without the need for bespoke theories to explain

disjunctive evidence.

Introduction

Neural responses are inherently variable[1,2]. What was once considered as "noise" is now increasingly being recognized as a crucial part of efficient neural processing[2–4]. A growing body of research has shown that cortical signal variability is key in higher-order cognition[5,6], allowing for flexible navigation of task-specific demands[5,7,8]. This is strongly supported by theoretical frameworks suggesting that neural variability reflects a statistically optimal representation of task uncertainty[9,10]. This interpretation of neural variability as a cognitive facilitator is leveraged in aging neuroscience to compare how cognitive demands affect this measure across lifespan[11–13]. However, studies often show highly region-specific[14] and task-specific results[6,15], making a generalized directional claim between neural variability and experience tenuous. This highlights the need to contextualize neural variability within specific regions and under relevant theoretical models.

Conversely, studies on intrinsic, resting-state signal variability make it difficult to link to experience and specific theoretical frameworks outlined above due to the absence of an explicit task[4]. Combining naturalistic neuroimaging with theoretical modeling offers a promising approach to exploring how variability-based regional differentiation relates to experience. In this study, we explore how aging alters this relationship.

A richly dynamic and socially complex movie requires one to navigate an array of internal and external affective states flexibly. Orbitofrontal subregions in the prefrontal cortex have been implicated in numerous affect-related studies[16,17] and have strong theoretical underpinnings to learning[18]. Specifically, its medial and lateral sectors are thought to play complementary roles in affective computations[16]. The medial orbitofrontal cortex (mOFC) or ventromedial PFC is a core region involved in learning schemas[19] and state estimation[20] and fluctuates between affective states[21]. In contrast, the lateral orbitofrontal cortex (lOFC) is mostly externally focused, predicts state transitions[22], stimulus-outcome associations[23] and is involved in predictive tracking of affect[16]. In short, both these regions show strong ties to affective experience in naturalistic experiences. Moreover, theoretical frameworks suggest that these regions are involved in estimating state uncertainty and its dysfunction can have implications in affective disorders[24]. Changes to BOLD signal variability in these regions with age, should then exhibit broader changes to affective experience (Figure. 1a). For example, the mean neural activity might be similar in both

young and older adults for a brain region. However, the neural variability of the same region can show differential patterns between the two groups. Such variability-based regional change would likely be specific to the 'task-evoked' variability rather than intrinsic, resting-state variability[4,6]. Linking this to theoretical models of optimal task variable representations would offer testable model predictions to compare with neural data.

In the present study, we explore this variability-based regional differentiation in the context of aging. We particularly investigate how the task-evoked neural variability relates to the age-associated changes in affective experience. Employing Bayesian modelling on large-scale neuroimaging and behavioral data, older adults show significantly higher BOLD variability in the lOFC. In contrast, they exhibit a concurrent reduction in variability within the mOFC, during naturalistic experience. Notably, these differences were specific to the stimulus-evoked neural variability rather than their resting-state neural variability. Crucially, the mean neural activity showed no difference between the two groups. A Bayesian learning model revealed that the increased neural variability in lOFC in older adults was linked to a suboptimal computation of the evolving valence estimations. Furthermore, older adults showed a scattered latent state representation within their lOFC compared to a highly coherent pattern in the young. This resembled the moment-by-moment subjective emotional experience in both groups. Together, these results highlight the biological importance of regional BOLD signal variability and its effect on the affective experience during healthy aging.

Results

Neural variability during naturalistic experience is distinct from resting-state variability

Our aim was to investigate how the neural variability alters with aging in response to a naturalistic affective task (Figure. 1a). For this, we quantified the neural variability as the standard deviation of the normalized, filtered and demeaned BOLD time series (SD_{BOLD}) for both young and older adults for the movie (~8mins) and the resting state (~9mins) conditions. This enabled us to assess whether changes in neural variability reflect intrinsic traits or are induced by the affective states elicited by the movie.

We focused our analyses primarily on the prefrontal regions, given their role in higher-order cognition and affective processing, as well as evidence from our previous study[16]. The regions of

interest included the prefrontal regions – anterior cingulate cortex (ACC), dorsomedial cortex (dmPFC), dorsolateral prefrontal cortex (dlPFC), medial prefrontal cortex (mPFC), ventrolateral prefrontal cortex (vlPFC), lOFC and mOFC, visual cortex (VC) and posterior cingulate cortex (PCC), a core Default Mode Network region. To determine whether the engagement in older adults varies as a function of the emotional content of the stimulus, we performed an engagement analysis (shown in Supplementary Figure 4). Next, we constructed a Bayesian hierarchical regression with the SD_{BOLD} from the movie and the rest as the dependent variables. The model also included random effects of participants, including random slopes for the fixed effects to capture participant-level variance across the movie and rest. This allowed us to assess whether the BOLD variability associated with these regions, is driven primarily by structural changes with age. In that case, SD_{BOLD} would significantly differ between the two groups for both conditions. Posterior evidence for each hypothesis was quantified through Bayes factors. However, we observed a significant increase in the SD_{BOLD} for the older individuals for the movie and not the rest (Movie: $P = 1$, BF >100; Rest: $P = 0.86$, BF $= 6.04$) (Figure. 1b, c).

Neural variability offers unique information not captured by mean neural activity

One possibility is that the BOLD signal varies as a function of age affecting both the mean activity and variability of the young and older adults during the movie-watching task. This led us to investigate if the neural variability reflects a distinct source of information in contrast to the mean neural activity between the two groups. We computed the averaged BOLD signal for the movie-watching task and applied a Bayesian hierarchical regression using the previous model structure. No significant difference was found between the mean BOLD activities of the two groups (Figure. 1d) (Movie: $P = 0.83$, BF $= 4.89$).

The above results suggest two key points. First, the increase in cortical BOLD signal variability observed in healthy aging represents a task-specific effect unobserved in the resting state. Second, within naturalistic settings, neural variability provides distinct insights than those captured by the mean neural activity.

Dissociable task-evoked neural variability changes within lOFC and mOFC in older adults

Our findings so far suggest a distinct change in the task-specific neural variability between the two groups. Next, we wanted to focus on how these changes manifest at the regional levels and affect

their corresponding functions in naturalistic experience. We particularly focused on the two

subregions of the OFC known to mediate affective computations in naturalistic experiences. This

is also evidenced from our previous study, which identified a distinct dissociative role of the lOFC

and the mOFC in mediating affective experience during movie watching[16]. We compared the

SD_{BOLD} of the lOFC and mOFC between the young and older adults during the movie-watching

task. We observed opposing trends in the neural variability of these two regions with age (Figure.

2a,b). Older adults exhibited significantly higher SD_{BOLD} in the lOFC (Figure. 2a) (Young: β_{mean}

= 0.03, 95% HDI = [-0.15, 0.82], $P = 0.9$; Old: β_{mean} = 0.18, 95% HDI = [0.11, 0.23], $P = 1$), while

the mOFC showed reduced variability in old compared to younger adults (Figure. 2b) (Young:

β_{mean} = -0.004, 95% HDI = [-0.05, 0.04], $P = 0.57$; Old: β_{mean} = -0.05, 95% HDI = [-0.11, -0.001],

$P = 0.97$).

To determine whether these task-evoked changes in neural variability in older adults represented

a general aging effect, we compared their mean neural activity for the movie-watching task. No

significant differences were found between the groups in the BOLD means for either the lOFC

(Young: β_{mean} = 0.003, 95% HDI = [-0.009, 0.02], $P = 0.70$; Old: β_{mean} = 0.002, 95% HDI = [-

0.008, 0.01], $P = 0.67$) or mOFC (Young: β_{mean} = -0.004, 95% HDI = [-0.01, 0.009], $P = 0.74$;

Old: β_{mean} = -0.005, 95% HDI = [-0.02, 0.006], $P = 0.81$) (Supplementary Figure. 2).

