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# The effects of age bias on neural correlates of successful and unsuccessful response inhibition in younger and older adults

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ABSTRACT

Facilitating communication between generations has become increasingly important. However, individuals often demonstrate a preference for their own age group, which can impact social interactions, and such bias in young adults even extends to inhibitory control. To assess whether older adults also experience this phenomenon, a group of younger and older adults completed a Go/NoGo task incorporating young and old faces, while undergoing functional magnetic resonance imaging. Within the networks subserving successful and unsuccessful response inhibition, patterns of activity demonstrated distinct neural age bias effects in each age group. During successful inhibition, the older adult group demonstrated significantly increased activity to other-age faces, whereas unsuccessful inhibition in the younger group produced significantly enhanced activity to other-age faces. Consequently, the findings of the study confirm that neural responses to successful and unsuccessful inhibition can be contingent on the stimulus-specific attribute of age in both younger and older adults. These findings have important implications in regard to minimizing the emergence of negative consequences, such as ageism, as a result of related implicit biases.



## 1. Introduction

Response inhibition has been shown to exhibit dramatic age-related deficits (i.e., in the context of paradigms such as Go/NoGo), whereby converging evidence suggests that advancing age produces longer response times during initiation and suppression of a response, as well as a larger extent of suppression errors (van de Laar et al., 2012; Smittenaar et al., 2015; Niessen et al., 2017; Gibson et al., 2018; Martin et al., 2021). Accurate or successful suppression of stimuli typically produces activation in a network comprising right inferior frontal gyrus (IFG; Aron et al., 2004), subthalamic nucleus (Aron, 2011), supplementary and pre-supplementary motor areas (SMA; Simmonds et al., 2008), premotor cortex (Watanabe et al., 2002), as well as subregions of the parietal cortex (Rubia et al., 2001). In contrast, additional recruitment of right anterior cingulate and insula cortices (Menon et al., 2001; Sharp et al., 2010), thought to represent mechanisms subserving error detection and conflict resolution, is evident in instances of failed or unsuccessful inhibition.

However, in the context of aging, the behavioral profile of results is accompanied by a reduction in the dynamic modulation of connectivity between prefrontal and sensorimotor regions of the response inhibition network, which differentiate trials that require the execution of action from those that necessitate action suppression (Tsvetanov et al., 2018). Deficient response inhibition may also be ascribed to age-related alterations in the relationship of regions both within and between the default mode network and dorsal attention network. For example, between posterior cingulate cortex (pCC; Persson et al., 2007; Spreng et al., 2016; Samu et al., 2017) and anterior cingulate cortex (aCC; Sambataro et al., 2010), as well as between the precuneus and the rest of the default mode network (Ng et al., 2016). Taken together, these findings suggest that the outlined neural changes have implications for the allocation of appropriate attentional resources to distinguish stimuli that require responses versus those that do not, translating to increased distractibility and the inhibitory deficits associated with aging.

*Abbreviations*: aCC, anterior cingulate cortex; ANOVA, analysis of variance; IFG, inferior frontal gyrus; LV, latent variable; PLS, Partial Least Squares; SMA, supplementary motor areas.

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Beyond a laboratory setting, failure to efficiently engage inhibitory mechanisms can impact how an individual interacts with the environment (Verbruggen and Logan, 2008; Erel and Levy, 2016). Therefore, age-related decline in effective action suppression is likely to impact adequate daily functioning (Wilkins et al., 2010). The frequent observation of dysfunction of the precuneus and pCC, integral for introspection and evaluations that guide communication with others (Cabanis et al., 2013; Wang et al., 2019), may compound these inhibitory deficits in a social setting. Such appraisals are commonly made on the basis of facial attributes, yet research suggests that adults demonstrate progressive impairments in facial recognition across the lifespan (Searcy et al., 1999; Lott et al., 2005; Lamont et al., 2005; Boutet and Faubert, 2006; Habak et al., 2008), which are likely to further impede interpersonal interactions, as faces provide vital cues required to successfully traverse social engagement (Leopold and Rhodes, 2010). Additionally, a range of evidence suggests the presence of a processing advantage for same-age faces compared to other-age faces, but there is much debate as to whether this phenomenon is maintained with aging. Young adults have been reported to find it easier to recognize and distinguish between young faces compared to faces from other age groups (Anastasi and Rhodes, 2005; Kuefner et al., 2008; Hills and Lewis, 2011). Neuroimaging studies indicate that greater activity in medial prefrontal cortex, insula, and amygdala for same-age faces, compared to other-age faces, underlies this own-age bias (OAB; Ebner et al., 2013), thereby signaling the salience of own-age faces within the bounds of social engagement (Sugiura et al., 2005; Bickart et al., 2014).

Our previous research in young adults further attests to the importance of in-group stimuli in relation to social cognition while also extending the influence of age bias from the modulation of stimulus-specific activity (e.g., fusiform gyrus in relation to face stimuli; Golby et al., 2001; Wheeler and Fiske, 2005) to global inhibitory processing (Hanley et al., 2022). Although our behavioral data did not support the existence of the OAB in the tested group, the study established altered neural responses to a Go/NoGo task in the response inhibition (successful trials) and dorsal salience (unsuccessful trials) networks. Crucially, the results were dependent on whether face stimuli belonged to the in- or out-group (younger vs. older adults), and participants appear to have made an implicit judgment based on the age of the stimulus, which was shown to modulate the accompanying network activity. For example, in-group stimuli increased activity in medial prefrontal cortex and temporoparietal junction (in relation to successful inhibition) and also increased activity in posterior insula (in conjunction with unsuccessful inhibition), thereby inferring the presence of an age bias effect in the context of inhibitory control. However, what remains unknown is whether such distinctions are also evident in older adults.

