The effects of age-bias on neural correlates of successful and unsuccessful response inhibition

Claire J. Hanley, Natasha Burns, Hannah R. Thomas, Lars Marstaller, Hana Burianová

PII: S0166-4328(22)00145-0

DOI: https://doi.org/10.1016/j.bbr.2022.113877

Reference: BBR113877

To appear in: *Behavioural Brain Research*

Received date: 7 June 2021
Revised date: 14 March 2022
Accepted date: 30 March 2022

Please cite this article as: Claire J. Hanley, Natasha Burns, Hannah R. Thomas, Lars Marstaller and Hana Burianová, The effects of age-bias on neural correlates of successful and unsuccessful response inhibition, *Behavioural Brain Research,* (2021) doi:https://doi.org/10.1016/j.bbr.2022.113877

The effects of age-bias on neural correlates of successful and unsuccessful response inhibition

Claire J. Hanley[a], Natasha Burns[a,b], Hannah R. Thomas[a], Lars Marstaller[b], Hana Burianová[a,b,c]

[a]Department of Psychology, Swansea University, UK
[b]Department of Psychology, Bournemouth University, UK
[c]Centre for Advanced Imaging, University of Queensland, Australia

Correspondence should be addressed to:

Claire J. Hanley, PhD
Department of Psychology
Swansea University, Singleton Park
Swansea, SA2 8PP, Wales, UK
c.j.hanley@swansea.ac.uk

Abstract

Response inhibition is important for adherence to social norms, especially when norms conflict with biases based on one's social identity. While previous studies have shown that in-group bias generally modulates neural activity related to stimulus appraisal, it is unclear whether and how an in-group bias based on age affects neural information processing during response inhibition. To assess this potential influence, young adults completed a Go/NoGo task incorporating younger face (in-group) and older face (out-group) stimuli while undergoing functional magnetic resonance imaging (fMRI). Our results replicated previous findings by demonstrating higher accuracy in successful Go compared to NoGo trials, as well as the engagement of nodes of the response inhibition network during successful response inhibition, and brain regions comprising the salience network during unsuccessful response inhibition. Importantly, despite a lack of behavioural differences, our results showed that younger and older face stimuli modulated activity in the response inhibition and salience networks during successful and unsuccessful inhibition, respectively. Interestingly, these effects were not uniform across networks. During successful response inhibition, in-group stimuli increased activity in medial prefrontal cortex and temporo-parietal junction, whereas out-group stimuli more strongly engaged pre-supplemental

motor area. During unsuccessful response inhibition, in-group stimuli increased activity in posterior insula, whereas out-group stimuli more strongly engaged angular gyrus and intraparietal sulcus. Consequently, the results infer the presence of an age-bias effect in the context of inhibitory control, which has substantial implications for future experimental design and may also provide the means of investigating the neural correlates of implicit beliefs that contribute to ageism.

Keywords:
Age-bias; Face processing; fMRI; Go/NoGo; Response inhibition; Social cognition

1. Introduction

Response inhibition is a crucial element of executive control, encompassing the suppression of information and related actions to support goal-directed behaviour in dynamic environments (Verbruggen & Logan, 2008). A range of deficits are associated with failure to inhibit a response, which can result in loss of sustained attention, increased distractibility, or impulsive behaviour (Booth et al., 2003; Horn et al., 2003; Hutton et al., 2002). In a social context, response inhibition forms part of an individual's ability to conform to social norms; in particular, norms that conflict with goals, beliefs, or attitudes, which are based on the individual's social identity and manifest as in-group bias.

Failure to inhibit in-group bias can perpetuate existing stereotypes, such as ageism, *i.e.*, explicit actions or implicit attitudes that discriminate against older adults (Butler, 1969). Analysis of written accounts by younger adults engaged in a senior mentoring programme revealed instances of negative discriminatory language towards older adults, while perceived attributes of younger adults were viewed in a favourable manner (Gendron et al., 2016). Failure to constrain such in-group versus out-group beliefs has been shown to be damaging to older adults themselves and to hinder active ageing due to the internalisation of these negative views

(Swift et al., 2017). This phenomenon also extends to a professional setting, where attitudes towards older adults held by health care workers have been established to produce discrimination in rehabilitation services (Rybarczyk et al., 2001). It is, therefore, crucial to understand the origins of age-based in-group bias and particularly its interaction with response inhibition, in order to prevent its detrimental consequences. Neuroscientific studies have demonstrated that in-group bias generally modulates brain activity and is associated with differences in brain systems that are specific to the stimulus or task, such as the amygdala and fusiform gyrus in response to face stimuli (Golby et al., 2001; Wheeler & Fiske, 2005), medial prefrontal and anterior cingulate cortices during conflict resolution (Dominguez et al., 2016; Fan et al., 2003), the salience network during empathy (Xun et al., 2009), or the temporo-parietal junction during mentalising (Van Overwalle, 2009). However, to date, no study has addressed the question of whether in-group bias modulates brain activity in regions associated with response inhibition.

Studies examining response inhibition most commonly utilise the Go/NoGo task (Drewe, 1975). Considered to be a measure of action restraint (as opposed to action cancelling, for which the Stop-Signal task is advocated: Schachar et al., 2007; Swick et al., 2011), Go/NoGo requires participants to respond to standard or frequent events (Go trials), but withhold their response to novel or infrequent events (NoGo trials). A network comprising fronto-parietal structures has consistently been reported to underlie such action suppression processes, with right lateral frontal cortex thought to play a critical role (Mostofsky et al., 2003). NoGo stimuli have been shown to activate right inferior frontal gyrus (IFG; Aron et al., 2004) in conjunction with the subthalamic nucleus (Aron, 2011), supplementary and pre-supplementary motor areas (SMA; Simmonds et al., 2008), premotor cortex (Watanabe et al., 2002), and subregions of the parietal cortex, such as inferior parietal lobule (IPL; Rubia et al., 2001). Dorsolateral prefrontal cortex (dlPFC) activity

is also often observed, although this may better reflect the influence of cognitive processes that aid inhibition, such as conflict monitoring (Graf et al., 2011), attention (Hampshire et al., 2010), working memory (Mostofsky et al., 2003), and response selection (Simmonds et al., 2008). Error detection, for example, is a distinct but related construct; resulting in largely overlapping activation while also triggering additional recruitment of right anterior cingulate and insula cortices (Menon et al., 2001; Sharp et al., 2010). Consequently, the pattern of neural co-activation, corresponding to the implemented behavioural paradigms, can be dramatically different depending on the nature of the stimuli; particularly where complex, top-down intensive tasks are utilised (often involving multiple Go and NoGo cues, Wager et al., 2005; Criaud & Boulinguez, 2013; Meffert et al., 2016).

Go/NoGo tasks have incorporated a variety of stimuli; including numbers, letters, and images (Donkers & van Boxtel, 2004; Kelly et al., 2004; Mosofsky et al., 2003). Within the image-based investigations, faces are particularly interesting for studies focusing on in-group bias. Facial perception is considered one of the most developed visual skills possessed by humans (Haxby et al., 2000), with faces representing a unique yet commonly viewed stimulus that can express a multitude of information (spanning identity, emotion, age, and gender; Quinn & Macrae, 2011). Therefore, faces provide vital cues required to successfully navigate social interactions (Leopold & Rhodes, 2010). Individuals often form static impressions of others based on superficial characteristics, such as appearance. For example, visual cues related to age have consequences for impression formation that can perpetuate negative stereotypes and ageism, in relation to judgments of mental and physical capacity. Studies of such ‘diagnostic facial cues’ (Zebrowitz et al., 2014) have shown that younger adults have an innate bias against older adults founded on facial appearance (Kaufmann et al., 2017). This implicit value judgement

corresponds to research that supports the assertion that expertise in face perception primarily applies to faces that are particularly salient (Young & Burton, 2018), as opposed to humans being equally adept at processing all faces (Carey, 1992).