Additionally, we also compared the SD_{BOLD} of VC and Precuneus between young and older adults,

to assess any sensory processing related effects. No significant differences were observed in the

neural variability between the two groups for these regions (Figure. 2c,d) (VC: Young: β_{mean} =

0.02, 95% HDI = [-0.02, 0.07], $P = 0.85$; Old: β_{mean} = -0.004, 95% HDI = [-0.06, 0.05], $P = 0.54$;

Precuneus: Young: β_{mean} = -0.005, 95% HDI = [-0.05, 0.04], $P = 0.58$; Old: β_{mean} = -0.03, 95%

HDI = [-0.09, 0.02], $P = 0.86$).

These above results indicate that regional BOLD variability provides distinct neural signatures of

aging that are not captured by mean BOLD activity alone. Additionally, the specific bidirectional

trends observed in the OFC may indicate an age-related shift in processing naturalistic movie

within this region.

Changes in neural variability underlie suboptimal computations of valence in the OFC in

older adults

Increased neural variability has been suggested to facilitate dynamic behavioral switching based
on task-specific demands. Parallely, theoretical frameworks propose that neural variability
supports efficient encoding of stimulus-specific uncertainty during tasks[10]. Our previous study
elaborated the role of orbitofrontal regions to encode uncertainty during affective processing[16].
Especially, we have shown that these regions are involved in optimally encoding the uncertainty
around the evolving valence in the movie. Thus, an altered BOLD variability in these regions may
reflect an altered valence processing during affective experience.

To investigate how this uncertainty around valence is computed by the young and older adults, we
implemented a Bayesian learning model termed as Hierarchical Gaussian Filter model (HGF)
(Figure. 3a). First, we collected the continuous valence ratings from two independent groups of
young and older adults for the movie (Figure. 3b). Next, we deployed multiple 3-level HGF models
to fit the averaged valence ratings of each group separately. This model has been extensively used
in learning, decision-making, and affective dynamics[25–27]. In this model, the averaged valence
time-course of each group is used as the input. With this input, the first layer, x_1, models the
probability of the valence at each time point. The next level, x_2, estimates the underlying
uncertainty associated with that of the predictions on the valence. Finally, the third level x_3,
estimates the overall volatility or the metavolatility associated with the valence. This indicates the
rate at which the belief in the uncertainty around valence changes. This can also be described as
one's belief in how stable are the movie contexts, given the valence dynamics. The belief updates
are primarily governed by 2 parameters - ω and ϑ, which influence the estimated uncertainty
(second-level) and volatility (third-level) trajectories about the valence respectively. Here, we
wanted to dynamically model the averaged valence rating of the elderly, by lesioning 2 free
parameters - ω and ϑ.

For this, we initially used the HGF model fitted to the young group (from our previous study)[16] as
the 'baseline' model. Following this, we simulated multiple models each with a specific lesioning
in ω and ϑ parameters. We then fit each of these models to the older cohort's group-averaged
valence time-course. We hypothesized that the model best-fitting the older adults' task-specific
variable (valence) would deviate from the 'baseline' parameters. This deviation would then reflect
specific changes in the estimation of uncertainty around the valence, reflective of their observed
differences in the OFC BOLD variability. A reduced ω in the older adults would suggest a

decreased prediction uncertainty around the valence dynamics, whereas an increased ω will signify increased uncertainty around the predictions of valence. The meta-volatility parameter ϑ, on the final level, determines the belief about the model's beliefs in the movie volatility. Lower values denote higher beliefs in the stability of the movie context, and vice versa.

Model inversion was conducted by variational inference, and model adjudication was done by selecting the one with the highest log-model evidence (LME) (Figure. 3c) (Table 2). The best-fitting model showed an increased ω (Figure. 4a) suggesting an increased variance (uncertainty) around the valence in the elderly. Concurrently it also showed a decreased ϑ, denoting an increased belief in the stability of the context of the movie. Figure. 2a,b shows that older adults exhibited increased variability in the lOFC and reduced variability in the mOFC than younger adults, mirroring the model parameters. This suggests that similar uncertainty processing trends occur in both the neural and model output from the same stimuli as a function of aging.

A more direct prediction of the model is that older adults would show more frequent prediction updates due to their increased ω (Figure. 4a). Based on our previous findings that the OFC tracks uncertainty around valence during naturalistic movie viewing[16], we hypothesized that older adults would show more frequent neural transitions in these regions compared to younger adults. We used Hidden Markov Models (HMMs) to obtain these neural transitions (see Methods for details). We found that both lOFC and mOFC transitions closely matched with the third-level updates in younger adults (Figure. 4b left) with more stable transitions. However, the lOFC and mOFC both showed frequent latent state transitions in older adults (Figure. 4b right).

We also compared the HMM state transitions of the visual cortex as a control ROI for the two groups (Figure. 4c and supplementary figure 5). This was to rule out the effect of sensory or perceptual uncertainty processing. Both groups exhibited similar transitions with no distinct pattern, suggesting that the observed differences in orbitofrontal regions are due to top-down processes rather than perceptual differences.

In summary, an increased neural variability in older adults within OFC reflected a suboptimal computation of the uncertainty around the valence. This also corresponded with faster latent state transitions within the older adults in contrast to more stable transitions within the OFC of the younger adults, aligning with Bayes-optimal prediction updates.

Disrupted OFC dynamics links to variable emotional experience in aging

Our findings so far suggest that older individuals exhibit a suboptimal computation of uncertainty around the valence, which may be linked to the altered neural variability in the lOFC and mOFC. While the computational model hinted at this relationship, we have not yet directly examined how these regions relate to affective experience. To explore this, we collected continuous ratings of Arousal for this movie from two independent groups of young and older adults. Arousal reflects the global emotional intensity of the movie, capturing elements beyond valence, such as attention-driven mechanisms. Unlike valence, the two groups showed significant difference between their arousal ratings, with older adults displaying lower and more variable arousal (Figure. 5a) ($r = 0.67$, $p < 0.001$). This effect was most pronounced during emotionally intense scenes, as rated by the young group.

The lOFC and mOFC exhibited distinct patterns of neural variability and qualitatively reflected different forms of prediction updates. This led us to hypothesise that these regions may show different latent representational patterns underlying the affective experience during the movie. The externally focused lOFC might exhibit heightened sensitivity due to its increased variability, while the mOFC, which processes internal states, might show reduced flexibility. To this end, we leveraged a non-linear dimensionality reduction method, Temporal-PHATE on the BOLD timeseries of these regions (see Methods for full description). This method has been shown to capture the sequential progression of neural activity onto a low-dimensional space, revealing how these regions transition across time. This would recover the sequential trajectory of 'latent states' these regions would navigate during naturalistic experience on a group level.

In the young adults, the latent representation in the lOFC followed a preserved temporal sequence during movie-watching, while in older adults, this sequence was disrupted (Figure. 5b). Crucially, the arousal responses exhibited the most differences between the groups at the time points where the lOFC sequence was most disrupted in the older adults. The consistency between neural data and behavioral ratings, despite originating from two distinct groups, underscores the reliability of these results. The latent representation in mOFC displayed different temporal trajectories between the two age groups as well (Supplementary Figure 3).