Evidence for behavioral OAB in older adults has been more inconsistent than that in younger adults. Some studies suggest that the phenomenon is robust and even intensifies with age, becoming engrained over the lifespan (Anastasi and Rhodes, 2005; Lamont et al., 2005; Rhodes and Anastasi, 2012; Verdichevski and Steeves, 2013). Other investigations, however, find that the OAB might be absent from middle age and that older adults potentially attend less to social information (including facial cues), with both younger and older adults being quicker and more accurate when making judgments on young faces (Wolff et al., 2012; Wiese et al., 2013; Denkinger and Kinn, 2018; De Lillo et al., 2021). Ultimately, the presence of an OAB in older adults may be contingent on novelty and exposure to those of other age groups (Melinder et al., 2010), the extent of age-related changes in the appraisal of faces to favor holistic processing (Konar et al., 2013) or the availability of sufficient processing resources (Macchi Cassia, 2011). Continued research is required to establish this, particularly at a neural level, in order to further advance the literature and extend our previous findings from a sample of young adults (Hanley et al., 2022).

Despite the lack of research in this specific area, older adults compared to younger adults have been demonstrated to engage alternative neural circuits to sustain face matching performance (Burianová et al., 2013), such that a similar discrimination may be evident in relation to a response inhibition task incorporating face stimuli. Indeed, where it is observed, distinct patterns of neural activity appear to underlie the OAB in younger and older adults, with older adults recruiting dorsal medial PFC and amygdala to a greater extent (Ebner et al., 2013). Given the importance of social connections to successful aging, the current study represents a timely investigation of age bias in a group of younger and older adults. It is also important to note that expressions of age bias have been established across the lifespan in a bidirectional manner (not simply from young to old but also from old to young; Chasteen et al., 2021), which suggests that investigations such as these—in both younger and older samples—are required to be able to design appropriate interventions and tackle ageism from all angles. Therefore, by strengthening evidence for a relationship between inhibitory control and social cognition, the outcomes could contribute to practical interventions to facilitate response inhibition (in a similar manner to the benefits of response inhibition training on social skills in those with attention-deficit/hyperactivity disorder; Razmi et al., 2021), with a view to encouraging social interaction between generations; known to minimize ageism and be beneficial for cognitive function, emotional, and social well-being (Bodner, 2009; Park et al., 2014).

The present study utilized the Go/NoGo paradigm devised for our previous investigation (Hanley et al., 2022), which features facial stimuli of young and old adults. Participants were instructed to respond each time a stimulus was presented (Go trial), unless the same stimulus was repeated immediately (NoGo trial). We aimed to determine the presence of age-related differences in neural activity during successful (accurate NoGo trials) and unsuccessful response inhibition (inaccurate NoGo trials), following the presentation of own-age and other-age stimuli. In accordance with the literature, we expected that (1) both groups would show higher accuracy on Go compared to NoGo trials, although it was projected that older adults would make more errors than younger adults; (2) younger adults would be faster on Go trials compared to older adults; however, both groups would show no difference in reaction times between trials featuring young and old faces, signaling the absence of a behavioral OAB (in correspondence with our previous findings in a sample of younger adults and the consensus in the literature with regard to older adults; Hanley et al, 2022); (3) there would be age-related distinctions in neural activity between NoGo and Go trials, specifically (3a) there would be differences in activity during correct NoGo trials in regions essential for response inhibition (e.g., parietal cortex, IFG, and pre-SMA), and (3b) a similar pattern of age-related differences corresponding to incorrect NoGo trials in structures associated with error detection (e.g., aCC and insula), with older adults exhibiting greater activity in these regions alongside a wider distribution of recruited resources than younger adults; and, finally, (4) that despite the absence of an OAB in the context of behavioral scores, distinctions in neural activity would be evident between trials featuring own-age and other-age faces (where increased activity was predicted to signify difficulty to accurately suppress responses or resolve conflict as a result of errors; Hanley et al., 2022). In the context of successful trials (4a), regions associated with response inhibition were predicted to demonstrate greater activity for same-age as opposed to other-age faces, and with regard to unsuccessful trials (4b), structures corresponding to error detection were projected to demonstrate greater activity for same-age as

opposed to other-age faces, thus representing evidence for the presence of age bias in neural responses.

## 2. Material and methods

### 2.1. Participants

We tested 23 older adults (mean age = 68.96 years, standard deviation [SD] = 5.80 years; 10 males) and 23 younger adults (mean age = 24.92 years, SD = 3.54 years; 11 males), representing an independent sample to that used in our previous work (Hanley et al., 2022). Participants were right handed, had normal or corrected-to-normal vision, were screened for magnetic resonance imaging (MRI) contraindications, and were excluded from the study if they had a history of neurological and/or psychiatric disorders (e.g., epilepsy, anxiety, or depression), alcohol and/or drug abuse, head trauma, or surgical implants incompatible with MRI. All participants provided informed consent upon entering the study, which was approved by the School of Psychology Ethics Committee at Swansea University.

### 2.2. Stimuli

As per an identical paradigm used in our previous study (Hanley et al., 2022), stimuli consisted of color images representing 12 young faces (20–30 years) and 12 old faces (aged ≥60 years) in a frontal orientation. Face images were obtained from the FACES database (Ebner et al., 2010; https://faces.mpdl.mpg.de/imeji/). Each stimulus set was balanced in relation to gender, and stimuli were selected on the basis of prior attractiveness and distinctiveness ratings (use of images with an SD in ratings of < 10) to ensure that there were no significant differences within and between the different age groups ($p > 0.05$). Additionally, all selected images featured neutral facial expressions to ensure responses were not confounded by valence (Hare et al., 2005; Verbruggen and De Houwer, 2007; Pessoa, 2009).