Accordingly, there appears to be a discernible processing advantage for same age faces (Kuefner et al., 2008), indicating that individuals tend to attribute greater importance to faces of those from their own demographic. Young participants, therefore, find it easier to recognise and distinguish between young faces (Anastasi & Rhodes, 2005), compared to faces from other age groups (Hills & Lewis, 2011). Neuroimaging studies suggest that greater activity in medial prefrontal cortex (mPFC), insula, and amygdala for same-age, compared to other-age faces, underlies this face processing preference (Ebner et al., 2013). Involvement of mPFC has also been demonstrated to be independent of emotional expression, indicating its role as fundamental to the own-age bias (Ziaei et al., 2019); a finding which is highly consistent with what is known of the mPFC in relation to salience within the bounds of social interactions (Sugiura et al., 2005; Bickart et al., 2014). Taken together, these results suggest that the observed bias in face processing may provide a unique opportunity to study inhibitory control in the context of interactions with other-age individuals.

In the context of the present study, a Go/NoGo paradigm with facial stimuli of younger and older adults was used to investigate the effects of age bias on response inhibition. Specifically, we aimed to determine whether the presentation of in-group stimuli (younger faces) and out-group stimuli (older faces) modulated neural activity during successful and unsuccessful response inhibition in a sample of young adults. Participants were asked to respond to the present stimulus unless it matched the previous one (separated by a brief interval of 500ms); making the task far less complex than those, for example, where participants must choose between two

possible NoGo cues after intervals of several seconds (Garavan, Ross, & Stein, 1999). Therefore, we considered working memory demand to be low, such that we were able to produce a simple manipulation of stimulus salience and minimise additional cognitive strategies, to better explore response inhibition in as isolated state as possible (Snyder et al., 2011). To our knowledge, there have been no such attempts to create a Go/NoGo task in this manner, yet this approach may provide the insight necessary to determine activity in subregions of the response inhibition network as being contingent upon specific stimulus attributes. In accordance with the literature, we expected (1) higher accuracy on Go trials than NoGo trials and (2) superior behavioural performance, particularly with regard to reaction time for trials featuring younger, compared to older, adult faces. We further anticipated (3) to replicate previous findings showing increased activity during correct NoGo trials in regions essential for response inhibition (e.g., parietal cortex, IFG, and pre-SMA), and during incorrect NoGo trials in structures associated with error detection (e.g., anterior cingulate cortex and insula). Finally, we predicted (4) that own-age face bias would modulate activity in mPFC, by establishing stronger responses to younger compared to older adult face stimuli.

2. *Material and Methods*

2.1. Participants

We tested 46 right-handed young adults with normal or corrected-to-normal vision. The final sample size was 44 (mean age = 24.27 years; SD = 3.55 years, 23 males) as two participants were excluded from all analyses due to a lack of understanding of the task instructions and consequent poor performance. Participants were screened and 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 Department of Psychology Ethics Board at Swansea University.

2.2. Stimuli

Stimuli consisted of colour images of younger and older adult faces, in a frontal orientation. Face images were obtained from the FACES database (Ebner, Riediger & Lindenberger, 2010; https://faces.mpdl.mpg.de/imeji/), representing 12 younger (20-30 years of age) and 12 older (60+ years of age) individuals. 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 a standard deviation in ratings of less than ten) to ensure that there were no significant differences within and between the different age groups ($p > .05$). Additionally, all selected images featured neutral facial expressions to ensure responses were not confounded by valence (Hare et al., 2005; Verbruggen & De Houwer, 2007; Pessoa, 2009).

2.3. Experimental Procedure

Stimuli 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 **Figure 1**). Each experimental session began with a structural scan (5 minutes), followed by 2 functional runs of the Go/NoGo task (6.5 minutes each), one run for younger adult and one run for older adult faces. The order of runs was counterbalanced across participants, as part of an event-related experimental design (which better enables the identification of brain activity unique to inhibition, compared to block designs; Liddle et al., 2001; Mostofsky et al., 2003). 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 s 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 or 4:1 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 trials and 4 NoGo trials. Each trial was 1000 ms in length, with an inter-stimulus interval (ISI) of 500 ms. The stimulus remained on screen once participants had responded, such that both stimulus onset and ISI were fixed. As per the aims of the study, trial presentation of this duration, and repeated presentation of a small selection of faces, was implemented to minimise cognitive load. The short, static ISI was adopted to facilitate a consistent and predictable response pattern during the task, in order to produce conditions where it is sufficiently effortful to adequately withhold responses (Mostofsky et al., 2003; Wager et al., 2005; Young, Sutherland, & McCoy, 2018). Furthermore, varied ISI would alter the length of time participants were expected to maintain representations of the faces in working memory, which would alter subsequent load.

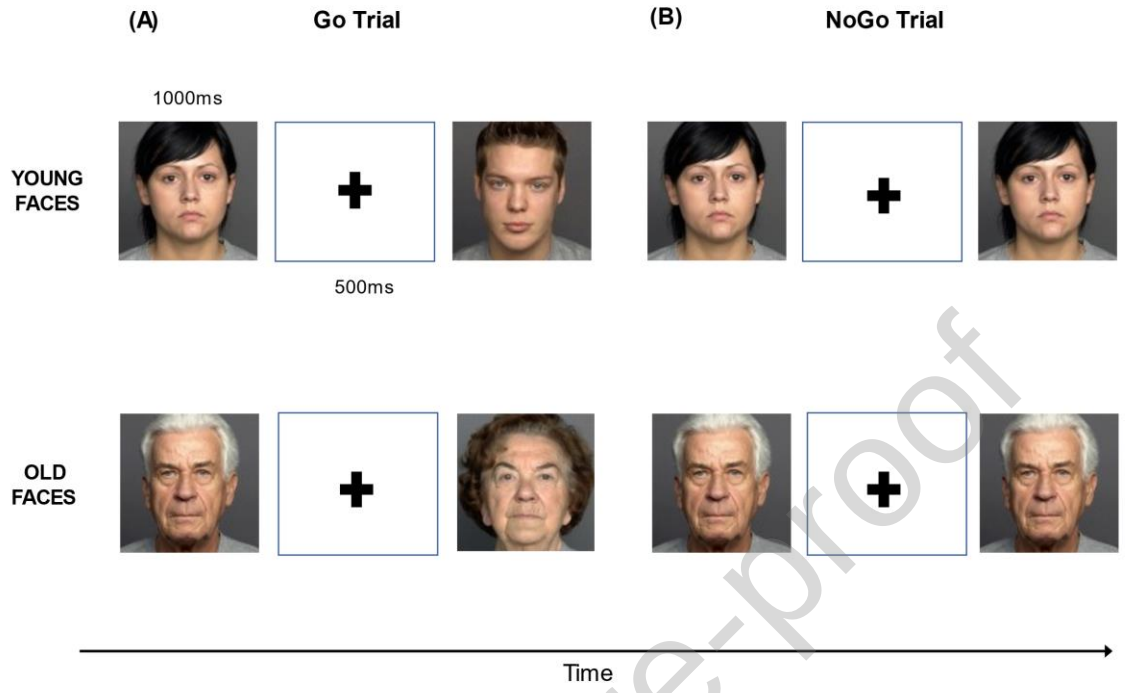

Figure 1. **Go/NoGo Task.** Participants were presented with a series of neutral face stimuli, between fixation screens, and were required to push a button each time a face was presented (GO trial; A) or to withhold their response if the same face was displayed in succession (NOGO trial; B). The task was presented twice, with separate experimental runs for younger adult (top) and older adult (bottom) faces.

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 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 (EPI) 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. No participants were excluded due to excessive motion (*i.e.*, > 2mm). The structural image of each participant was then segmented into three tissue types (grey matter, white matter, and cerebrospinal fluid), using tissue probability maps. Spatial normalisation into standard stereotaxic space was completed using the Montreal Neurological Institute (MNI) 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

The data were analysed with Principal Component Analysis using Partial Least Squares (PLS; McIntosh et al., 1996, 2004; Krishnan et al., 2011); a multivariate approach, which is optimal for extracting distributed signal changes in relation to task demands. PLS analysis was conducted using a free software (PLSGUI; https://www.rotman-baycrest.on.ca/) implemented via Matlab. PLS reduces the dimensionality of large data sets by decomposing the data into orthogonal dimensions by conducting singular value decomposition (SVD) and outputting a set of latent variables (LVs), i.e., patterns of brain activity related to the experimental design, which account for maximum covariance in the data. This identification of spatiotemporal patterns of whole-brain activity that covary with task effects requires only a single analytical step, as patterns of activity are evaluated across all voxels and timepoints at the same time.