245 Overall, these results provide novel insights into the nature of regional neural variability linking

246 to healthy aging, optimal computations and most importantly our affective experience.

247 Generalizing age-related emotional variability to multiple tasks

Next, we considered whether the emotional variability observed in the movie task could be

generalized to other emotional tasks with different formats. It is important to rule out the possibility

that the neural variability observed was specific to movie demands (plot complexity, working

memory load etc). For this, we analyzed data from the scanning cohort on two separate behavioral

tasks.

First, we examined a task in which participants reported the displayed emotion on a morphed image

of a facial expression (FER). Participants chose from six emotion categories: Happy, Sad, Anger,

Fear, Disgust, and Surprise. We compared the individual variability of each participant by

computing the standard deviation (SD) of their accuracy over all 6 categories. Older adults had a

significantly higher SD than young (mean-SD_Y = 11.08, mean-SD_O = 17.44, t = -5.17, p < 0.0001,

Cohen's d = 0.73) (Figure. 6a). Interestingly, between-group variability for each of the 6 emotions

showed a similar pattern of increased idiosyncrasy in older adults (Happy: SD_Y = 2.68, SD_O =

5.99; Sad: SD_Y = 5.02, SD_O = 19.31; Anger: SD_Y = 19.52, SD_O = 27.4; Fear: SD_Y = 15.4, SD_O =

23.54; Disgust: SD_Y = 20.28, SD_O = 20.63; Surprise: SD_Y = 8.04, SD_O = 13.32) (Figure. 6b). Thus

the emotional variability was not only present but it showed aging related effects in each of the

separate emotions.

Next, we analyzed data from a task where participants watched short video clips (~30s) of Neutral,

Negative, and Positive valence and provided a single rating (0-100) of their emotional experience.

Here we could not obtain the individual variability due to the nature of the task but instead obtained

the between-group SD of their ratings for each condition. All 6 conditions (see Methods for details)

showed a consistent increase in variability in old irrespective of the valence (NegW_pos: SD_Y =

0.47, SD_O = 1.75, NegW_neg: SD_Y = 1.38, SD_O = 2.43; PosW_pos: SD_Y = 1.90, SD_O = 2.36;

PosW_neg: SD_Y = 0.74, SD_O = 1.47; NeuW_pos: SD_Y = 1.18, SD_O = 2.29; NeuW_neg: SD_Y =

0.40, SD_O = 1.42) (Figure. 6c).

Discussion

The key advance of our work is to show how regional BOLD variability indicates a physiologically unique signature in aging. Importantly, the changes to cortical neural variability in older adults show distinct patterns in naturalistic experience compared to mean neural activity as well as resting-state variability. This is in line with theoretical frameworks that posit task-variable computations require navigating different regimes flexibly, which may be compromised in aging[12]. We found valence-related processing in orbital prefrontal regions shows specific age-related changes in their neural variability in its medial (mOFC) and lateral (lOFC) subregions. Moreover, a Bayesian learning model suggested older adults had increased uncertainty around valence computations. Additionally, the model showed concordance with neural transitions within OFC in young, but much less in old, suggesting deviation from optimal computations. Changes to the latent representations in the regions closely resembled the affective experiences of both young and older adults. These results advance our understanding of how neural variability might carry unique information in aging, particularly with regards to their idiosyncratic affective experiences.

Neural variability is usually studied on cognitively demanding tasks (e.g. working memory) or resting-state variability[6,7,11,12,14]. These studies provide a wealth of results in terms of its various neurobiological properties and alterations in healthy aging[28]. While some studies link increased neural variability to deteriorating performance in tasks like working memory[8], others demonstrate the opposite trend. The pattern of change also varies across different brain regions. Unlike specific task-based studies, naturalistic paradigms require coordinated dynamics across multiple forms of higher-order cognition, making them more ecologically similar to real-life experiences[29,30]. Leveraging Bayesian hierarchical modelling allowed us to incorporate multiple, related sources of information within the data. Specifically, this ensured that we captured both individual, group-level and condition-specific effects on neural variability. In doing so, we found a significant increase in neural variability in older adults compared to young. Critically the evidence for this increase was much smaller in intrinsic, resting-state BOLD variability. This comparison provides strong evidence that neural variability modulated by naturalistic experiences differs from spontaneous, resting-state activity. In contrast, the mean neural responses (BOLD mean) showed no differences among the young and old. This strongly suggests that the mean and SD of the physiological BOLD signal carry fundamentally different sources of information in aging[28].

A variety of information is processed during naturalistic stimulation. We focused on an important

variable related to emotion processing - continuous valence information. In addition, we focused

on the OFC because of its critical role in affective processing[16]. Studies have shown that its lateral

subregions (lOFC) underpin distinct functional roles than its medial counterparts (mOFC)[31,32].

Here, we observed a distinct trend within the OFC for these two regions. lOFC exhibited much

higher neural variability than younger adults, while the mOFC showed reduced variability with

age. Importantly, these differences in variability could not be attributed to the differences in

perceptual processing in the visual cortex. Moreover, the mean neural activity showed no

differences among the groups, in both these regions. These results suggest that variability in BOLD

signals during movie viewing may reflect age-related alterations in affective processing.

Theoretical models posit that neural variability represents optimal task computations and

uncertainty representations[4,9,10]. Optimally representing task-uncertainty comes under the purview

of Bayesian frameworks of cognition[33]. To explore the effect of increased neural variability at the

computational level during naturalistic affective experience, we used a hierarchical Bayesian

learner [27] which was given the valence responses in the movie. In our previous study, a normative

variant of this model showed how uncertainty computations arise from valence in the same

younger individuals[16]. Using this as our baseline, we adjusted two key parameters underlying

uncertainty computations in different ways. This was to test several competing accounts of

suboptimal computations happening in aging[25,34,35]. This allowed us to use the same model

architecture to assess deviations in older adults compared to young. The winning variant showed

considerably higher variance around predicting valence for the older adults. That is, older adults

had a heightened uncertainty around predicting how the valence changes in the movie. To link the

neural findings with the model output, we compared prediction updates in the model to that of the

latent state transitions in the OFC. Neural state changes during naturalistic stimuli are closely

linked to the movie experience, although several factors might underlie these changes within a

region. Here, we found qualitative similarities between OFC transitions and prediction updates to

valence in the young. In contrast, the older adults showed more variable neural transitions. This

suggests that neural transitions here may reflect suboptimal estimation of valence uncertainty in

these regions. Overall, increased uncertainty around the valence coupled with increased neural

variability in lOFC suggests that older adults may experience less stable or more variable

emotional experiences.

Neural variability indexes how adaptive a region is to task variable changes and demands. Although a one-to-one correlation might be misleading, changes to this measure are expected to have an impact on the general cognition the specific task variable governs. In our study, we hypothesised that a suboptimal computation of emotional valence might affect the overall affective experience. Using T-PHATE, we projected neural representations of the OFC regions onto a low-dimensional space, uncovering latent state trajectories across the two groups. The stark differences observed in the lOFC were highly similar to their respective arousal time-courses. Specifically, a sequentially preserved representation observed in the young group mirrored their stable arousal dynamics. In contrast, the distorted patterns observed in older adults' lOFC paralleled their lower and more variable arousal. Cognitively demanding tasks such as working memory require representing and navigating a higher dynamic range of states to perform optimally. Affective tasks, in contrast, are more inferential in nature[36]. As a result, there is an inherent uncertainty in one's interpretations of emotional experiences. Here, representing a wider gamut might actually be misleading (at best) or paralyzing (at worst). Indeed, misestimation of uncertainty, a known factor in psychiatric disorders [24,37], may similarly underlie the idiosyncratic affective experiences in aging. In affective tasks, the lOFC helps predict how emotional states will change over time, integrating information about uncertainty to guide decision-making[18,22]. The higher variability observed here in the older cohorts seems to be consistent with our model results and reward learning studies. Taken together, this suggests that a failure to compute the uncertainty around the valence by the OFC might underlie the consistently idiosyncratic affective experiences seen in aging.