### 2.3. Experimental procedure

The stimuli outlined above were used to create the Go/NoGo task, whereby participants responded each time a face was presented but withheld responses when the same face was displayed in direct succession (see Fig. 1, as featured in Hanley et al., 2022). Each experimental session began with a structural scan (5 minutes), followed by 2 functional runs of the Go/NoGo task (6.5 minutes each), 1 run for young faces and 1 run for old faces. The order of runs was counterbalanced across participants as part of an event-related experimental design. Stimuli were presented on a screen positioned behind the MRI scanner and viewed via a mirror mounted onto the head coil. Participants were instructed on how to complete the task before entering the MRI scanner, and a reprisal of the instructions was presented for 9 seconds prior to each experimental run, which advised participants to press a response button with their right index finger each time a stimulus was presented (Go trial) unless the same stimulus was repeated immediately (NoGo trial). Within each run, 240 trials were split into 192 Go trials and 48 NoGo trials, thus representing an 80:20 ratio, sufficient to generate the necessary prepotent tendency for Go responses to facilitate the novelty of NoGo trials (Wessel, 2018). Face stimuli were displayed an equal number of times, such that each image featured in 16 Go and 4 NoGo trials. Each trial was 1000 ms in length, with an interstimulus interval of 500 ms. The stimulus remained on screen once participants had responded, such that both stimulus onset and interstimulus interval were fixed (for further discussion of the rationale, see Hanley et al., 2022).

### 2.4. Acquisition and preprocessing of neuroimaging data

Anatomical and whole-brain functional images were acquired at the Swansea University Clinical Imaging Facility using a 3-Tesla Siemens Magnetom Skyra MRI Scanner with a 32-channel head coil. T1-weighted anatomical images were acquired using an MP2RAGE

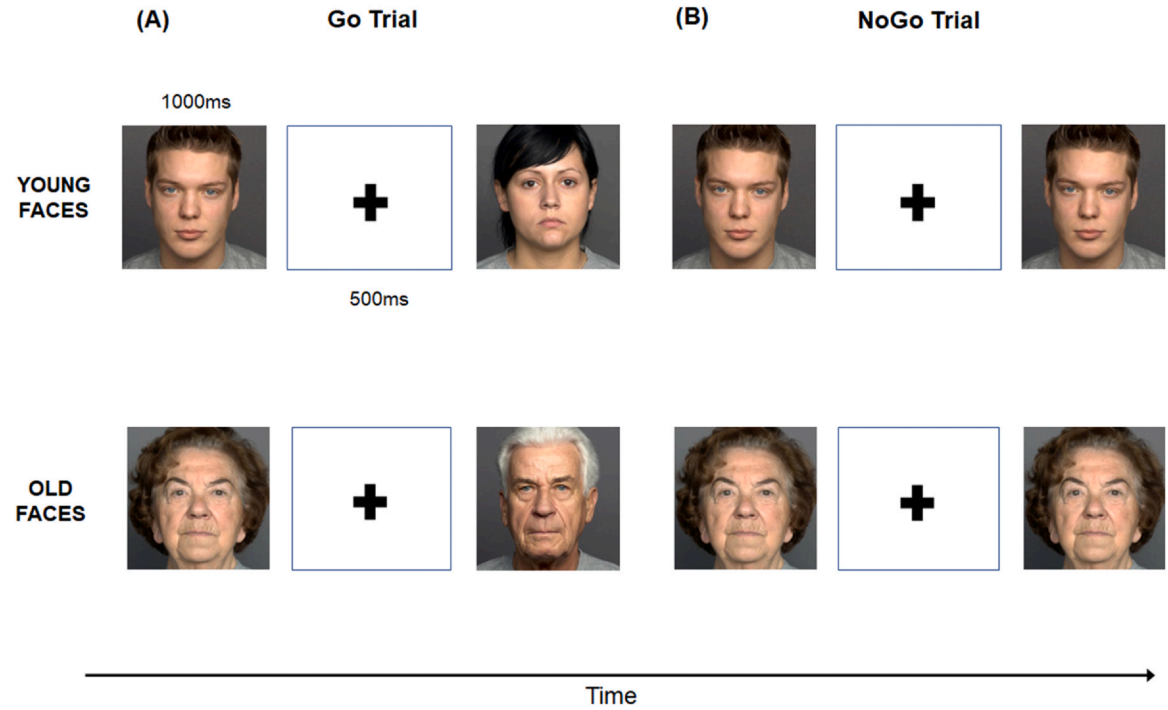


**Fig. 1. Go/NoGo Task.** Participants were presented with a series of neutral face stimuli, between fixation screens, and were required to press a button each time a face was presented (Go trial; A) or to withhold their response if the same face was displayed in succession (NoGo trial; B). The task was presented twice, with separate experimental runs for young (top) and old (bottom) faces (as depicted in Hanley et al., 2022).

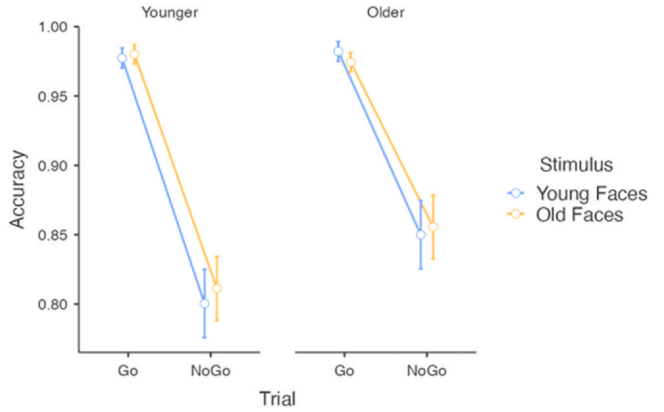


**Fig. 2. Accuracy results.** Split by group (younger participants /older participants), the graph shows accuracy scores on the Go & NoGo trials in response to young/old face stimuli. The error bars represent the standard error of the mean.