Consequently, correction for multiple comparisons is not necessary, which results in higher statistical power than mass-univariate analyses (which consider each voxel separately; Habeck, 2010).

Here, we used task-based PLS, examining spatial and temporal dependencies among voxels, thus allowing inferences regarding differences across time and space between the experimental conditions. For each condition, we conducted analysis of activity across five TRs, starting at the onset of the face stimulus. Activity at each time point was normalised to the onset TR (i.e., stimulus presentation) and, thus, activity in each condition was uninfluenced by activity in another condition. In an event-related paradigm, PLS provides a set of brain regions related to the experimental conditions for each TR on each LV. At each TR, for each participant, a brain score is calculated by multiplying the salience (i.e., the degree of covariance of activity with the task condition on each LV) of each voxel by the signal of each brain voxel, and summing these across the entire brain. We plotted the mean brain scores at each TR to show overall brain activity fluctuations across the different conditions expressed over the 15 s period, which is analogous to hemodynamic response functions.

To determine statistical significance, we conducted 500 permutation tests to estimate the probability of each LV and 100 bootstraps to estimate the standard errors of the salience for each voxel in order to assess the reliability and robustness of each voxel's contribution to a pattern of brain activity (McIntosh et al., 2004). We used the mean-centering approach, which involves subtracting the grand mean of the data matrix from the task means. We restricted the bootstrap ratio threshold to +/-3 (statistical significance at $p < 0.001$; Sampson et al., 1989) and reported areas with a cluster size of 50 or more voxels. Confidence intervals (95%) were calculated from

the bootstrap; for the mean brain scores in each condition across the five TRs, with significant differences between conditions determined by a lack of overlap in the confidence intervals.

In the current study, we utilised event-related PLS to explore the relations among the following experimental conditions: **GO-YF** (successful Go trials; younger faces), **GO-OF** (successful Go trials, older faces), **NOGO-YF** (successful NoGo trials, younger faces), **NOGO-OF** (successful NoGo trials, older faces), **NOGO-ERR-YF** (unsuccessful NoGo trials, younger faces), and **NOGO-ERR-OF** (unsuccessful NoGo trials, older faces) to examine the presence of an own-age face bias during successful and unsuccessful response inhibition. Specifically, two whole-brain analyses were conducted: first, we examined the relations between the GO and NOGO conditions (GO as baseline), identifying brain activity during successful response inhibition to younger and older faces (n = 44); and, second, we examined the relations between the NOGO and NOGO-ERR conditions (NOGO as baseline), identifying brain activity during unsuccessful response inhibition to younger and older faces (n = 36). For the second analysis, participants with less than four unsuccessful NOGO trials in either face condition were excluded from the analysis.

*3. **Results***

3.1.Behavioural Results

To assess performance on the Go/NoGo task, two repeated-measures ANOVAs were conducted: one on the accuracy of responses to successful GO and NOGO trials, and the other on the reaction times to successful GO trials and unsuccessful NOGO trials. For accuracy, the 2 (**Trial**: Go/NoGo) x 2 (**Stimulus**: Younger Faces/Older Faces) ANOVA yielded a significant main effect of Trial ($F_{1,43}$ = 66.52, $p < 0.001$; η_p^2 = .61), demonstrating significantly better performance on the Go trials in comparison to the NoGo trials. The main effect of Stimulus and

Trial x Stimulus interaction were not significant (*p*s > 0.05). For reaction times, the 2 (**Response**: Successful Go/Unsuccessful NoGo) x 2 (**Stimulus**: Younger Faces/Older Faces) ANOVA did not reveal any significant main effects or interaction (*p*s > 0.05; **Table 1**).

Table 1. Means, standard deviations, and standard errors during the task (accuracy & RT)

ACCURACY	**GO-YF**	**GO-OF**	**NOGO-YF**	**NOGO-OF**
Mean	0.981	0.981	0.833	0.828
SD	0.033	0.027	0.123	0.122
SE	0.005	0.002	0.019	0.018
RT	**GO-YF**	**GO-OF**	**NOGO-ERR-YF**	**NOGO-ERR-OF**
Mean	489	487	482	511
SD	63.1	60.7	85.7	133.0
SE	9.5	9.2	13.1	20.0

3.2. fMRI Results

3.2.1. Whole-brain Activity: Successful Response Inhibition

The whole-brain analysis of the GO and NOGO conditions (successful trials only) yielded two significant LVs. LV1 accounted for 71.79% of covariance in the data and delineated a pattern of activity common to the NOGO conditions, in contrast to the GO conditions (see **Figure 2**). Response inhibition to both younger and older faces engaged a common network of brain regions, including bilateral hippocampus, ventral and dorsal striatum, anterior insula, frontoparietal areas, cuneus, somatosensory cortices, and pre-SMA.

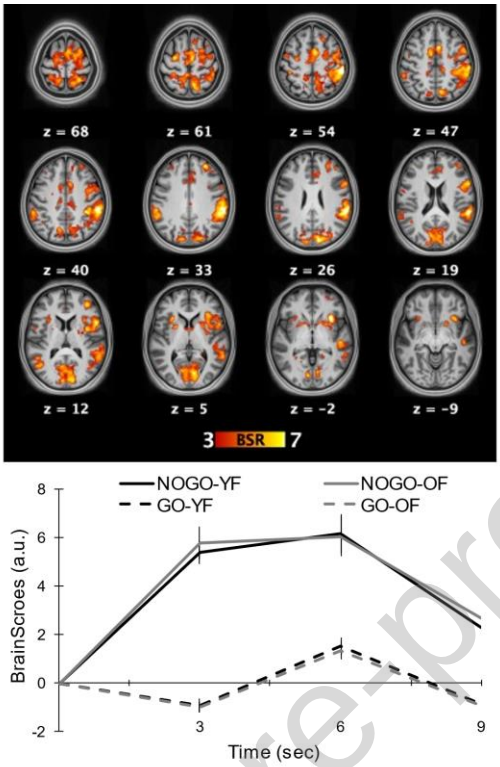

Figure 2. Successful response inhibition: shared brain activity across age stimuli. Top: A pattern of whole-brain activity depicting areas active during NOGO *vs*. GO trials ($p < 0.001$). Below: Mean brain scores related to the whole-brain activity across four experimental conditions (NOGO-YF, NOGO-OF, GO-YF, and GO-OF). Error bars denote 95% confidence intervals for correlations calculated from the bootstrap procedure; **BSR** = bootstrap ratio; **a.u.** = arbitrary units; **z** coordinate = superior/inferior orientation.

LV2 accounted for 24.78% of covariance in the data and delineated a pattern of activity different for NOGO-YF and NOGO-OF. Successful response inhibition to younger faces engaged orbitofrontal, ventromedial & ventrolateral PFC, bilateral anterior insula, left temporal pole, striatum, right inferior frontal gyrus (BA 9/46), and right temporoparietal junction, whereas successful response inhibition to older faces engaged parahippocampus, left inferior frontal gyrus (BA 45), middle temporal gyrus, precuneus, and pre-SMA (see **Figure 3**).