There are inherent limitations to interpreting BOLD signal variability in any task. For example vascular and non-cognitive process may play a significant role[28]. We took steps to mitigate these influences, by regressing motion as well as the CSF and white matter signals. Another potential critique is the use of two separate behavioral and neuroimaging groups in this study. However, the alignment between model prediction updates and neural transitions supports the validity of this approach. Moreover, we generalized the results of variability in emotions in the scanning cohort to two separate tasks requiring processing of valence. Our confirmation of similar patterns of shared neural responses in the movie for the two groups also rules out attentional processing-related accounts.

365   Overall, we contribute a strong case for the physiological BOLD signal variability as a readout of

366   regional computations, separate from resting-state and neural mean activity. The changes to this

367   signal in healthy aging, captured in a naturalistic setting offered a window to their idiosyncratic

368   experience. More nuanced questions on various forms of uncertainty can affect the variability

369   remain – but we hope to have furnished a potential framework for answering them.

Methods

Participants

We divided our participant pool into two groups – Young (18-35 years) and Old (60-88 years). After preprocessing, a total of 209 individuals (Young: N = 111, μage = 28.5±4.9, Male = 48; Old: N = 98, μage = 77±5, Male = 45) were selected from the healthy population derived Cambridge Centre for Aging and Neuroscience (CamCan) cohort for this study[38,39]. We extracted the behavioral responses of these participants for the Facial Emotion Recognition (FER) and Emotional Reactivity and Regulation (EmoR) tasks. Owing to missing data, the final sample size for the FER was 203 (Y = 108, O = 95) and that of EmoR was 91 (Y = 49, μage = 28±5; O = 42, μage = 76.9±5.7). All participants provided their informed consent, and the data was collected in accordance with the Cambridgeshire Research Ethics Committee.

Additionally, we recruited independent groups of participants on an online platform (Prolific) to collect continuous ratings for arousal, valence and uncertainty for the same movie shown to the neuroimaging participants. 40 participants were recruited for each group (N=80), age and demographically matched with the fMRI individuals (UK). All participants were screened based on educational qualification and mental health status to reduce potential confounds and reported no previous history of watching this movie. The study was approved by the Institutional Human Ethics Committee of the National Brain Research Centre, India (NBRC).

Stimulus

Our main behavioral and neuroimaging analyses were centred on a short, suspenseful movie called "Bang! You're dead" (~8mins) by Alfred Hitchcock.

Continuous behavioral rating task

Four independent groups of participants continuously rated the movie for valence and arousal using a vertical slider on Prolific (Table 1). After rejecting subjects with missing data, this resulted in a final sample of 97 participants (Y: N = 34, μage = 24.5, Male =16; O: N = 30, μage = 67.8, Male = 14). For each group, we z-scored the participants' responses and smoothed the averaged time courses using local regression smoothing (loess).

fMRI acquisition and preprocessing

The fMRI data for the movie-watching and the resting state sessions were provided by the CamCan[38]. The functional scans for the movie-watching session were acquired using a T2∗-weighted echo planar imaging pulse sequence (TR = 2470 ms; TE = 9.4 ms, 21.2 ms,33 ms, 45 ms, 57 ms; 32 axial slices; slice thickness = 3.7 mm; FOV = 192 × 192 mm; voxel size = 3 × 3 × 4.44 mm), leading to a total of 193 volumes. The functional data for resting state was acquired using the same pulse sequence and acquisition parameters with a TR of 1970 ms. The acquisition time for this session was 8 min 40 s, which resulted in 261 functional volumes. The first 4 functional volumes of both sessions were discarded from the main analyses.

Neuroimaging data from both sessions were preprocessed in MATLAB (2019b) using Statistical Parametric Mapping (SPM12) (https://www.fil.ion.ucl.ac.uk/spm). The preprocessing steps included spatial realignment, slice-timing correction, coregistration of functional (T2) to anatomical (T1) scans, affine transformation to Montreal Neurological Institute template (MNI152), resampling to 2 mm isotropic voxels, and spatial smoothing with a 6 × 6 × 9-mm full-width at half-maximum Gaussian kernel. Whole-movie GLM was computed by regressing six motion parameters (X-, Y-, Z-displacement and pitch, roll, and yaw parameters) by least square regression. We excluded subjects with maximum framewise displacement >2.5 mm or 1.5° from further analysis. The extracted BOLD data were detrended and band-pass filtered (0.01–0.1 Hz) using a second-order Butterworth filter.

Region-of-interest (ROI) definition

We focused our analyses on the prefrontal cortical regions due to their critical role in mediating higher-order cognitive functions, such as affect[16,40,41], and their involvement in naturalistic tasks[42,43].

For the neural variability analyses of the movie and resting state, we included 7 prefrontal ROIs – anterior cingulate cortex (ACC), dorsolateral PFC (dlPFC), dorsomedial (dmPFC), ventrolateral PFC (vlPFC), medial PFC (mPFC), medial orbitofrontal cortex (mOFC) and lateral orbitofrontal cortex (lOFC). We also incorporated the visual cortex (VC) and Precuneus because of their roles

in sensory and multi-sensory processing. All ROI masks were adapted from our previous work,

where additional details can be found [16].

Bayesian Hierarchical Regression (BHR) to model the effect of movie and resting state on

neural variability and mean neural activity

First, we computed the neural variability as the standard deviation of the BOLD signal (SD_{BOLD})

for the movie and the resting state. BOLD signals were extracted for each session and each ROI

after regressing out signals from white matter, cerebrospinal fluid (CSF), and motion-related

artifacts. Thereafter, the BOLD timeseries was normalised, filtered and demeaned for each ROI

for both groups. Next, we modelled the effect of rest and movie with age on the BOLD variability

of the participants, using a BHR. The dependent variable for the model input was given by the

SD_{BOLD} of 9 ROIs which included all prefrontal ROIs (mOFC, mPFC, dmPFC, lOFC, vlPFC,

dlPFC, ACC) along with VC and Precuneus.

The SD_{BOLD} of each session (Rest/Movie) for each subject was modeled as a Student t-distribution:

$SD_{BOLD} = $ Student $t\ (v, \mu, \sigma),$

Where v is the degrees of freedom, σ is the scale parameter of the distribution, and μ is the mean,

which can be expressed as:

$\mu = \alpha + \alpha_j + \alpha_i + \beta_1.\text{Age} + \beta_2.\text{Condition} + \beta_3.\text{Age : Condition}$

$+ \gamma_{1j}.\ \text{Age} \mid \text{ROI}$

$+ \gamma_{2j}.\ \text{Condition} \mid \text{ROI}$

$+ \gamma_{3j}.\ \text{Age: Condition} \mid \text{ROI}$

$+ \gamma_{4i}.\ \text{Age} \mid \text{Subject}$

$+ \gamma_{5i}.\ \text{Condition} \mid \text{Subject} + \sigma_i + \varepsilon.$

Here, α is the intercept, α_j is the varying intercept over j ROIs, α_i is the varying intercept over i

participants. β and γ reflect the slope and varying slope of the predictors, respectively. β_1 represents

the slope for the age (given as a categorical variable), β_2 denotes the slope for the conditions (given

as categorical variables - Rest and Movie), β_3 denotes the slope for the cross-level interaction term of age and condition. γ_{1j} and γ_{2j} indicate the varying slope terms where the age and conditions vary across all the ROIs. γ_{3j} indicates the varying slope term where the cross-level interaction term (age and condition) varies across all the ROIs. Likewise, γ_{4i}, and γ_{5i} are varying slopes where each of the 2 predictors is allowed to vary across all i (=209) participants. σ_i and ε connote subject-level and population-level variance terms, respectively. Weak, noninformative priors were applied over the model terms. The model incorporated the effect of rest and movies as their interaction with age (categorically defined as Young and Old) while accounting for within-group and between-group variability on ROIs. For more details, see supplementary section 1 (Supplementary Figure 1).

