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Age Differences in Intuitive Moral Decision-Making: Associations with Inter-Network Neural Connectivity

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Abstract

Positions of power involving moral decision-making are often held by older adults (OAs). However, little is known about age differences in moral decision-making and the intrinsic organization of the aging brain. In this study, younger adults (YAs; n=117, M_{age}=22.11) and OAs (n=82, M_{age}=67.54) made decisions in hypothetical moral dilemmas and completed resting-state multi-echo fMRI scans. Relative to YAs, OAs were more likely to endorse deontological decisions (i.e., decisions based on adherence to a moral principle or duty), but only when the choice was immediately compelling or *intuitive*. By contrast, there was no difference between YAs and OAs in utilitarian decisions (i.e., decisions aimed at maximizing collective well-being) when the utilitarian choice was intuitive. Enhanced connections between the posterior medial core of the default network (pmDN) and the dorsal attention network, and overall reduced segregation of pmDN from the rest of the brain, were associated with this increased deontological-intuitive moral decision-making style in OAs. The present study contributes to our understanding of age differences in decision-making styles by taking into account the intuitiveness of the moral choice, and it offers further insights as to how age differences in intrinsic brain connectivity relate to these distinct moral decision-making styles in YAs and OAs.

Keywords: aging, moral cognition, decision-making, resting-state fMRI, functional connectivity

Older adults (OAs) constitute an increasingly large share of the population, with recent US population projections showing that, for the first time, OAs will outnumber children by the year 2034 (Vespa et al., 2020). OAs are also overrepresented in positions of higher power in both the government and the private sector relative to younger adults (YAs). A recent study showed that the average age at the time of hire among Fortune 500 and S&P 500 company CEOs was 58.3 years, an increase of almost 14 years over the last decade and a half (*Crist|Kolder Volatility Report*, 2019). Indeed, at the time of writing this manuscript, the average age of leaders of the United Nations Security Council Permanent Five is 62.4 years and that of Senators of the 117th United States Congress is 64.3 years. As a result, OAs are increasingly making decisions of significant moral consequence. However, while extensive research has focused on how normal aging contributes to changes in cognitive abilities such as working memory and attention that accompany altered structural and functional connections in the brain (Cabeza et al., 2018; Murman, 2015), much less is known about age differences in moral cognition.

The few extant studies investigating age differences in moral reasoning focus on two general theories of moral decision-making, *utilitarianism* and *deontology*. To illustrate, consider the well-known thought experiment in which a runaway trolley is on its way to kill five unaware railroad workers (Foot, 1967; Thomson, 1985). You have enough time to pull a lever and divert the trolley onto a different track, where there is only one worker. If you do so, the five would be saved, but the one would die. Is it morally permissible to pull the lever? Pulling the lever to kill the one and save the five is to decide in agreement with utilitarianism, which holds that one should strive to maximize well-being for most people, without partiality for anyone (Bentham, 1789; Mill, 1861). By contrast, not pulling the lever is to decide in agreement with deontology, which holds that one should always adhere to certain moral principles or duties—such as not to kill—even if doing so leads to less well-being overall (Kant, 1797).

Differences in these approaches to moral decision-making can influence a range of behaviors, and the outcome that follows from emphasizing a rigid moral code often differs from that in which overall well-being is favored. Some recent studies have observed age differences in moral reasoning styles, with OAs' moral decisions appearing to be more *deontological* or less *utilitarian* than YAs (Arutyunova et al., 2016; Hannikainen et al., 2018; McNair et al., 2019). This tendency to adhere to rule-based thinking may arise from a greater reliance on stored deontic knowledge. Indeed, neural regions associated with semantic rule retrieval are also activated while processing statements of personal, sacred values (Berns et al., 2012). Accordingly, differences in moral reasoning between OAs and YAs may reflect broad age-related changes in affective and cognitive processing that collectively influence the strategies that guide decision-making. For instance, emotional functioning and semantic memory are generally preserved with age (Carstensen et al., 2006; Mather, 2016), despite accompanying declines in cognitive domains such as working memory and executive control (Braver & West, 2008). When faced with difficult moral decisions, OAs may therefore rely more on immediate emotional reactions and stored semantic representations as opposed to lengthy, cognitively taxing deliberation. Indeed, this emotionally intuitive tendency has been observed among several non-moral decision-making studies with OAs (Lighthall, 2020; Mikels et al., 2010, 2013; Peters et al., 2008). With regard to moral reasoning, a recent study by McNair and colleagues showed that OAs not only endorse more deontological moral principles (i.e., moral idealism), but also experience more negative affect in response to utilitarian interventions wherein the death or misfortune of one individual benefits the majority. Importantly, heightened moral idealism and emotional response to such dilemmas were associated with the tendency for OAs to accept fewer interventions and rate these interventions as less acceptable (McNair et al., 2019). Thus, age differences in moral reasoning may reflect differing emotional appraisal and information processing styles that ultimately influence the decision-making process.