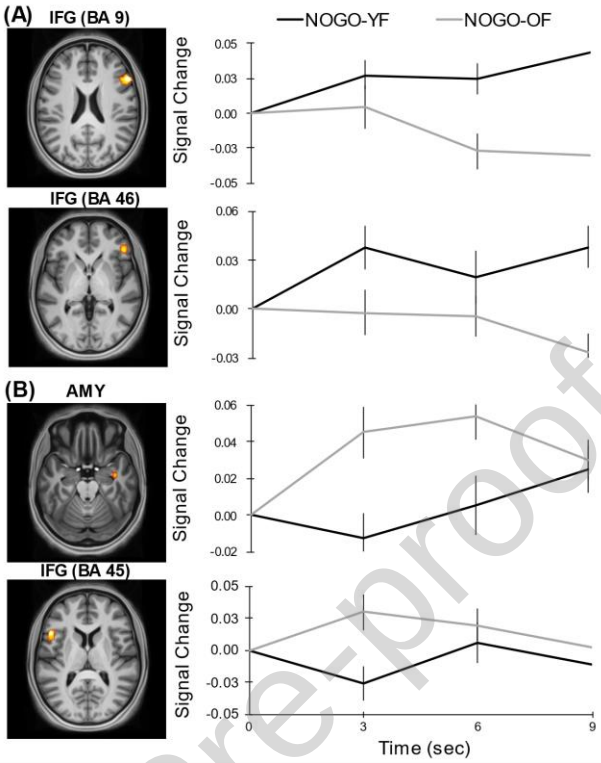

Figure 3. Successful response inhibition: differences in brain activity due to age bias. (A) During response inhibition to younger face stimuli (NOGO-YF), significantly more activity was found in right inferior frontal gyrus (BA 9 [maximal divergence at 6s] and BA 46 [maximal divergence at 3s] than during response inhibition to older face stimuli (NOGO-OF); (B) During response inhibition to older face stimuli (NOGO-OF), significantly more activity was found in right amygdala (maximal divergence at 3s) and left inferior frontal gyrus (BA 45: maximal divergence at 3s) than during response inhibition to younger face stimuli (NOGO-YF). Error bars denote 95% confidence intervals for correlations calculated from the bootstrap procedure; **BA** = Brodmann area; **IFG** = inferior frontal gyrus; **AMY** = amygdala.

3.2.2. Whole-brain Activity: Unsuccessful Response Inhibition

The whole brain analysis of the NOGO and NOGO-ERR conditions yielded two significant LVs. LV1 accounted for 72.32% of covariance in the data and delineated a pattern of activity common to the NOGO-ERR conditions, in contrast to the NOGO conditions (see **Figure 4**). Unsuccessful response inhibition to both younger and older faces engaged a common network

of brain regions, including bilateral anterior insula, dorsal ACC, intraparietal sulcus, temporoparietal junction, superior temporal gyrus, and pre-SMA.

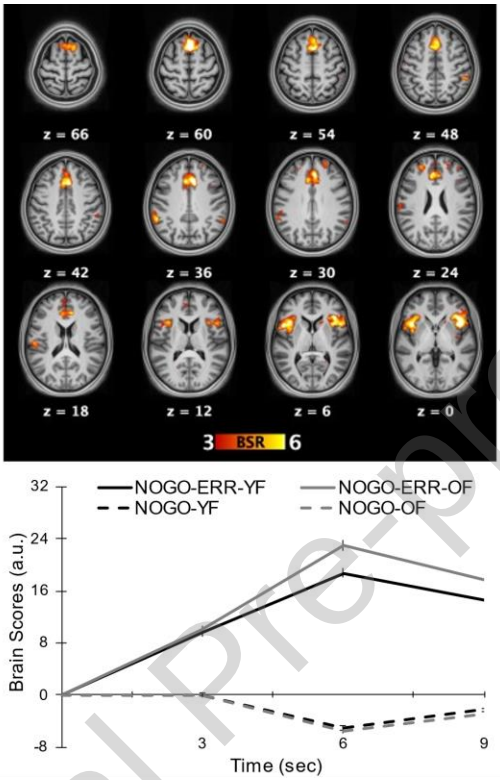

Figure 4. Unsuccessful response inhibition: shared brain activity across age stimuli. Top: A pattern of whole-brain activity depicting areas active during NOGO-ERR *vs*. NOGO trials. Below: Mean brain scores related to the whole-brain activity across four experimental conditions (NOGO-ERR-YF, NOGO-ERR-OF, NOGO-YF, and NOGO-OF). Error bars denote 95% confidence intervals for correlations calculated from the bootstrap procedure; **BSR** = bootstrap ratio; **a.u.** = arbitrary units; **z** coordinate = superior/inferior orientation.

LV2 accounted for 25.65% of covariance in the data and delineated a pattern of activity different for NOGO-ERR-YF and NOGO-ERR-OF. Unsuccessful response inhibition to younger faces engaged temporal pole, bilateral posterior insula, parahippocampus, thalamus, supramarginal gyrus, premotor cortex, and bilateral precuneus more strongly, whereas unsuccessful response inhibition to older faces resulted in increased activity in caudate nucleus,

inferior frontal gyrus (BA 47), angular gyrus, intraparietal sulcus, and superior frontal gyrus (see **Figure 5**).

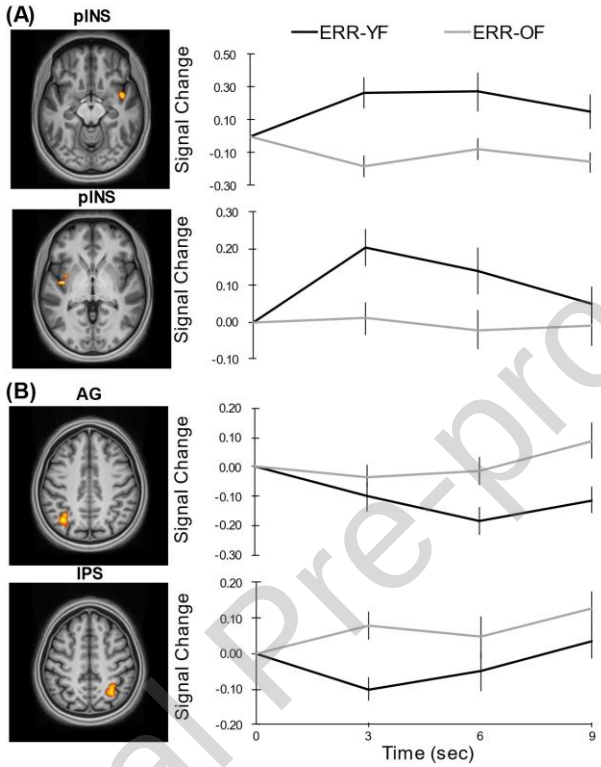

Figure 5. Unsuccessful response inhibition: differences in brain activity due to age bias. (A) During unsuccessful response inhibition to younger face stimuli (ERR-YF), significantly more activity was found in bilateral posterior insula [maximal divergence at 3s] than during unsuccessful response inhibition to older face stimuli (ERR-OF); (B) During unsuccessful response inhibition to older face stimuli (ERR-OF), significantly more activity was found in left angular gyrus [maximal divergence at 6s] and right intraparietal sulcus [maximal divergence at 3s] than during unsuccessful response inhibition to younger face stimuli (ERR-YF). Error bars denote 95% confidence intervals for correlations calculated from the bootstrap procedure; **BA** = Brodmann area; **pINS** = posterior insula; **AG** = angular gyrus; **IPS** = intraparietal sulcus.

4. Discussion

A Go/NoGo paradigm, with faces of younger and older adults as stimuli, was used to determine the effects of an age-based in-group bias on the neural responses associated with successful and unsuccessful response inhibition. Behaviourally, we replicated the response inhibition effect, with results showing that participants made more errors in their NoGo compared to their Go responses but did not show any differences when responding to younger or older face stimuli. The neuroimaging results showed sustained activity in regions of the response inhibition network for successful response inhibition (compared to response execution) and in regions of the dorsal salience network for unsuccessful response inhibition (compared to successful response inhibition). Importantly, the results further demonstrated that activity within some regions of these networks was modulated by stimulus type. Thus, the results suggest that age-based in-group bias affects neural information processing during successful response inhibition, as well as during the detection of response inhibition errors.

4.1. Successful NoGo trials

4.1.1. Activation of the Response inhibition Network

Replicating previous findings, the neuroimaging analyses revealed that successful suppression of prepotent actions was subserved by activity in the main nodes of the response inhibition network, including bilateral anterior insula, right IFG, MFG, bilateral striatum, and pre-SMA (Aron et al., 2003; Nelson et al., 2010; Swann et al., 2012; Steele et al., 2013; Janes et al., 2015; Morein-Zamir & Robbins, 2015; Zhang, Geng & Lee, 2017). This sustained brain activity across the functional network was evident for both types of age stimuli, reflecting the response inhibition effect, rather than in/out-group modulation.