$\alpha \sim$ Student $t(3, 0.5, 2.5)$

$\beta \sim$ Student $t(3, 0.5, 2.5)$

$\gamma \sim$ Student $t(3, 0.5, 2.5)$

$\sigma_j \sim$ Half Student $t(3, 0, 2.5)$

$\varepsilon \sim$ Half Student $t(3, 0, 2.5)$

Evidence of P > 95% is equivalent to the frequentist depiction of significant *P*-values. In addition, we also quantified the effect size by computing the BF (calculated by the Savage-Dickey ratio).

A similar model was used to examine the effect of movie and resting-state conditions on mean neural activity across age groups, using the same ROIs. In this model, the standard deviation of BOLD (SD$_{BOLD}$) was replaced with the average BOLD activity for each ROI.

Behavioral modelling - Hierarchical Gaussian Filter (HGF)

To investigate how the age-associated changes in task-evoked neural variability affect the computation during affective experience, we compared and contrasted multiple variants of the 3-level hierarchical Gaussian Filter (HGF)[27]. The HGF is a Bayesian learning model [27], which can be used to fit and recover parameters from a participant's behavioral data or simulate models with different parameter configurations, scored on Log Model Evidence (LME). In brief, by employing variational Bayes, this model can infer an individual's belief and uncertainty trajectory of hidden

environmental states, which are modelled as a hierarchy of coupled Gaussian random walks. Since we did not have any behavioral response from the neuroimaging participants, we only used a perceptual model on a Bayes-optimal agent with the average valence ratings of each group as the input using the TAPAS toolbox (http://www. translationalneuromodeling.org/tapas/). With this input, the first layer, x_1, models the probability of the valence at each time point. The next level, x_2, estimates the underlying uncertainty associated with the predictions on the valence. Finally, the third level x_3, estimates the overall volatility associated with the valence, i.e., the rate at which the belief on the uncertainty around valence changes. In this study, this level can signify the belief on the environmental stability or the context of the movie. These levels are related to each other with regard to the step-size of a Gaussian random walk. A prediction error i.e. a misestimation of the valence at the lower level will cause an update at the higher levels. These levels are coupled to each other by parameter $\boldsymbol{\kappa}$, which denotes a phasic, temporally varying parameter that determines the scaling of the volatility. Since we did not have any specific hypotheses on how this coupling might change with age, we kept the $\boldsymbol{\kappa}$ same for both groups. Our main hypotheses rested with the $\boldsymbol{\omega}$ and $\boldsymbol{\vartheta}$ parameters that denote a tonic, time-invariant parameter for the second and third levels, respectively. $\boldsymbol{\Omega}$ captures the degree to which an agent updates his belief about the rate of change of valence $x_2^{(k)}$ independent of the volatility and $\boldsymbol{\vartheta}$ determines meta-volatility or the variance of the agent's volatility.

The HGF is commonly implemented to dynamically model learning under uncertainty. However, previously this model had enabled us to uncover a predictive architecture where volatility trajectory estimated from the valence ratings reflected the subjective uncertainty of the participants[16] during affective experiences. In this study, our goal was to test a few competing hypotheses, especially, whether the older adults differed with regards to – 1) computation of the variance around the fluctuating valence across the movie and 2) updating their belief trajectory in the face of changing uncertainty on the valence. Thus, this can be construed as a form of model 'lesioning' wherein a normative model that explains a behavioural quantity and its latent parameters are altered, such that qualitative predictions similar to the data can be assessed.

To formalize these predictions, we simulated multiple models manipulating 2 free parameters $\boldsymbol{\omega}$ and $\boldsymbol{\vartheta}$ (Table 2), the tonic parameters for the second and third level respectively. An increase in $\boldsymbol{\omega}$ would indicate a higher uncertainty estimate (at the 2nd level) on the changing valence, whereas

its decrease would indicate vice-versa. The meta-volatility parameter ϑ, influences the belief
updates on the volatility (3rd level) of the valence. The resultant belief trajectories were visually
inspected and after considering the Log-Model Evidence (LME), we selected the best model which
could offer a parsimonious explanation of the age-associated changes during naturalistic
experience in older adults.

To analyse the effect of ω on the variance of belief around the changing valence we compared the
variance of the x_2 trajectories of both groups. Furthermore, we also compared how the ω affected
the belief updates in these two groups, by binarizing their update trajectories (ud3) with a threshold
of 1 SD.

Hidden Markov Model (HMM)

Next, we wanted to explore how the age-associated computational changes are reflected in the
latent state representations of the orbitofrontal cortex during naturalistic experience. For this, we
fit an HMM to the individual subject's BOLD time series of lOFC, mOFC and VC (for control)
for both groups, generating a single emission sequence across all participants of a group. Multiple
models were created from pre-specified states of range 2 to 10 which were then adjudicated by
selecting the one with the least Bayesian information criteria (BIC). Parameter estimation for the
models was done using the Baum-Welch algorithm (a variant of the Expectation-Maximization
algorithm) by iteratively maximizing the expected joint log-likelihood of the parameters, given the
observations and states. Decoding was done by the Viterbi algorithm by computing the maximum
a posteriori state sequence for each of the HMMs. Thereafter, we compared the update trajectories
from the HGF with the HMM state transitions of the orbitofrontal cortex subregions for the two
groups.

Temporal Potential of Heat-diffusion for Affinity-based Transition Embedding (PHATE)

Finally, we sought to explore, how these representational changes in the OFC affect the subjective
experience in the two groups. We implemented a non-linear, unsupervised dimensional-reduction
technique called temporal PHATE (T-PHATE) [44]. PHATE is recognized for its distinct advantages
compared to conventional dimensional-reduction techniques like PCA and tSNE, as it effectively
preserves both local and global data structures. Additionally, its non-linear nature and ability to

capture the temporal evolution of a component present in the stimulus makes it well-suited for

naturalistic paradigm.

It considers an input matrix of TR x Voxel, on which it computes the Euclidean distance D between

two TRs, where, $D(i, j) = \|X_i, - X_j,\|^2$. Then it converts this matrix into a local affinity matrix K

using an adaptive bandwidth Gaussian kernel. The affinity matrix K is then row-normalized to get

the initial probabilities P, which are used for the Markovian random-walk diffusion process. The

diffusion operator P is then raised to the $t_D{}^{\text{th}}$ power, where t_D is the PHATE optimal diffusion time

scale, to perform a t_D-step random walk over the data. This specific diffusion process effectively

infers more global relations beyond the local affinities. To further preserve both the local and

manifold-intrinsic global structure of data, PHATE computes the diffusion potential distance P_D

between the distribution at the ith row $P^{tD}{}_i$ and the distribution at the jth row $P^{tD}{}_j$.

$$P_D(i,j) = \sqrt{\sum_k \square \left(\log\!\left(P^{t_D}(i,k) - P^{t_D}(j,k)\right)\right)^2}$$

The potential distance is finally embedded with a distance embedding method (multidimensional

scaling - MDS) for final visualisation. This embedding accurately visualizes trajectories and data

distances, without requiring strict assumptions typically used by path-finding and tree-fitting

algorithms. T-PHATE is a modified PHATE algorithm which is able to capture the temporal aspect

of the data. The algorithm works the same as the original PHATE except for the temporal

component infused in the diffusion matrix using the auto-covariance function in a Temporal

Affinity Matrix[44].