Unfortunately, the few studies mentioned thus far have primarily employed sacrificial dilemmas that fail to distinguish between intuitive and counterintuitive decisions—that is, dilemmas in which one of the alternatives elicits an automatic and unreflective response among most respondents (intuitive) versus a more controlled and reflective one (counterintuitive). Specifically, many moral dilemmas pit one intuitive and one counterintuitive option against each other, making it unclear whether the moral decision reflects utilitarian or deontological tendencies, or rather a response to the intuitiveness of the moral decision (Kahane, 2014; Kahane et al., 2012, 2015). When the intuitiveness of the moral decision is taken into account, a moral decision is no longer merely deontological or utilitarian, but rather one of four types: 1) deontological-intuitive, 2) deontological-counterintuitive, 3) utilitarian-intuitive, and 4) utilitarian-counterintuitive (see **Table 1**). In fact, previous findings that were allegedly due to differences in moral preferences turned out to be accounted for by differences in the intuitiveness of the moral decision (Rowley et al., 2018). As a result, accounting for intuitiveness may provide a more accurate perspective on differences in moral decision-making between YAs and OAs.

Table 1. Examples of moral dilemma vignettes by dilemma category

Deontological Intuitive (DI)	You are a doctor. You have five patients, each of whom is about to die due to a failing organ of some kind. You have another patient who is healthy. The only way that you can save the lives of the first five patients is to transplant five of this young man’s organs (against his will) into the bodies of the other five patients. If you do this, the young man will die, but the other five patients will live. Should you perform this transplant in order to save five of your patients? Option A [deontological-intuitive]: not performing the transplant Option B [utilitarian-counterintuitive]: performing the transplant
Utilitarian Intuitive (UI)	You are a waiter. You overhear one of your customers say that he is about to go to jail and that in his last forty-eight hours of freedom he plans to infect as many people as possible with HIV. You know him well enough to know that he is telling the truth and that he has access to many potential victims. You happen to know that he has a very strong allergy to poppy seeds. If he eats even one he will go into convulsions and have to be hospitalized for at least forty-eight hours. Should you cause this man to have a serious allergy attack in order to prevent him from spreading HIV? Option A [utilitarian-intuitive]: causing an allergy attack Option B [deontological-counterintuitive]: not causing an allergy attack

Note. The first moral dilemma is classified as “deontological intuitive” because the deontological decision in this scenario—not performing the transplant—is intuitive, in the sense of being immediately compelling to most people. Similarly, the second moral dilemma is classified as “utilitarian intuitive” because the utilitarian decision in this scenario—causing the man to have a serious allergy attack—is intuitive too, as most people find it immediately compelling (for more of these definitions, and their norming procedures, see Kahane et al., 2012).