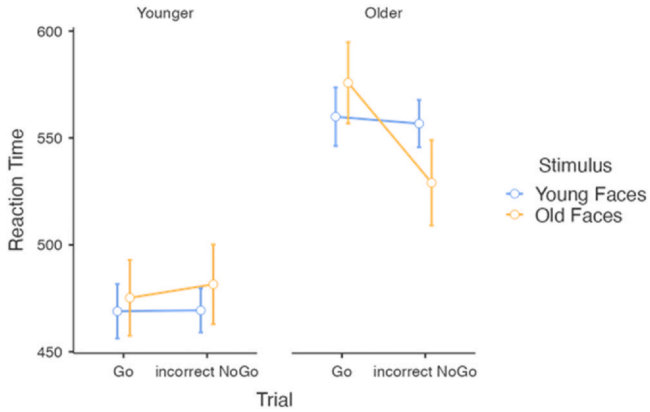


**Fig. 3. Reaction time results.** Split by group (younger participants/older participants), the graph shows reaction time scores (in milliseconds) to the Go & incorrect NoGo trials in response to young/old face stimuli. The error bars represent the standard error of the mean.

sequence (176 axial slices, voxel size = 1 $mm^3$, 50% distance factor, FOV = 256 mm, TR = 4000 ms, TE = 2.98 ms, 3 PAT GRAPPA, flip angle = 6º). T2*-weighted echo planar imaging sequences were used to measure the BOLD response (Ogawa et al., 1990; 45 axial slices, voxel size = 2.5 $mm^3$, 10% distance factor, FOV = 190 mm, TR = 3000 ms, TE = 30 ms, 2 PAT GRAPPA, flip angle = 90º).

Preprocessing of the obtained images was completed using Statistical Parametric Mapping software (SPM12; http://www.fil.ion.ucl.ac.uk/spm). Functional images were realigned using rigid-body transformation to correct for participant head motion between volumes, and the mean image of each run was co-registered to the structural image. One participant from the older adult group was removed from the imaging analysis due to excessive motion (above 2 mm). Structural images of each participant were segmented into constituent parts of gray matter, white matter, and cerebrospinal fluid using tissue probability maps. One older adult participant was removed from the imaging analysis due to segmentation issues. Images were then spatially normalized into standard stereotaxic space using the Montreal Neurological Institute template with a voxel size of 2 $mm^3$. Finally, each volume was spatially smoothed using a 6 mm FWHM, isotropic Gaussian kernel (Della-Maggiore et al., 2002; Weissenbacher et al., 2009).

### 2.5. Analysis of neuroimaging data

As per our previous work (Hanley et al., 2022), the data were analyzed with Principal Component Analysis using Partial Least Squares (PLS; McIntosh et al., 1996; McIntosh and Lobaugh, 2004; Krishnan et al., 2011) analysis, a multivariate approach, which is optimal for extracting distributed signal changes in relation to task demands. PLS reduces the dimensionality of large data sets by transforming correlated variables into sets of uncorrelated components, which are ordered by the amount of variability in the data they explain. Task-based PLS examines spatial and temporal dependencies among voxels, thus allowing inferences regarding differences across time and space between experimental conditions. Thus, this method utilizes the assumption that cognition engages a consolidated and spatially distributed pattern of neural activations. A single matrix is decomposed by singular value decomposition, generating a hierarchical arrangement of latent variables (LVs), which delineate both the common and unique patterns between brain activations and experimental design. Contrary to univariate methods, contrasts are not defined; instead, interpretation relies on the accounted covariance of significant LVs. For each LV, PLS produces an image of voxel saliences (i.e., indication of neural activity modification according to experimental condition or behavior), a profile of task saliences (i.e., the influence of brain activity over conditions), and a singular value (i.e., the percentage of LV accounted covariance). As such, correcting for multiple comparisons is not necessary since all voxels and conditions are entered into a single analysis. To acquire a summary measure of the spatial pattern of every condition across each LV, brain scores are calculated, indicating the salience of each voxel and BOLD signal. Saliences are represented in positive or negative values, depending on the voxel's relation to the pattern of task-dependent differences identified by the LV.

Statistical significance of each LV is assessed with permutation testing, repeated 500 times. To further evaluate the reliability of activations identified by permutation testing, bootstrap estimates of the salience standard errors are used and repeated 100 times. Voxels with a bootstrap ratio > 3.0 are considered reliable, approximating $p < 0.001$ (Sampson et al., 1989). Confidence intervals of brain scores for each LV are calculated at 95%.

For the purposes of the current study, we conducted event-related PLS analysis to investigate age-related differences in OAB during (1) successful response inhibition—here, we compared activity during accurate NoGo trials (response inhibition to young/old face stimuli) with activity during accurate Go trials (a baseline; response to young/old face stimuli); and (2) unsuccessful response inhibition, signifying error detection—here, we compared activity during inaccurate NoGo trials (Err NoGo; erroneous response to young/old face stimuli) with activity during accurate NoGo trials (a baseline; response inhibition to young/old face stimuli).

## 3. Results

### 3.1. Behavioral results

To assess behavioral performance on the Go/NoGo task across the 2 groups, we conducted a repeated-measures analysis of variance (ANOVA) on the accuracy of responses to successful Go and NoGo trials and a repeated-measures ANOVA on reaction times on successful Go and unsuccessful NoGo trials. For accuracy, the 2 (trial: Go/NoGo) × 2 (stimulus: young faces/old faces) × 2 (group: younger participants/older participants) ANOVA yielded a significant main effect of trial ($F_{1,44} = 73.85$, $p < 0.001$; $\eta_p^2 = 0.63$), demonstrating significantly better performance on the Go trials in comparison to the NoGo trials for both age groups (see Fig. 2). The main effects of stimulus and group were not significant, and neither were any of the interactions (*ps* > 0.05).