Behavioral tasks on Emotion processing

Behavioral tasks on Emotion processing

Facial Emotion Recognition task

Participants were presented with a series of emotional faces and for each trial, they had to

characterize the emotion from six emotion categories – happy, sad, anger, fear, disgust, and

surprise. Ee investigated the within-group and between-group behavioral variability (SD) across
all categories and for each category respectively for both groups.

Emotional Reactivity and Regulation task

Participants viewed short video clips of 30 seconds, chosen from a wide range of videos
categorized into Positive (e.g. Babies playing), Negative (e.g. Accident) or Neutral (e.g.
Workplace demonstration) clips. The presentation of the video was preceded by a cue to watch or
regulate. For our study, we only selected the responses to the Watch condition, where participants
were instructed to rate their emotional response on scales of 0 – 100 on how positive and negative
they felt after each clip. Thereby, for each group, their behavioral ratings were classified into 6
types – Negative-watch-Negative (NegW_neg), Negative-watch-Positive (NegW_pos), Positive-
watch-Negative (PosW_neg), Positive-watch-Positive (PosW_pos), Neutral-watch-Negative
(NeuW_neg) and Neutral-watch-Positive (NeuW_pos). We compared the between-group
variability of their responses for each condition.

References:

1. Neumann, J., Lohmann, G., Zysset, S. & von Cramon, D. Y. Within-subject variability of BOLD response dynamics. *NeuroImage* **19**, 784–796 (2003).

2. Garrett, D. D., Kovacevic, N., McIntosh, A. R. & Grady, C. L. Blood oxygen level-dependent signal variability is more than just noise. *J Neurosci* **30**, 4914–4921 (2010).

3. Garrett, D. D., Kovacevic, N., McIntosh, A. R. & Grady, C. L. The importance of being variable. *J Neurosci* **31**, 4496–4503 (2011).

4. Waschke, L., Kloosterman, N. A., Obleser, J. & Garrett, D. D. Behavior needs neural variability. *Neuron* **109**, 751–766 (2021).

5. Garrett, D. D., Kovacevic, N., McIntosh, A. R. & Grady, C. L. The modulation of BOLD variability between cognitive states varies by age and processing speed. *Cereb Cortex* **23**, 684–693 (2013).

6. Millar, P. R. *et al.* Evaluating Cognitive Relationships with Resting-State and Task-driven Blood Oxygen Level-Dependent Variability. *Journal of Cognitive Neuroscience* **33**, 279–302 (2021).

7. Armbruster-Genç, D. J. N., Ueltzhöffer, K. & Fiebach, C. J. Brain Signal Variability Differentially Affects Cognitive Flexibility and Cognitive Stability. *J. Neurosci.* **36**, 3978–3987 (2016).

8. Steinberg, S. N., Malins, J. G., Liu, J. & King, T. Z. Within-individual BOLD signal variability in the N-back task and its associations with vigilance and working memory. *Neuropsychologia* **173**, 108280 (2022).

9. Festa, D., Aschner, A., Davila, A., Kohn, A. & Coen-Cagli, R. Neuronal variability reflects probabilistic inference tuned to natural image statistics. *Nat Commun* **12**, 3635 (2021).

10. Orbán, G., Berkes, P., Fiser, J. & Lengyel, M. Neural Variability and Sampling-Based Probabilistic Representations in the Visual Cortex. *Neuron* **92**, 530–543 (2016).

11. Grady, C. L. & Garrett, D. D. Brain signal variability is modulated as a function of internal and external demand in younger and older adults. *Neuroimage* **169**, 510–523 (2018).

12. Boylan, M. A. *et al.* Greater BOLD Variability is Associated With Poorer Cognitive Function in an Adult Lifespan Sample. *Cereb Cortex* **31**, 562–574 (2021).

13. Rieck, J. R., DeSouza, B., Baracchini, G. & Grady, C. L. Reduced modulation of BOLD variability as a function of cognitive load in healthy aging. *Neurobiology of Aging* **112**, 215–230 (2022).

14. Nomi, J. S., Bolt, T. S., Ezie, C. E. C., Uddin, L. Q. & Heller, A. S. Moment-to-Moment BOLD Signal Variability Reflects Regional Changes in Neural Flexibility across the Lifespan. *J Neurosci* **37**, 5539–5548 (2017).

15. Gaut, G. *et al.* Predicting Task and Subject Differences with Functional Connectivity and Blood-Oxygen-Level-Dependent Variability. *Brain Connectivity* **9**, 451–463 (2019).

16. Majumdar, G., Yazin, F., Banerjee, A. & Roy, D. Emotion dynamics as hierarchical Bayesian inference in time. *Cerebral Cortex* **33**, 3750–3772 (2023).

17. Rolls, E. T., Cheng, W. & Feng, J. The orbitofrontal cortex: reward, emotion and depression. *Brain Communications* **2**, fcaa196 (2020).

18. Chan, S. C. Y., Schuck, N. W., Lopatina, N., Schoenbaum, G. & Niv, Y. Orbitofrontal cortex and learning predictions of state transitions. *Behav Neurosci* **135**, 487–497 (2021).

19. Mack, M. L., Preston, A. R. & Love, B. C. Ventromedial prefrontal cortex compression during concept learning. *Nat Commun* **11**, 46 (2020).

20. Moneta, N., Garvert, M. M., Heekeren, H. R. & Schuck, N. W. Task state representations in vmPFC mediate relevant and irrelevant value signals and their behavioral influence. *Nat Commun* **14**, 3156 (2023).

21. Hiser, J. & Koenigs, M. The multifaceted role of ventromedial prefrontal cortex in emotion, decision-making, social cognition, and psychopathology. *Biol Psychiatry* **83**, 638–647 (2018).

22. Elliott Wimmer, G. & Büchel, C. Learning of distant state predictions by the orbitofrontal cortex in humans. *Nat Commun* **10**, 2554 (2019).

23. Wang, B. A., Veismann, M., Banerjee, A. & Pleger, B. Human orbitofrontal cortex signals decision outcomes to sensory cortex during behavioral adaptations. *Nat Commun* **14**, 3552 (2023).

24. Pulcu, E. & Browning, M. The Misestimation of Uncertainty in Affective Disorders. *Trends Cogn Sci* **23**, 865–875 (2019).

25. Reiter, A. M. F., Diaconescu, A. O., Eppinger, B. & Li, S.-C. Human aging alters social inference about others' changing intentions. *Neurobiology of Aging* **103**, 98–108 (2021).

26. Siegel, J. Z., Mathys, C., Rutledge, R. B. & Crockett, M. J. Beliefs about bad people are volatile. *Nat Hum Behav* **2**, 750–756 (2018).

27. Mathys, C., Daunizeau, J., Friston, K. J. & Stephan, K. E. A bayesian foundation for individual learning under uncertainty. *Front Hum Neurosci* **5**, 39 (2011).

28. Baracchini, G. *et al.* The biological role of local and global fMRI BOLD signal variability in human brain organization. Preprint at https://doi.org/10.1101/2023.10.22.563476 (2023).