4.1.2. In-/Out-group Modulation of the Response Inhibition Network

The presentation of younger and older faces differentially modulated the activity in several nodes of the response inhibition network, highlighting more specific (regional) rather than network-level differences. In particular, we observed increased vmPFC activity during successful NoGo trials featuring younger faces, compared to older faces. The mPFC is thought to be involved in the detection of socially salient information and has previously been found to display increased activation when viewing faces of a similar age group to the viewer (Ebner et al., 2013; Bickart et al., 2014). Similarly, our results showed increased activity in the temporoparietal junction, which has been consistently linked to social perception (Santiesteban et al., 2012) and attention (Corbetta & Shulman, 2011). The findings of the present study, therefore, provide empirical evidence to support the roles of mPFC and TPJ as key structures underlying age-based, in-group processing. In contrast, our results showed that activity was significantly increased during successful response inhibition to older face stimuli within pre-SMA (widely regarded as a core structure underlying motor inhibition, with high connectivity to prefrontal as well as motor regions; Nachev, Kennard & Hussain, 2008). This modulation of activity suggests that out-group stimuli require stronger activation of pre-SMA in order to effectively inhibit motor responses.

4.2. Unsuccessful NoGo trials

4.2.1. Activation of the Dorsal Salience Network

The analysis of unsuccessful response inhibition (for stimuli of both age groups) revealed a pattern of activity representative of the dorsal salience network, comprising bilateral anterior insula, dorsal ACC, temporoparietal junction, superior temporal gyrus, and pre-SMA (Downar et

al., 2002; Orr & Hester, 2012). Many of these regions were also found to govern successful response inhibition but it is important to note that a degree of overlap in network activation is to be expected, between trial types, having been produced by the same task (Xu et al., 2016). For example, pre-SMA was active in both the response inhibition and salience networks because preparation of a response is characteristic of the general demands of the Go/NoGo task. Similarly, as previously stated, TPJ activation is primarily proposed to reflect the social relevance of stimuli, irrespective of trial type.

Activity in regions of dorsal salience network in relation to unsuccessful inhibition is not surprising; especially given the executive role of the anterior insula, shown to execute specialised and integrative functions pertaining to error monitoring (Bastin et al., 2016). Additionally, while the dorsal region reflects cognitive control processes, the ventral area responds to social and emotional stimulus attributes (Uddin et al., 2017). This distinction is also evident across hemispheres, with right anterior insula adopting a more affective role; suggesting the bilateral activity observed in the current study is indicative of our stimuli evoking responses requiring the integration of external top-down, cue-dependent information with internal social signals. Likewise, TPJ is also engaged during domain-general salience processing and that involving social cognition, having been shown to be integral to "self and other" discriminations (Uddin et al., 2006; Geng & Vossel, 2013). Regarded as a mediator between dorsal and ventral attention networks; an anterior node of TPJ projects to dorsal ACC and MFG, and a posterior node connects to IFG, MFG and precuneus – both of which extend to anterior insula (Decety & Lamm, 2007; Igelstrom & Graziano, 2017), highlighting the interplay of these regions in utilising social cues to construct appropriate responses.

4.2.2. In-/Out-group Modulation of the Dorsal Salience Network

Activity in several nodes of the dorsal salience network was differentially modulated by the presentation of younger and older faces, again highlighting more specific (regional) rather than network-level differences. Unsuccessful response inhibition to younger faces engaged bilateral posterior insula significantly more strongly. Posterior insula projects to parietal and sensorimotor cortices that are instrumental within the ventral system in adjusting responses based on personal attributes (Uddin et al., 2017). Furthermore, bilateral involvement of precuneus, within superior parietal lobule, also attests to the importance of internal mental representations in response to the stimuli, as this region has a notable role in introspection (Cabanis et al., 2013; Wang et al., 2019). Therefore, the observed pattern of activity underpinning responses to younger faces indicates that they were regarded as more important, and of higher personal value than those of older adults (Kuefner et al., 2008; Ebner et al., 2013; Young & Burton, 2018). Accordingly, our neural results suggest that it is more salient, or socially detrimental, to make an error in response to faces depicting one's own age group, although this bias is likely to be implicit (given the non-significant behavioural result related to the stimuli). Socially relevant stimuli, particularly those representing in- vs. out-group distinctions, are therefore highly likely to enhance error awareness and define responses to incorrect trials. For example, the extent of involvement of dorsal ACC has also been linked to the salience of the withholding response (Manza et al., 2016). Consequently, age as a stimulus feature should signify a key consideration in future experimental designs relating to response inhibition, and perhaps other executive tasks.

Unsuccessful response inhibition to older faces most notably resulted in increased activity in angular gyrus and intraparietal sulcus. Linked to components of both the ventral (e.g., IFG) and dorsal (e.g., IPS/SFG) attention networks via branches of the superior longitudinal

fasciculus (Makris et al., 2005; de Schotten et al., 2011), angular gyrus has been shown to be implicated in conflict resolution and failed inhibition resulting from numerous Go/NoGo tasks (Wager et al., 2005; Nee et al., 2007; Singh-Curry & Husain, 2009). The activity pattern corresponding to errors involving older faces does not appear to be based on social cognition *per se* (instead implicating salience purely within the bounds of attention; representing novelty from the perspective of the infrequency of error responses, as opposed to being contingent on the nature of the stimuli). However, the age-related distinction in face stimuli must have been sufficient to evoke the substantial contextual conflict proposed to be required to activate left angular gyrus in this manner (as typically only right hemisphere is shown to be engaged; Seghier et al., 2013). Furthermore, connections via the inferior occipitofrontal fasciculus extend from angular gyrus to the caudate nucleus (Uddin et al., 2010), while parahippocampal gyrus is linked to angular gyrus via the inferior longitudinal fasciculus (Rushworth et al., 2006). These structures were also part of the network in question and are instrumental in the chain of events required to integrate perception, recognition, and action control, which angular gyrus is reported to coordinate (Nelson et al., 2010). Therefore, NoGo errors to stimuli featuring older faces appear to be important in the context of cognitive control but may not be socially meaningful.

4.3. Limitations & Future Directions

With regard to the stimuli, it is important to consider that interpretation of neutral facial expressions may be dependent on the age of the stimulus. For example, younger adults may interpret neutral expressions in older adults as emotional due to the physical changes associated with ageing (e.g., loss of plasticity of the skin, slanting of the eyebrows). While we did not obtain independent ratings of the stimuli in our participant sample, we are confident that the

images used would have been interpreted as neutral by the vast majority of participants. This is because the database from which the stimuli were sourced provides accompanying ratings of the facial expressions, which - for the neutral images - were validated in an age-representative sample of 154 participants (comprising equal numbers of younger, middle aged, and older adults; Ebner et al., 2010).

Whilst the results attest to an age-bias in neural activation patterns, distinguishing between the processing of younger and older face stimuli in the context of both successful and unsuccessful attempts to inhibit, the lack of behavioural age-bias effect is somewhat surprising. It is speculated that this may have been due to the following. (1) We chose to separate the presentation of younger and older adult faces into distinct functional runs, as opposed to intermixing stimuli, but designed the paradigm in this way for both clarity and brevity. On the subject of clarity, when task responses are based on comparisons and relationships to prior stimuli (as is the case for Go/NoGo paradigms), it becomes essential to block images by defining characteristics, such as age group. As such, intermixing the stimuli would be predicted to alter the basic premise of the task, and may result in participants using bottom-up surface-level age cues to facilitate responses as opposed to engaging top-down inhibition. Previous research has also utilised separate presentations of adult/new born, and adult/child stimuli; generating a statistically significant interaction between the variables (e.g., Kuefner et al., 2008), suggesting that although it is a possibility, it is unlikely that the manner in which we presented the stimuli contributed to the non-significant own-age bias results. Additionally, in relation to brevity, intermixing the stimuli, while gathering equivalent data, would result in a functional run of ~13 minutes; demonstrated to induce fatigue and increase the likelihood of motion artefacts (Amaro Jr and Barker, 2006).