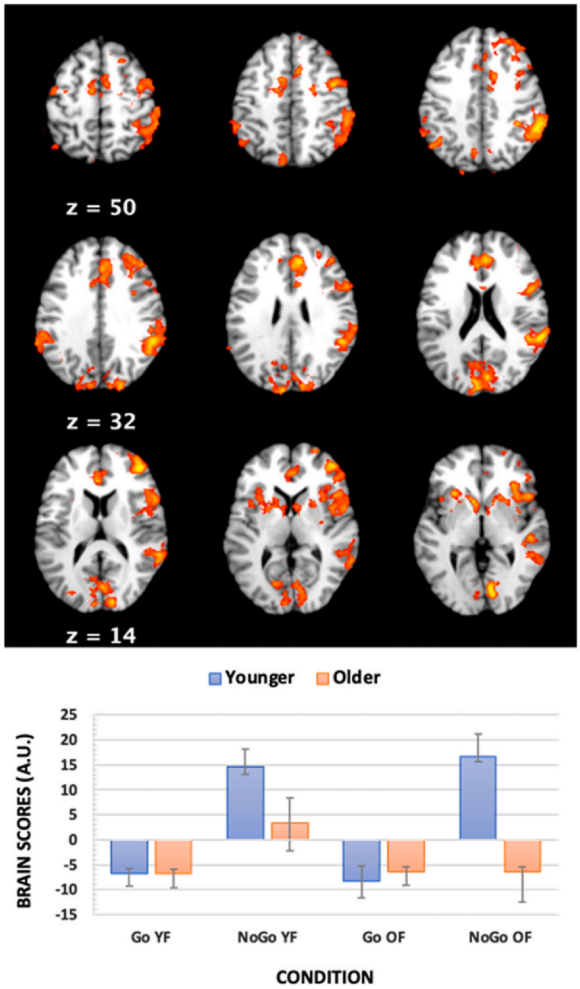


**Fig. 4. Successful response inhibition: younger and older adults, latent variable 1.** Top: A pattern of whole-brain activity depicting areas active during NoGo versus Go trials. Below: Mean brain scores related to whole-brain activity seen above across the 4 experimental conditions for each group. Error bars denote the standard error of the mean. Abbreviations: A.U., arbitrary units; OF, old faces; YF, young faces.

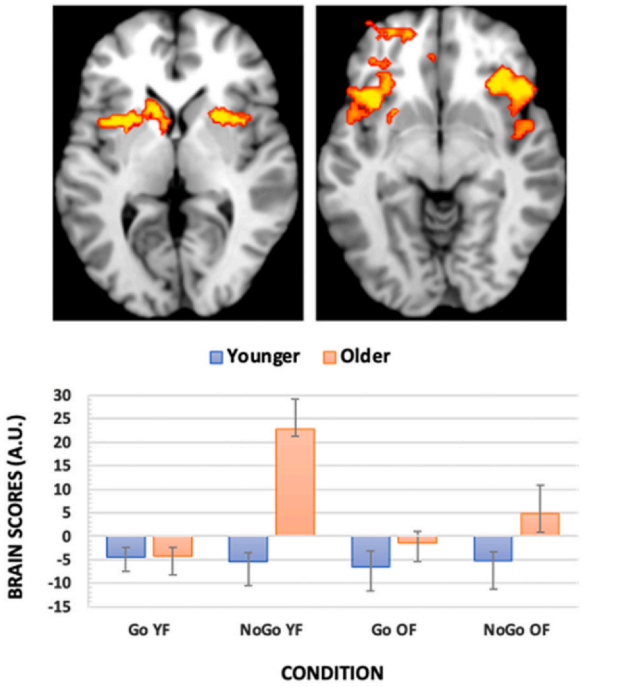


**Fig. 5. Successful response inhibition: younger and older adults, latent variable 2.** Top: Examples of brain activity (putamen and insula & IFG) depicting areas active during NoGo versus Go trials in older versus younger adults. Below: Mean brain scores related to whole-brain activity seen above across the 4 experimental conditions for each group. Error bars denote the standard error of the mean. Abbreviations: A.U., arbitrary units; OF, old faces; YF, young faces.

For reaction times, the 2 (trial: Go/incorrect NoGo) × 2 (stimulus: young faces/old faces) × 2 (group: younger participants/older participants) ANOVA yielded no significant within-subjects effects or interactions ($ps > 0.05$). The between-subjects factor group was significant at $F_{1,41} = 16.30$, $p < 0.001$; $\eta_p^2 = 0.28$, demonstrating an overall slower performance of the older participants compared to the younger group (see Fig. 3).

### 3.2. Functional MRI results

#### 3.2.1. Whole-brain activity: successful response inhibition

The whole-brain analysis comparing activity during the Go and NoGo conditions (successful trials only) across the 2 age groups yielded 2 significant LVs. LV1 accounted for 30.81% of covariance in the data ($p < 0.001$) and, for the younger participants, differentiated a pattern of activity during the NoGo conditions in contrast to the Go conditions (see Fig. 4). Activated brain areas during response inhibition of the younger participants, as opposed to the older participants, included bilateral cuneus, right anterior insula, frontoparietal areas, somatosensory cortices, right supramarginal gyrus, ACC, and superior temporal gyrus. Older adults did not show this pattern of brain activity differentiating the Go and NoGo trials, suggesting evidence of dedifferentiation within the response inhibition network. Additionally, LV1 showed no evidence of age bias in either age group.

LV2 accounted for 28.47% of covariance in the data ($p < 0.001$) and, for the older participants, differentiated a pattern of activity during the NoGo conditions in contrast to the Go conditions. Brain areas involved in response inhibition of the older participants, in contrast to younger participants, included bilateral insula and IFG, bilateral putamen, and right inferior parietal lobule (see Fig. 5). In addition, this network of brain regions was activated significantly more during response inhibition to young stimuli, providing evidence of age bias in the older age group.

#### 3.2.2. Whole-brain activity: unsuccessful response inhibition

The whole-brain analysis comparing activity during inaccurate NoGo trials with activity during accurate NoGo trials yielded 2 significant LVs. LV1 accounted for 34.17% of covariance in the data ($p < 0.001$) and, for both age groups, delineated a pattern of activity underlying unsuccessful response inhibition to old but not young face stimuli (see Fig. 6). Unsuccessful response inhibition to old faces engaged a common network of brain regions, including bilateral anterior insula, dorsal ACC, bilateral temporoparietal junction, bilateral postcentral gyrus, and pre-SMA.

LV2 accounted for 27.53% of covariance in the data ($p < 0.001$) and delineated unique activity during unsuccessful response inhibition of younger, as opposed to older adults. Younger adults engaged inferior temporal cortex, temporal pole, striatum, dorsal frontoparietal areas, precuneus, ventral ACC, and precentral gyrus (see Fig. 7). Importantly, younger adults engaged these areas significantly more strongly for old faces than for young faces (error bars did not overlap), whereas older adults did not show this difference.