29. Ghaderi, A. H., Wang, H. & Protzner, A. Exploring the Interplay between BOLD Signal Variability, Complexity, and Static and Dynamic Functional Brain Network Features during Movie Viewing. Preprint at https://doi.org/10.1101/2023.02.28.530546 (2023).

30. Hasson, U., Malach, R. & Heeger, D. J. Reliability of cortical activity during natural
stimulation. *Trends Cogn Sci* **14**, 40 (2010).

31. Elliott, R. Dissociable Functions in the Medial and Lateral Orbitofrontal Cortex:
Evidence from Human Neuroimaging Studies. *Cerebral Cortex* **10**, 308–317 (2000).

32. Qiu, L. *et al.* Functional specialization of medial and lateral orbitofrontal cortex in
inferential decision-making. *iScience* **27**, 110007 (2024).

33. Knill, D. C. & Pouget, A. The Bayesian brain: the role of uncertainty in neural coding
and computation. *Trends in Neurosciences* **27**, 712–719 (2004).

34. Nassar, M. R. *et al.* Age differences in learning emerge from an insufficient
representation of uncertainty in older adults. *Nat Commun* **7**, 11609 (2016).

35. Bruckner, R., Nassar, M. R., Li, S.-C. & Eppinger, B. Default beliefs guide learning
under uncertainty in children and older adults. Preprint at https://doi.org/10.31234/osf.io/we3ct
(2020).

36. Tracking the affective state of unseen persons | PNAS.
https://www.pnas.org/doi/10.1073/pnas.1812250116.

37. Pulcu, E. *et al.* Using a generative model of affect to characterize affective variability and
its response to treatment in bipolar disorder. *Proc Natl Acad Sci U S A* **119**, e2202983119
(2022).

38. Shafto, M. A. *et al.* The Cambridge Centre for Ageing and Neuroscience (Cam-CAN)
study protocol: a cross-sectional, lifespan, multidisciplinary examination of healthy cognitive
ageing. *BMC Neurology* **14**, 204 (2014).

39. Taylor, J. R. *et al.* The Cambridge Centre for Ageing and Neuroscience (Cam-CAN) data
repository: Structural and functional MRI, MEG, and cognitive data from a cross-sectional adult
lifespan sample. *Neuroimage* **144**, 262–269 (2017).

40. Chang, L. J. *et al.* Endogenous variation in ventromedial prefrontal cortex state dynamics
during naturalistic viewing reflects affective experience. *Science Advances* **7**, eabf7129 (2021).

41. Jääskeläinen, I. P., Sams, M., Glerean, E. & Ahveninen, J. Movies and narratives as
naturalistic stimuli in neuroimaging. *NeuroImage* **224**, 117445 (2021).

42. Brandman, T., Malach, R. & Simony, E. The surprising role of the default mode network
in naturalistic perception. *Commun Biol* **4**, 1–9 (2021).

43. Saarimäki, H. Naturalistic Stimuli in Affective Neuroimaging: A Review. *Front. Hum.*
Neurosci. **15**, (2021).

44. Busch, E. L. *et al.* Multi-view manifold learning of human brain-state trajectories. *Nat*
Comput Sci **3**, 240–253 (2023).

Table 1. Instructions for the continuous rating task conducted in Prolific

Arousal: Click the white button (and hold it throughout) and drag it up or down depending on the intensity of emotion you feel while watching the movie, irrespective of whether you feel a positive or negative emotion.

Valence: Click the white button (and hold it throughout) and drag it up or down depending on whether you feel – positive (up) or negative (down). If it gets increasingly negative, you drag it further down from the centre and vice versa.

680   **Table 2: Prior parameters for all simulated HGF models.**

	$\omega_1\ \mu$	$\omega_2\ \mu$	$\omega_1\ \sigma$	$\omega_2\ \sigma$	$\theta\ \mu$	$\theta\ \sigma$	LME
Baseline Model	99993	-8	1	0.05	2	0.05	1703
Increased Uncertainty at both levels	99993	-4	1	0.05	4	0.05	1717
Decreased Uncertainty at both levels	99993	-10	1	0.05	0	0.05	1678
Increased Uncertainty around Valence and decreased metavolatility	99993	-4	1	0.05	0.05	0.05	1737
Decreased Uncertainty around Valence, increased metavolatility	99993	-10	1	0.05	4	0.05	1497

Figure 1: Neural Variability during Naturalistic Experience shows Unique Changes in Aging.
(a) Illustration depicting the regional differentiation based on neural variability across two age
groups. We analysed average neural activity (μ_{BOLD}) and the neural variability (SD_{BOLD}) during
movie-watching and resting state sessions in young (N=111, 18-35yrs) and older adults (N=98,
60-88 yrs). (Bottom) The illustration demonstrates that while the μ_{BOLD} and the SD_{BOLD} might be
similar across age groups for ROI_1. In contrast, ROI_2 may show differing levels of SD_{BOLD}
between the age groups while maintaining similar μ_{BOLD} values. This highlights that average
neural activity and its variability provide distinct and complementary information about neural
functioning. Main effect of (b) Movie and (c) Rest on SD_{BOLD} across young and older adults.
Posterior density estimates shows significantly more evidence for increased SD_{BOLD} in old than

694   young ($P = 1$, BF >100) in movie than that in the rest ($P = 0.86$, BF $= 6.04$). (d) Main effect of

695   movie on μ_{BOLD}. No significant difference was observed between the two groups ($P = 0.83$, BF $=$

696   4.89).

Figure 2: Neural Variability shows functionally distinct trend in the Orbitofrontal cortex in
aging. ROI-level effect of the movie on the SD_{BOLD} across the two groups. (a) Posterior density
estimates of lOFC shows significantly more evidence in old than young (Young: $\beta_{mean} = 0.03$, P
$= 0.9$; Old: $\beta_{mean} = 0.18$, $P = 1$). (b) In contrast, the posterior density estimates of mOFC showed
reduced variability in old compared to younger adults (Young: $\beta_{mean} = -0.004$, $P = 0.57$; Old:
$\beta_{mean} = -0.05$, $P = 0.97$). No significant differences were observed in the neural variability
between the two groups for (c) the VC and (d) Precuneus, to rule out sensory-driven changes.

Figure 3: (a) Graphical illustration of the HGF. x_1 represents beliefs about the observed valence, which in turn is affected by x_2, representing the belief of how the valence changes. x_3 estimates the metavolatility related to the valence timecourse, which in turn affects x_2. The levels are coupled via a phasic, time-varying parameter kappa (κ). A tonic, time-invariant parameter omega (ω) influences the variance of the Gaussian walk at x_2, while theta (ϑ) determines the variance of the volatility. (b) Continuous ratings of Valence during the Movie in young and older adults. Older adults exhibit more variable valence than young adults although they show a strong correlation (r=0.91, p<0.001). (c) We simulated multiple 3-level HGF models for older adults and selected the models based on the highest LME. These models were simulated by lesioning two free parameters - ω and ϑ affecting the second and the third level trajectories simultaneously.

Figure 4: Bayesian model predictions and Orbitofrontal Neural variability in Aging. (a)
Parameter comparisons from the final HGF model reveal an increased ω and reduced ϑ in the
older adults. (b) Model prediction updates and neural state transitions of the lOFC and mOFC
(from HMM). Younger adults show much more stable and synchronised latent state transitions of
the OFC (qualitatively) which were replaced by much faster transitions in the older adults. (c)
The latent state transitions of the Visual Cortex (VC) between the two groups, showed a similar
transition pattern in both groups. This might reflect that the processing of sensory uncertainty
(changing of visual features) is similar in both groups.