(2) To minimise cognitive load and simplify the Go/NoGo task, the study utilised a small number of face images combined with a relatively slow stimulus presentation rate (1000 ms, compared to 250 ms used elsewhere; e.g., Steele et al., 2013). Nevertheless, it should be noted that the stimulus set size used here is equivalent to that found in other Go/NoGo studies (e.g., those adopting letters stimuli, presenting a total of 12 items; Wager et al., 2005), and across the wider literature investigating the own age-bias (utilising 8-16 images of faces; Anastasi & Rhodes, 2005; Ebner et al., 2013). While we cannot eliminate the possibility of habituation, if habituation were to occur, we would predict that it would influence younger and older adult stimuli in a similar manner (and would, as such, not pose a problem for the purpose of the study). Furthermore, as response inhibition effects were demonstrated behaviourally and neurally, the results suggest that the task was sufficiently challenging to produce errors and distinguish Go from NoGo trials (Crauid & Boulinguez, 2013; Peatfield et al., 2015; Young, Sutherland, & McCoy, 2018). Importantly, these elements did not influence the fundamental nature of the task, which evoked activity in response inhibition and salience networks. The fact that age-related distinctions were noted in regions central to action suppression and not in peripheral, face processing regions, also confirms that the paradigm served the intended purpose.

Future research in this area may benefit from the use of skin conductance measures and electroencephalography to further evaluate the effects of error processing (Harsay et al., 2012). For example, “error-related negativity” (ERN), which is commonly associated with increased autonomic arousal (Ladouceur et al., 2006; Olvet & Hajcak, 2008). Advancing age is often accompanied by an increased difficulty to recognise faces and engage inhibition mechanisms (Chaby & Narme, 2009; Chaby, Narme, & George, 2011; Hsieh, Wu, & Tang, 2016), such that investigating the responses of older participant samples would also be advantageous in

distinguishing whether they use similar or alternative strategies to process out-group stimuli (Wiese, Schweinberger, & Hansen, 2008; Hildebrandt et al., 2011).

*5. **Conclusions***

The results of the study provide new insight into patterns of neural responses underlying inhibitory control processes; confirming that both successful and unsuccessful inhibition can be modulated by the stimulus-specific attribute of age and related in-group/out-group biases. Greater activity of mPFC and TPJ to younger faces during successful NoGo trials demonstrates the presence of an own-age bias in the response inhibition network. Furthermore, responses to younger faces during unsuccessful NoGo trials exhibited more prominent involvement of posterior insula and precuneus, indicative of an own-age bias in the dorsal salience network in relation to failed inhibition. Therefore, in generating successful and unsuccessful inhibitory responses, participants appear to have made an implicit appraisal of the age of the stimulus, which was shown to modulate the accompanying network activity. In the context of errors, these findings suggest that young adults found unsuccessful trials involving their own age group particularly salient, possibly attaching a higher degree of value and significance to their processing. Beyond laboratory investigations of response inhibition, this finding has the potential to contribute towards understanding the neural mechanisms of ageism; regarded as a prominent societal concern. As a way of counteracting such implicit bias, training individuals to consciously regulate such introspective processing to view all errors as equal could help to minimise the prospective detrimental impact.

Ethical Approval

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

Publication Ethics

The manuscript adheres to Elsevier's policy.

Sources of Funding

No external sources of funding. The research was supported by Department of Psychology, Swansea University. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Data Availability

Upon acceptance of the manuscript, the data will be uploaded to a public repository.

Declarations of Interest: None.

References

Amaro Jr, E., & Barker, G. J. (2006). Study design in fMRI: basic principles. *Brain and Cognition*, *60*(3), 220-232.

Anastasi, J. S., & Rhodes, M. G. (2005). An own-age bias in face recognition for children and older adults. *Psychonomic Bulletin & Review*, *12*(6), 1043-1047.

Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature Neuroscience*, *6*(2), 115-116.

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*(4), 170-177.

Aron, A. R. (2011). From reactive to proactive and selective control: developing a richer model for stopping inappropriate responses. *Biological Psychiatry*, *69*(12), e55-e68.

Bastin, J., Deman, P., David, O., Gueguen, M., Benis, D., Minotti, L., ... & Kahane, P. (2016). Direct recordings from human anterior insula reveal its leading role within the error-monitoring network. *Cerebral Cortex*, bhv352.

Bickart, K. C., Dickerson, B. C., & Barrett, L. F. (2014). The amygdala as a hub in brain networks that support social life. *Neuropsychologia*, *63*, 235-248.

Booth, J. R., Burman, D. D., Meyer, J. R., Lei, Z., Trommer, B. L., Davenport, N. D., ... & Mesulam, M. M. (2003). Neural development of selective attention and response inhibition. *Neuroimage*, *20*(2), 737-751.

Butler, R. N. (1969). Age-ism: Another form of bigotry. *The Gerontologist,* **9** (4), 243–246.

Cabanis, M., Pyka, M., Mehl, S., Müller, B. W., Loos-Jankowiak, S., Winterer, G., ... & Langohr, K. (2013). The precuneus and the insula in self-attributional processes. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(2), 330-345.

Carey, S. (1992). Becoming a face expert. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *335*(1273), 95-103.

Chaby, L., & Narme, P. (2009). Processing facial identity and emotional expression in normal aging and neurodegenerative diseases. *Psychologie & NeuroPsychiatrie du Vieillissement*, *7*(1), 31-42.

Chaby, L., Narme, P., & George, N. (2011). Older adults' configural processing of faces: Role of second-order information. *Psychology and Aging*, *26*(1), 71.

Corbetta, M., & Shulman, G. L. (2011). Spatial neglect and attention networks. *Annual Review of Neuroscience*, *34*, 569-599.

Criaud, M., & Boulinguez, P. (2013). Have we been asking the right questions when assessing response inhibition in go/no-go tasks with fMRI? A meta-analysis and critical review. *Neuroscience & Biobehavioral Reviews*, *37*(1), 11-23.

Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. *The Neuroscientist*, *13*(6), 580-593.

Della-Maggiore, V., Chau, W., Peres-Neto, P. R., & McIntosh, A. R. (2002). An empirical comparison of SPM preprocessing parameters to the analysis of fMRI data. *Neuroimage*, *17*(1), 19-28.

de Schotten, M. T., Dell'Acqua, F., Forkel, S., Simmons, A., Vergani, F., Murphy, D. G., & Catani, M. (2011). A lateralized brain network for visuo-spatial attention. *Nature Neuroscience*, 1-1.

Dominguez, D., Juan, F., Taing, S.A., & Molengberghs, P. (2016). Why do some find it hard to disagree? An fMRI study. *Frontiers in Human Neuroscience*, 9:718.

Donkers, F. C., & Van Boxtel, G. J. (2004). The N2 in go/no-go tasks reflects conflict monitoring not response inhibition. *Brain and Cognition*, *56*(2), 165-176.

Downar, J., Crawley, A. P., Mikulis, D. J., & Davis, K. D. (2002). A cortical network sensitive to stimulus salience in a neutral behavioral context across multiple sensory modalities. *Journal of Neurophysiology*, *87*(1), 615-620.

Drewe, E. A. (1975). Go-no go learning after frontal lobe lesions in humans. *Cortex*, *11*(1), 8-16.

Ebner, N. C., Johnson, M. R., Rieckmann, A., Durbin, K. A., Johnson, M. K., & Fischer, H. (2013). Processing own-age vs. other-age faces: neuro-behavioral correlates and effects of emotion. *Neuroimage*, *78*, 363-371.

Ebner, N. C., Riediger, M., & Lindenberger, U. (2010). FACES—A database of facial expressions in young, middle-aged, and older women and men: Development and validation. *Behavior Research Methods*, *42*(1), 351-362.

Fan, J., Flombaum, J.I., McCandliss, B.D., Thomas, K.M., & Posner, M.I. (2003). Cognitive and brain consequences of conflict. *NeuroImage*, *18*, 42-57.

Garavan, H., Ross, T. J., & Stein, E. A. (1999). Right hemispheric dominance of inhibitory control: an event-related functional MRI study. *Proceedings of the National Academy of Sciences*, *96*(14), 8301-8306.

Gendron, T. L., Welleford, E. A., Inker, J., & White, J. T. (2016). The language of ageism: Why we need to use words carefully. *The Gerontologist*, *56*(6), 997-1006.

Geng, J. J., & Vossel, S. (2013). Re-evaluating the role of TPJ in attentional control: contextual updating?. *Neuroscience & Biobehavioral Reviews*, *37*(10), 2608-2620.