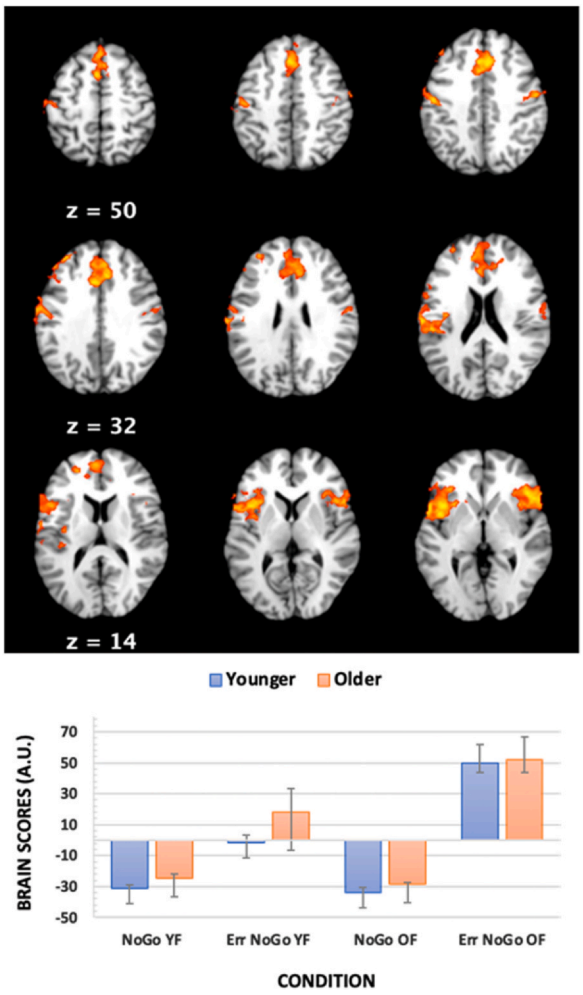


**Fig. 6. Unsuccessful response inhibition: younger and older adults, latent variable 1.** Top: A pattern of whole-brain activity depicting areas active during Err NoGo versus NoGo trials. Below: Mean brain scores related to whole-brain activity seen above across the 4 experimental conditions for each group. Error bars denote the standard error of the mean. Abbreviations: A.U., arbitrary units; OF, old faces; YF, young faces.

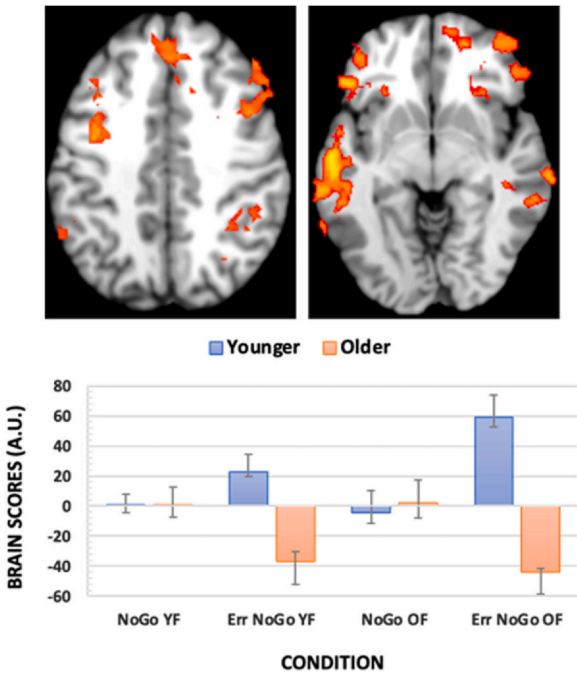


**Fig. 7. Unsuccessful response inhibition: younger and older adults, latent variable 2.** Top: Examples of brain activity (inferior temporal cortex, ventral ACC, and precentral gyrus) depicting areas active during Err NoGo versus NoGo trials in younger versus older adults. Below: Mean brain scores related to whole-brain activity seen above across the 4 experimental conditions for each group. Error bars denote the standard error of the mean. Abbreviations: A.U., arbitrary units; OF, old faces; YF, young faces.

## 4. Discussion

A novel Go/NoGo paradigm, incorporating faces of young and old adults, was used to determine age-related differences in the influence of these stimuli on successful and unsuccessful response inhibition. Behavioral findings (1, 2) were as predicted, and no significant stimulus-related (young/old faces) differences were established in either group (van de Laar et al., 2012; Hanley et al., 2022). During successful response inhibition (3a), distinctions in neural activity were evident in the response inhibition network of the younger group with regard to the type of face stimuli, whereas neural responses of the older adults were more uniform (displaying reduced hemispheric asymmetry and signs of dedifferentiation; Cabeza, 2002; Daselaar et al., 2013). During unsuccessful response inhibition (3b), age-related similarities in responses of the dorsal salience network were related only to the processing of old, and not young, faces. Furthermore, during successful inhibition (4a), young compared to old faces evoked significantly more activation in nodes of the response inhibition network in older adults, while the younger adults displayed no such stimulus distinctions in processing. In contrast, during unsuccessful inhibition (4b), regions of the dorsal salience network were significantly more active in response to old, as opposed to young, faces in the younger group, which the older sample did not exhibit. Therefore, for the first time, the study provides evidence for a neural age bias effect that differentially influenced each age group, depending on both the nature of the response and stimulus type.