Figure 5: (a) Older adults exhibit lower and more variable arousal ratings than younger adults (r=0.67, p<0.001). (b) Manifold embedding of the lOFC using T-PHATE. Each data point is indexed by TR. The latent temporal trajectory of the lOFC shows a conserved and sequential representation during a movie-watching task in young. In contrast, the older adults exhibit a disrupted latent trajectory, indicating alterations in their temporal dynamics of the lOFC. Notably, the disrupted segments in their latent trajectory correspond to their differential emotional experiences during those specific parts of the movie (coloured bars in the ratings correspond to the TRs in T-PHATE embeddings). Importantly, despite the neural and behavioral data being from two independent groups of participants, a similar pattern is observed in both.

Figure 6: Generalizing age-related emotional variability to multiple tasks. (a) In the Facial Emotion Recognition (FER) task, individual variability, computed as the standard deviation (SD) of each participant's accuracy over all 6 categories depicts significantly higher behavioral variability in older adults compared to young (mean-SD$_{Young}$ = 11.08, mean-SD$_{Old}$ = 17.44, P<0.0001). (b) All emotion categories show increased variability in older adults compared to the younger individuals using between-participant SD separately for each emotion category. (c) Between-participant SD during Emotion Reappraisal task shows increased variability in behavioral responses in the old compared to young for all conditions.

Supplementary Material

Bayesian Hierarchical Regression to model the effect of uncertainty and valence on the neural activity

For this analysis, we defined 5 Ascent (high-intensity scenes marked by positive arousal slopes), 5 Descent (low-intensity scenes marked by negative arousal slopes), and 1 Control (neutral scene) segments from the arousal ratings of the young in a data-driven way. Here, we employed a Bayesian hierarchical regression model to delineate the age-related effects of uncertainty and valence on emotion dynamics (Supplementary Figure 1). The dependent measure of the model input was given by the % BOLD signal for each of the 8 ROIs (mentioned in the ROI definition) for each group relative to Control and was modeled as a Student t-distribution:

$$PSC = \text{Student } t\,(v, \mu, \sigma)\,,$$

where v is the degrees of freedom, σ is the scale parameter of the distribution, and μ is the mean, which can be expressed as:

$$\mu = \alpha + \alpha_j + \alpha_i + \beta_1.\text{Age} + \beta_2.\text{Uncertainty} + \beta_3.\text{Valence} + \beta_4.\text{ Age: Uncertainty}$$

$$+ \beta_5.\text{Age : Valence}$$

$$+ \gamma_{1j} \text{ Age | ROI}$$

$$+ \gamma_{2j}.\text{ Uncertainty | ROI}$$

$$+ \gamma_{3j}.\text{ Valence | ROI}$$

$$+ \gamma_{4j}.\text{ Age : Uncertainty | ROI}$$

$$+ \gamma_{5j}.\text{ Age : Valence | ROI}$$

$$+ \gamma_{6j}.\text{ Age | Subject}$$

$$+ \gamma_{7j}.\text{ Uncertainty | Subject}$$

$$+ \gamma_{8j}.\text{ Valence | Subject} + \sigma_i + \varepsilon.$$

Here, α is the intercept, α_j is the varying intercept over j ROIs, α_i is the varying intercept over i participants. β and γ reflect the slope and varying slope of the predictors, respectively. β_1 represents the slope for the age parameter (which was defined as a categorical variable -Y and O), β_2 and β_3 denote the slope for the Uncertainty and Valence respectively. β_4 and β_5 denote the slope for the cross-level interaction term of age with valence and uncertainty respectively. γ_{1j}, γ_{2j} and γ_{3j} are varying slopes where each of the 3 predictors is allowed to vary across all j ROIs. γ_{4j} and γ_{5j} are varying slopes for the cross-level interaction terms of age with uncertainty and valence, allowed to vary across the ROIs. γ_{6i}, γ_{7i}, and γ_{8i} are varying slopes where each of the 3 predictors is allowed to vary across all i (=209) participants. The way we constructed the model enabled us to consider the effect of uncertainty and valence for the two conditions (we only show the Ascent here) across age and ROIs. Since the classification of scenes is based on the behavioral ratings of the young adults, we considered the entire movie for the main study. Here, we showed only the main effect of uncertainty and valence across age in modulating the neural activity.

Supplementary Figure 1: (a) Graphical illustration represents the architecture of the Hierarchical Bayesian model. BOLD % signal change was modeled to be drawn from a Student *t*-distribution and varied across, groups, participants and ROIs. Main effects of interest were the age-associated effect (categorically defined as Young and old) with the interaction terms of arousal (categorical predictor) with each of uncertainty and valence (as continuous predictors). (b) Main effect of Valence and Uncertainty in modulating the neural activity between the two groups. Posterior density estimates showing the effect of uncertainty is significantly difference (Young: P = 0.98; Old: P= 0.98) between the two groups compared to the valence (Young: P = 0.77; Old: P = 0.64). A potential point of critique may pertain to the stimulus classification, which is based on the ratings provided by the young participants. To address this concern, we refrained from scene categorization in our main analyses and incorporated the entire movie series for both behavioral and neural inferences.

Supplementary Figure 2: Mean neural activity of both lOFC and mOFC shows no significant difference between the two groups for the movie-watching task. ROI-level effect of the movie on the μ_{BOLD} (averaged BOLD signal) across the two groups. Posterior density estimates of (a) lOFC and (b) mOFC shows no significant difference between the two groups during movie.

Supplementary Figure 3: Latent state representations in mOFC for (a) young and (b) older individuals during the movie-watching task. Manifold embedding of mOFC show differential representational patterns in the two groups. Each dot indicates a timepoint in the movie.

Engagement analysis with whole-brain temporal intersubject correlation (ISC)

To determine whether the engagement in older adults varies as a function of the emotional content of the stimulus, we performed an engagement analysis. For each condition (Ascent, Descent and Control) we computed the whole brain temporal ISC of the older adults to compare their neural engagement with that of the Young as well as how it differed with the conditions. The whole-brain whole-brain BOLD signal for each subject was extracted using the Power Atlas with 264 cortical and subcortical ROIs (Fig. S3).

Supplementary Figure 4: Shared neural engagement of Ascent, Descent and Control computed from the whole-brain ISC of the two groups. If attentional processes were the main modulators of the neural activity in the old, we would expect a lower ISC in older adults affected in a similar way for all 3 conditions, irrespective of the emotional saliency of the scenes. Whole brain temporal ISC (whole brain parcellation by Power Atlas, 264 ROIs) on the movie watching data for both groups (Y = 111; O = 98) revealed that (a)

although the older individuals had lower ISC than Young for the entire movie (Young: r = 0.40; Old: r = 0.27;
P < 0.0001) as well as (b) for all conditions (Ascent: Y – r = 0.41, O – r = 0.27, P < 0.0001; Descent: Y – r
= 0.41, O – r = 0.24, P < 0.0001; Control: Y – r = 0.26, O – r = 0.12, P < 0.0001), within-group ISC of the
old were higher for the Ascent and Descent compared to Control (similar pattern as Young). This suggests
that the decreased neural engagement in the elderly varied as a function of the emotional saliency of the
conditions.

Supplementary Figure 5: Comparison of the HMM state transitions of the Visual Cortex (VC) between the
two groups, showed faster transitions in both. This might reflect that the processing of sensory uncertainty
(changing of visual features) is similar in both groups and cannot be attributed to the misestimation of
higher-order uncertainty in the elderly.

90