Golby, A.J., Gabrieli, J.D., Chiao, J.Y., & Eberhardt, J.L. (2001). Differential responses in the fusiform region to same-race and other-race faces. *Nature Neuroscience*, *4*, 845-850.

Graf, H., Abler, B., Freudenmann, R., Beschoner, P., Schaeffeler, E., Spitzer, M., ... & Grön, G. (2011). Neural correlates of error monitoring modulated by atomoxetine in healthy volunteers. *Biological Psychiatry*, *69*(9), 890-897.

Habeck, C. G. (2010). Basics of multivariate analysis in neuroimaging data. *JoVE (Journal of Visualized Experiments)*, 41, e1988.

Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: inhibition and attentional control. *Neuroimage*, *50*(3), 1313-1319.

Hare, T. A., Tottenham, N., Davidson, M. C., Glover, G. H., & Casey, B. J. (2005). Contributions of amygdala and striatal activity in emotion regulation. *Biological Psychiatry*, *57*(6), 624-632.

Harsay, H. A., Spaan, M., Wijnen, J. G., & Ridderinkhof, K. R. (2012). Error awareness and salience processing in the oddball task: shared neural mechanisms. *Frontiers in Human Neuroscience*, *6*, 246.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*(6), 223-233.

Hildebrandt, A., Wilhelm, O., Schmiedek, F., Herzmann, G., & Sommer, W. (2011). On the specificity of face cognition compared with general cognitive functioning across adult age. *Psychology and Aging*, *26*(3), 701.

Hills, P. J., & Lewis, M. B. (2011). Rapid communication: the own-age face recognition bias in children and adults. *Quarterly Journal of Experimental Psychology*, *64*(1), 17-23.

Horn, N. R., Dolan, M., Elliott, R., Deakin, J. F., & Woodruff, P. W. R. (2003). Response inhibition and impulsivity: an fMRI study. *Neuropsychologia*, *41*(14), 1959-1966.

Hsieh, S., Wu, M., & Tang, C. H. (2016). Adaptive strategies for the elderly in inhibiting irrelevant and conflict no-go trials while performing the go/no-go task. *Frontiers in Aging Neuroscience*, *7*, 243.

Hutton, S. B., Joyce, E. M., Barnes, T. R. E., & Kennard, C. (2002). Saccadic distractibility in first-episode schizophrenia. *Neuropsychologia*, *40*(10), 1729-1736.

Igelström, K. M., & Graziano, M. S. (2017). The inferior parietal lobule and temporoparietal junction: a network perspective. *Neuropsychologia*, *105*, 70-83.

Janes, A. C., Farmer, S., Peechatka, A. L., de B Frederick, B., & Lukas, S. E. (2015). Insula–dorsal anterior cingulate cortex coupling is associated with enhanced brain reactivity to smoking cues. *Neuropsychopharmacology*, *40*(7), 1561-1568.

Kaufmann, M. C., Krings, F., Zebrowitz, L. A., & Sczesny, S. (2017). Age bias in selection decisions: the role of facial appearance and fitness impressions. *Frontiers in Psychology*, *8*, 2065.

Kelly, A. C., Hester, R., Murphy, K., Javitt, D. C., Foxe, J. J., & Garavan, H. (2004). Prefrontal-subcortical dissociations underlying inhibitory control revealed by event-related fMRI. *European Journal of Neuroscience*, *19*(11), 3105-3112.

Krishnan, A., Williams, L. J., McIntosh, A. R., & Abdi, H. (2011). Partial Least Squares (PLS) methods for neuroimaging: a tutorial and review. *NeuroImage*, *56*(2), 455-475.

Kuefner, D., Macchi Cassia, V., Picozzi, M., & Bricolo, E. (2008). Do all kids look alike? Evidence for an other-age effect in adults. *Journal of Experimental Psychology: Human Perception and Performance*, *34*(4), 811.

Ladouceur, C. D., Dahl, R. E., Birmaher, B., Axelson, D. A., & Ryan, N. D. (2006). Increased error-related negativity (ERN) in childhood anxiety disorders: ERP and source localization. *Journal of Child Psychology and Psychiatry*, *47*(10), 1073-1082.

Leopold, D. A., & Rhodes, G. (2010). A comparative view of face perception. *Journal of Comparative Psychology*, *124*(3), 233.

Liddle, P. F., Kiehl, K. A., & Smith, A. M. (2001). Event-related fMRI study of response inhibition. *Human Brain Mapping*, *12*(2), 100-109.

Manza, P., Hu, S., Chao, H. H., Zhang, S., Leung, H. C., & Chiang-shan, R. L. (2016). A dual but asymmetric role of the dorsal anterior cingulate cortex in response inhibition and switching from a non-salient to salient action. *Neuroimage*, *134*, 466-474.

Makris, N., Kennedy, D. N., McInerney, S., Sorensen, A. G., Wang, R., Caviness Jr, V. S., & Pandya, D. N. (2005). Segmentation of subcomponents within the superior longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. *Cerebral Cortex*, *15*(6), 854-869.

McIntosh, A. R., Bookstein, F. L., Haxby, J. V., & Grady, C. L. (1996). Spatial pattern analysis of functional brain images using partial least squares. *Neuroimage*, *3*(3), 143-157.

McIntosh, A. R., & Lobaugh, N. J. (2004). Partial least squares analysis of neuroimaging data: applications and advances. *Neuroimage*, *23*, 250-263.

Meffert, H., Hwang, S., Nolan, Z. T., Chen, G., & Blair, J. R. (2016). Segregating attention from response control when performing a motor inhibition task: segregating attention from response control. *Neuroimage*, *126*, 27-38.

Menon, V., Adleman, N. E., White, C. D., Glover, G. H., & Reiss, A. L. (2001). Error-related brain activation during a Go/NoGo response inhibition task. *Human Brain Mapping*, *12*(3), 131-143.

Morein-Zamir, S., & Robbins, T. W. (2015). Fronto-striatal circuits in response-inhibition: Relevance to addiction. *Brain Research*, *1628*, 117-129.

Mostofsky, S. H., Schafer, J. G., Abrams, M. T., Goldberg, M. C., Flower, A. A., Boyce, A., ... & Pekar, J. J. (2003). fMRI evidence that the neural basis of response inhibition is task-dependent. *Cognitive Brain Research*, *17*(2), 419-430.

Nachev, P., Kennard, C., & Husain, M. (2008). Functional role of the supplementary and pre-supplementary motor areas. *Nature Reviews Neuroscience*, *9*(11), 856-869.

Nee, D. E., Wager, T. D., & Jonides, J. (2007). Interference resolution: insights from a meta-analysis of neuroimaging tasks. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(1), 1-17.

Nelson, S. M., Dosenbach, N. U., Cohen, A. L., Wheeler, M. E., Schlaggar, B. L., & Petersen, S. E. (2010). Role of the anterior insula in task-level control and focal attention. *Brain Structure and Function*, *214*(5-6), 669-680.

Ogawa, S., Lee, T. M., Kay, A. R., & Tank, D. W. (1990). Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proceedings of the National Academy of Sciences*, *87*(24), 9868-9872.

Olvet, D. M., & Hajcak, G. (2008). The error-related negativity (ERN) and psychopathology: Toward an endophenotype. *Clinical Psychology Review*, *28*(8), 1343-1354.

Orr, C., & Hester, R. (2012). Error-related anterior cingulate cortex activity and the prediction of conscious error awareness. *Frontiers in Human Neuroscience*, *6*, 177.

Peatfield, N., Caulfield, J., Parkinson, J., & Intriligator, J. (2015). Brands and Inhibition: A Go/No-Go Task Reveals the Power of Brand Influence. *PloS One*, *10*(11), e0141787.

Pessoa, L. (2009). How do emotion and motivation direct executive control?. *Trends in Cognitive Sciences*, *13*(4), 160-166.

Quinn, K. A., & Macrae, C. N. (2011). The face and person perception: Insights from social cognition. *British Journal of Psychology*, *102*(4), 849-867.

Rubia, K., Russell, T., Overmeyer, S., Brammer, M. J., Bullmore, E. T., Sharma, T., ... & Taylor, E. (2001). Mapping motor inhibition: conjunctive brain activations across different versions of go/no-go and stop tasks. *Neuroimage*, *13*(2), 250-261.