### 4.1. Successful NoGo trials

#### 4.1.1. Activation of the response inhibition network

In accordance with previous findings, including our own, the neuroimaging analyses revealed that successful suppression of prepotent actions was subserved by activity in core nodes of the response inhibition network (Aron et al., 2003; Nelson et al., 2010; Swann et al., 2012; Steele et al., 2013; Janes et al., 2015; Morein-Zamir and Robbins, 2015; Zhang et al., 2017; Hanley et al., 2022). Furthermore, as proposed in hypothesis 3a, distinct regional age-related differences were noted. While younger adults displayed distinct responses to each trial type, the neural responses of older adults suggest dedifferentiation (Cabeza, 2002; Burianová et al., 2013; Daselaar et al., 2013). For the younger, compared to older group, NoGo and Go trials were distinguished by activity exhibited in bilateral cuneus, right anterior insula, frontoparietal cortex, somatosensory cortices, right supramarginal gyrus, anterior cingulate cortex, and superior temporal gyrus. This sustained brain activity across the functional network was evident for both types of face stimuli, reflecting a response inhibition effect rather than in-/out-group modulation. Therefore, younger and older adults appear to rely on qualitatively different regions of the response inhibition network to successfully perform the Go/NoGo task, rather than demonstrating alterations in the extent of activity in the same brain areas (thus complimenting current knowledge of age-related change in inhibitory control mechanisms; Tsvetanov et al., 2018).

#### 4.1.2. In-/out-group modulation of the response inhibition network

While the pattern of results unique to the younger adults did not infer the presence of a stimulus-specific age bias, structures subserving older adult responses were activated significantly more during response inhibition to stimuli of young compared to old faces. For the older, compared to younger group, successful inhibition was characterized by activity in bilateral insula, inferior frontal gyrus, bilateral putamen, and right inferior parietal lobule. This novel finding points to an age-related difference in task processing but one that is specific to the type of stimuli used, indicating that the older participants had to recruit additional resources, thereby working harder to successfully process trials featuring young, but not old, faces (Lamont et al., 2005; Rhodes and Anastasi, 2012). For example, the involvement of bilateral insula and putamen during young face trials signifies compensation via a reduction in the asymmetry of responses (e.g., the HAROLD model; Cabeza, 2002). Consequently, for the older participants, successful responses to the Go/NoGo task were defined by a neural age-related stimulus bias, which conversely does not appear to be the case for the younger group (emulating the presence of alternative neural circuits established to underlie age-related differences in face matching performance; Burianová et al., 2013).

We had predicted it would be harder to successfully inhibit own-age faces due to familiarity with such in-group stimuli (in line with hypothesis 4a); however, the data suggest it was more difficult to suppress NoGo trials to other-age faces (which evoke a subsequent increase in demands for resource recruitment, likely due to novelty and lack of exposure to out-group stimuli; Melinder et al., 2010). Contrary to our initial hypothesis, while still representing a processing advantage for same-age compared to other-age faces, the aforementioned result is better conceptualized as evidence for an other-age bias as opposed to an own-age bias. Despite this nuance, we have established that the presentation of young and old faces differentially modulated activity in nodes of the response inhibition network, which exclusively altered the suppression of associated motor responses in our older sample (suggesting that age bias may manifest differently in older adults).

### 4.2. Unsuccessful NoGo trials

#### 4.2.1. Activation of the dorsal salience network

The analysis of unsuccessful response inhibition resulted in a common activity pattern across age groups, comprising regions of the dorsal salience network, specifically bilateral anterior insula, dorsal ACC, bilateral temporoparietal junction, bilateral postcentral gyrus, and pre-SMA (Downar et al., 2002; Orr and Hester, 2012). While salience network activity had been predicted in relation to unsuccessful trials, this finding is contrary to our prediction (hypothesis 3b), where age-related differences had been put forward. Furthermore, the observed pattern of results demonstrates a similarity in unsuccessful response inhibition specifically to old, compared to young, faces, highlighting stimulus modulation of basic error processing mechanisms (likely based on the impact of in-group/out-group classifications on task difficulty and the extent of required cognitive control resources; Kuefner et al., 2008; Hills and Lewis, 2011; Rhodes and Anastasi, 2012; Verdichevski and Steeves, 2013). Therefore, the nature of the face stimuli appears to have altered unsuccessful inhibition responses in the same manner in both age groups and resulted in all participants processing these errors by engaging identical regions to a similar extent.

#### 4.2.2. In-/out-group modulation of the dorsal salience network

While unsuccessful trials evoked a common pattern of activation to old faces, an age-related difference was apparent with regard to the extent of activity in specific regions of the dorsal salience network. Activity in several nodes was differentially modulated by the presentation of young and old faces; compared to older adults, younger adults engaged temporal pole, striatum, dorsal frontoparietal areas, precuneus, ventral anterior cingulate cortex, and precentral gyrus significantly more strongly for old, as opposed to young faces. This greater activity in the dorsal salience network suggests that the younger adult group exhibited a neural age-related bias in relation to the processing of errors. Although younger adults show greater activity to old faces, supported by additional frontal activity in the right hemisphere, older adults displayed similar responses to each stimulus type of a more distributed nature than the younger adults (which may be attributed to dedifferentiation; Cabeza, 2002; Burianová et al., 2013; Daselaar et al., 2013). Involvement of precuneus and ventral anterior cingulate cortex infers responses to old face errors were evaluated in a social context, suggesting accompanying demands on cognitive control were modulated on the basis of the subjective value of the stimuli (Cai and Padoa-Schioppa, 2012; Cabanis et al., 2013; Lockwood and Wittmann, 2018; Wang et al., 2019). Although we had proposed it would be harder to resolve inhibition errors to own-age faces due to familiarity with such in-group stimuli (in line with hypothesis 4b), it appears to be more difficult to do so in the context of other-age faces (as evidenced by the significant increase in demands for cognitive control resource recruitment, attributed to the novelty of out-group stimuli; Melinder et al., 2010).

It is also intriguing that the nature of the stimuli was only shown to alter error-related activity in the younger group. While young adults are at their peak in terms of neural recruitment capacity, beyond evoking heightened activity to sustain performance, stimulus-related modulation of processing errors may represent a level of cognitive effort that older adults are not capable of devoting adequate resources to, such that social cues appear to be less relevant (Cabeza, 2002; Daselaar et al., 2013). While our results are contrary to reports that older adults generally exhibit reduced value in attending to social information (De Lillo et al., 2021), the circumstances in which they do so are likely to be more specific. Indeed, any prioritization of this nature—based on factors such as task difficulty and cognitive load—could account for the conflicting findings in the literature and seldom reduced or absent age bias effects across the lifespan (Macchi Cassia, 2011).

### 4.3. Limitations and future directions

As previously addressed, the lack of age bias effect in the behavioral data is not considered surprising, as the emergence of this phenomenon is by no means robust (particularly in older adults; Wolff et al., 2012; Wiese et al., 2013; Denkinger and Kinn, 2018; De Lillo et al., 2021), and we did not observe the effect in younger adults during our previous study (Hanley et al., 2022). In the corresponding paper, we outline a number of methodological factors (relating to aspects of stimulus presentation and task demands) that may have influenced the behavioral results. However, we provide evidence to suggest that related experimental design decisions were unlikely to have fundamentally prevented the age bias effect and, importantly, that the Go/NoGo task served its intended purpose (all of which is also applicable to the present study).

It is possible that individual variations in exposure to members of the out-group may underlie the present findings (Melinder et al., 2010). In accordance with the contact hypothesis, used to account for the own-race bias (Meissner and Brigham, 2001), greater exposure to the out-group diminishes implicit bias. In the context of aging, the extent of own-age bias has also been related to such exposure (Harrison and Hole, 2009). For example, through variations in daily contact with own- and out-group individuals and as a product of interactions across the lifespan as in-groups change (He et al., 2011; Wiese et al., 2013). In the future, a measurement of out-group

exposure could be embedded into the study to assess related influences on the results.

Equally, an alternative explanation relates to the influence of age-related deterioration in face processing (Grady et al., 2000; Chaby et al., 2011), and a shift in strategy toward holistic appraisal (Konar et al., 2013), whereby fine-grain aspects, such as second-order configural processing (the ability to process distances between facial features), are more efficient for own-group faces rather than out-group faces (Wiese et al., 2013). The absence of behavioral age bias suggests that any such changes in our sample were not sufficient to alter the speed and accuracy of responses to the different stimulus types. Yet, our neural data clearly represent implicit characteristics of age bias, and the fact that these signatures of age bias were observed in both younger and older adult samples suggests that the phenomenon cannot be driven entirely by age-related changes.

On a related note, neural age-related comparisons were assessed on the basis of the BOLD response (dependent on neurovascular coupling, known to change over the lifespan; D'Esposito et al., 2003; Logothetis, 2008; Tsvetanov et al., 2015). While it is important to interpret the findings of any such studies within the bounds of this knowledge, several elements of the present study likely minimized the influence of this potential caveat (e.g., participants were screened for major vascular complications and related medications, a multivariate statistical method was adopted, and such approaches are far less affected by potential intrinsic group differences in the signal-to-noise ratio; Rypma and D'Esposito, 2000; Muller et al., 2001).

Lastly, addressing the interplay between cognition and emotion may further understanding into the context in which the younger and older adults demonstrate a neural age bias via the so-called positivity effect (Mather and Carstensen, 2005). Neutral expressions were featured in the present study, which—in the older adults—were sufficient to evoke an age bias effect for successful response inhibition but may not have maximized the likelihood of inducing a consistent age bias. Face recognition in older adults has previously been shown to improve with positive stimuli, which are thought to be attributed greater importance as opposed to items that are perceived to be neutral or negative (Denkinger and Kinn, 2018). Therefore, to establish the contribution of stimulus valence to the observation of age bias, future research could incorporate a variety of expressions, with face stimuli of a positive nature being predicted to capture processing priority in the older sample.

## 5. Conclusions

The findings of the study provide further insight into patterns of neural responses underlying inhibitory control processes, confirming that successful and unsuccessful inhibition can be modulated by the stimulus-specific attribute of age in both younger and older adults. Successful response inhibition appears to be underpinned by age-related differences (in the way NoGo and Go trials are processed and in regard to whether the face stimuli alter responses), whereas unsuccessful response inhibition is characterized by age-related similarities in network activity (with regard to older faces) alongside regionally specific distinctions (nodes displaying greater activity in younger adults only, relating to old faces). Consequently, the results indicate that enhanced activation is needed to process Go/NoGo trials featuring other-age faces, although there are age-related caveats. Older adults require greater resources in order to successfully inhibit responses to faces of younger adults to support the heightened cognitive demand, whereas this outcome was only evident in younger adults when processing errors to old faces, which are likely to be regarded as more effortful due to their novelty. In view of evidence further linking response inhibition and aspects of social cognition, these findings have important implications in relation to the emergence of negative consequences, such as ageism. Implicit biases could be minimized via the facilitation of adaptive response inhibition processes by designing interventions for both age groups to maximize neural resources and reduce processing effort in older adults (e.g., engagement with beneficial lifestyle changes or via external means, such as noninvasive brain stimulation techniques) and by enhancing exposure to out-group members with the aim of reducing novelty, which may be particularly useful for younger adults (e.g., involvement with schemes that encourage intergenerational interactions).

## Ethical Approval

The study was approved by the Department of Psychology Ethics Board at Swansea University (in line with the Declaration of Helsinki).

## Disclosure statement

The authors have no actual or potential conflicts of interest.

## Verification

The work described has not been published previously, it is not under consideration for publication elsewhere, and its publication is approved by all authors and tacitly or explicitly by the responsible authorities where the work was carried out. If accepted, it will not be published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyright holder. The authors acknowledge that to verify originality, Elsevier may check the article using the originality detection service Crossref Similarity Check and share the results with the Editor-in-Chief.

## CRediT authorship contribution statement

**Claire J. Hanley:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Supervision; Visualization; Writing - original draft; Writing - review & editing. **Natasha Burns:** Data curation; Formal analysis; Investigation; Resources; Visualization; Writing - original draft; Writing - review & editing. **Hannah R. Thomas:** Data curation; Formal analysis; Investigation; Resources; Visualization; Writing - original draft; Writing - review & editing. **Lars Marstaller:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Supervision; Visualization; Writing - original draft; Writing - review & editing. **Hana Burianová:** Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project administration; Resources; Software; Supervision; Visualization; Writing - original draft; Writing - review & editing.

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