Rushworth, M. F. S., Behrens, T. E. J., & Johansen-Berg, H. (2006). Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral Cortex*, *16*(10), 1418-1430.

Rybarczyk, B., Haut, A., Lacey, R. F., Fogg, L. F., & Nicholas, J. J. (2001). A multifactorial study of age bias among rehabilitation professionals. *Archives of Physical Medicine and Rehabilitation*, *82*(5), 625-632.

Sampson, P. D., Streissguth, A. P., Barr, H. M., & Bookstein, F. L. (1989). Neurobehavioral effects of prenatal alcohol: Part II. Partial least squares analysis. *Neurotoxicology and Teratology*, *11*(5), 477-491.

Santiesteban, I., Banissy, M. J., Catmur, C., & Bird, G. (2012). Enhancing social ability by stimulating right temporoparietal junction. *Current Biology*, *22*(23), 2274-2277.

Schachar, R., Logan, G. D., Robaey, P., Chen, S., Ickowicz, A., & Barr, C. (2007). Restraint and cancellation: multiple inhibition deficits in attention deficit hyperactivity disorder. *Journal of Abnormal Child Psychology*, *35*(2), 229-238.

Seghier, M. L. (2013). The angular gyrus: multiple functions and multiple subdivisions. *The Neuroscientist*, *19*(1), 43-61.

Sharp, D. J., Bonnelle, V., De Boissezon, X., Beckmann, C. F., James, S. G., Patel, M. C., & Mehta, M. A. (2010). Distinct frontal systems for response inhibition, attentional capture, and error processing. *Proceedings of the National Academy of Sciences*, *107*(13), 6106-6111.

Simmonds, D. J., Pekar, J. J., & Mostofsky, S. H. (2008). Meta-analysis of Go/No-go tasks demonstrating that fMRI activation associated with response inhibition is task-dependent. *Neuropsychologia*, *46*(1), 224-232.

Singh-Curry, V., & Husain, M. (2009). The functional role of the inferior parietal lobe in the dorsal and ventral stream dichotomy. *Neuropsychologia*, *47*(6), 1434-1448.

Snyder, J. S., Pasinski, A. C., & McAuley, J. D. (2011). Listening strategy for auditory rhythms modulates neural correlates of expectancy and cognitive processing. *Psychophysiology*, *48*(2), 198-207.

Steele, V. R., Aharoni, E., Munro, G. E., Calhoun, V. D., Nyalakanti, P., Stevens, M. C., ... & Kiehl, K. A. (2013). A large scale (N= 102) functional neuroimaging study of response inhibition in a Go/NoGo task. *Behavioural Brain Research*, *256*, 529-536.

Sugiura, M., Watanabe, J., Maeda, Y., Matsue, Y., Fukuda, H., & Kawashima, R. (2005). Cortical mechanisms of visual self-recognition. *Neuroimage*, *24*(1), 143-149.

Swann, N. C., Cai, W., Conner, C. R., Pieters, T. A., Claffey, M. P., George, J. S., ... & Tandon, N. (2012). Roles for the pre-supplementary motor area and the right inferior frontal gyrus in stopping action: electrophysiological responses and functional and structural connectivity. *Neuroimage*, *59*(3), 2860-2870.

Swick, D., Ashley, V., & Turken, U. (2011). Are the neural correlates of stopping and not going identical? Quantitative meta-analysis of two response inhibition tasks. *Neuroimage*, *56*(3), 1655-1665.

Swift, H. J., Abrams, D., Lamont, R. A., & Drury, L. (2017). The risks of ageism model: How ageism and negative attitudes toward age can be a barrier to active aging. *Social Issues and Policy Review*, *11*(1), 195-231.

Uddin, L. Q., Molnar-Szakacs, I., Zaidel, E., & Iacoboni, M. (2006). rTMS to the right inferior parietal lobule disrupts self–other discrimination. *Social Cognitive and Affective Neuroscience*, *1*(1), 65-71.

Uddin, L. Q., Supekar, K., Amin, H., Rykhlevskaia, E., Nguyen, D. A., Greicius, M. D., & Menon, V. (2010). Dissociable connectivity within human angular gyrus and intraparietal sulcus: evidence from functional and structural connectivity. *Cerebral Cortex*, *20*(11), 2636-2646.

Uddin, L. Q., Nomi, J. S., Hébert-Seropian, B., Ghaziri, J., & Boucher, O. (2017). Structure and function of the human insula. *Journal of Clinical Neurophysiology*, *34*(4), 300.

Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping*, *30*, 829-858.

Verbruggen, F., & De Houwer, J. (2007). Do emotional stimuli interfere with response inhibition? Evidence from the stop signal paradigm. *Cognition and Emotion*, *21*(2), 391-403.

Verbruggen, F., & Logan, G. D. (2008). Response inhibition in the stop-signal paradigm. *Trends in Cognitive Sciences*, *12*(11), 418-424.

Wager, T. D., Sylvester, C. Y. C., Lacey, S. C., Nee, D. E., Franklin, M., & Jonides, J. (2005). Common and unique components of response inhibition revealed by fMRI. *Neuroimage*, *27*(2), 323-340.

Wang, X., Wu, Q., Egan, L., Gu, X., Liu, P., Gu, H., ... & Fan, J. (2019). Anterior insular cortex plays a critical role in interoceptive attention. *ELife*, *8*, e42265.

Watanabe, J., Sugiura, M., Sato, K., Sato, Y., Maeda, Y., Matsue, Y., ... & Kawashima, R. (2002). The human prefrontal and parietal association cortices are involved in NO-GO performances: an event-related fMRI study. *Neuroimage*, *17*(3), 1207-1216.

Weissenbacher, A., Kasess, C., Gerstl, F., Lanzenberger, R., Moser, E., & Windischberger, C. (2009). Correlations and anticorrelations in resting-state functional connectivity MRI: a quantitative comparison of preprocessing strategies. *Neuroimage*, *47*(4), 1408-1416.

Wessel, J. R. (2018). Prepotent motor activity and inhibitory control demands in different variants of the go/no-go paradigm. *Psychophysiology*, *55*(3), e12871.

Wheeler, M.E. & Fiske, S.T. (2005). Controlling racial prejudice: Social-cognitive goals affect amygdala and stereotype activation. *Psychological Science*, *16*, 56-63.

Wiese, H., Schweinberger, S. R., & Hansen, K. (2008). The age of the beholder: ERP evidence of an own-age bias in face memory. *Neuropsychologia*, *46*(12), 2973-2985.

Xu, J., Potenza, M.N., & Calhoun, V.D., Zhang, R., Yip, S.W., Wall, J.T., … & Moran, J.M. (2016). Large-scale functional network overlap is a general property of brain functional organization: Reconciling inconsistent fMRI findings from general-linear-model-based analyses. *Neuroscience & Biobehavioral Reviews*, *71*, 83-100.

Xun, X., Zuo, X., Wang, X., & Han, S. (2009). Do you feel my pain? Racial group membership modulates empathic neural responses. *Journal of Neuroscience*, *29*, 8525-8529.

Young, A. W., & Burton, A. M. (2018). Are we face experts?. *Trends in Cognitive Sciences*, *22*(2), 100-110.

Young, M. E., Sutherland, S. C., & McCoy, A. W. (2018). Optimal go/no-go ratios to maximize false alarms. *Behavior Research Methods*, *50*(3), 1020-1029.

Zebrowitz, L. A., Franklin Jr, R. G., Boshyan, J., Luevano, V., Agrigoroaei, S., Milosavljevic, B., & Lachman, M. E. (2014). Older and younger adults' accuracy in discerning health and competence in older and younger faces. *Psychology and Aging*, *29*(3), 454.

Zhang, R., Geng, X., & Lee, T. M. (2017). Large-scale functional neural network correlates of response inhibition: an fMRI meta-analysis. *Brain Structure and Function*, *222*(9), 3973-3990.

Ziaei, M., Persson, J., Bonyadi, M. R., Reutens, D. C., & Ebner, N. C. (2019). Amygdala functional network during recognition of own-age vs. other-age faces in younger and older adults. *Neuropsychologia*, *129*, 10-20.

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.