Previous work with YAs shows that considering the intuitiveness of decisions changes how we think about extant dual-process models of moral reasoning, which distinguish between a rapid, prepotent emotional response and a slower, more deliberate cost-benefit analysis (Evans, 2008; Greene, 2007; Kahneman, 2013). Prevailing psychological accounts suggest that moral dilemmas initially evoke a negative social-emotional reaction that disapproves of committing moral violations (i.e., deontological), although utilitarian decisions can still be reached by recruiting executive control processes to reconcile a harmful action with a helpful outcome, ultimately overriding this conflict (Greene et al., 2004, 2008). These associations are questioned, however, when the *counterintuitive* (controlled) response to a dilemma is deontological. In these cases, a deontological response is considered to be the conflicting option to a more intuitive utilitarian response, often in cases where less severe moral violations (e.g., lying) are deemed permissible. Recently proposed adjustments to the dual-process model suggest that fast and effortless intuitive responses can be either deontological or utilitarian, but still undergo subsequent deliberation to confirm the intuition or consider conflicting options (Bago & De Neys, 2019). Given that OAs have been shown to exhibit enhanced emotional reactivity to utilitarian interventions but also concomitant changes to executive control abilities, these effects may interact to uniquely influence moral decision-making as a function of intuitiveness. For instance, OAs may be more likely to exhibit a response bias when the deontological response is intuitive, but show no difference compared to YAs when the deontological response is counterintuitive. Thus, a first objective of the current study is to help to clarify this issue.

Research on the neuropsychological mechanisms that underlie age differences in moral reasoning is also lacking, as most neuroimaging investigations have been conducted exclusively with YAs. Nevertheless, these studies with YAs have consistently identified activity within the default network (DN) as relevant to moral reasoning (Pujol et al., 2008; Reniers et al., 2012; Sevinc & Spreng, 2014), presumably because of this network's association with internally-directed, self-referential processing (Andrews-Hanna et al., 2014), social cognition (Mars et al., 2012), and the generation of past, future, and counterfactual episodic simulations (Schacter et al., 2012, 2015; De Brigard & Parikh, 2019). For instance, Kahane et al. (2012) found increased activation in the posterior cingulate cortex (PCC) and right temporo-parietal junction—regions within the posterior DN—when deontological moral decisions were made. Accordingly, recruitment of the DN during moral decision-making has been suggested to facilitate perceptions of the moral self, social norms, and the simulation of possible outcomes when deciding how to act in response to a dilemma (Cushman et al., 2013; Ellemers et al., 2019). Moreover, during this deliberation, top-down executive control networks such as the frontoparietal control network (FPCN), dorsal attention network (DAN), and salience network (SN) help to guide introspective processing by monitoring and maintaining task goals throughout the decision-making process (Dixon et al., 2018), as well as regulating self-generated thoughts and emotional response (Andrews-Hanna et al., 2014). The anterior cingulate cortex (ACC), a node within the SN, has been implicated in conflict detection among cognitive and emotional responses during deliberation on difficult moral dilemmas, consequently recruiting top-down executive regions in the FPCN and DAN to deploy conflict control operations (Greene et al., 2004). In fact, an investigation of large-scale brain networks during moral processing demonstrated early engagement of SN during the detection of moral information, and later modulation of downstream DN and FPCN interactions in the service of complex moral reasoning processes (Sevinc et al., 2017). Thus, moral reasoning, like other higher-level cognitive operations (e.g., mentalizing), stems from functional communication within the DN, as well as between the DN and executive control networks.

Similar findings have been observed among the few extant task-based neuroimaging studies on moral reasoning in healthy OAs. OAs show increased activation in DN regions during deliberation on moral dilemmas (Chiong et al., 2013; Moran et al., 2012), as well as directed, Granger causal influence from nodes in the SN (ACC and frontoinsular cortex) to nodes in the default (PCC and medial prefrontal cortex) and executive control (middle frontal gyrus and intraparietal sulcus) networks (Chiong et al., 2013). These inter-network interactions are also predictive of behavioral responses to moral dilemmas. For instance, compared to OAs with a behavioral variant frontotemporal dementia, healthy OAs display greater activation in the PCC and enhanced directed connectivity of the SN with the PCC during moral reasoning, both associated with a reduced likelihood of endorsing utilitarian decisions (Chiong et al., 2013). Hence, findings within YAs and OAs both suggest network-level interactions that associate with moral reasoning styles, although to our knowledge no study has explicitly evaluated how such interactions might interplay with age differences in moral decisions.

Research on the intrinsic functional organization of the brain during resting-state provides further insight into how neural network architecture co-varies with shifts in cognition. Accumulating evidence suggests that aging is associated with decreased intra-network and increased inter-network functional connectivity during rest and task performance, which collectively contribute to less segregated, or more integrated, neural networks in OAs (Chan et al., 2014; Geerligs et al., 2014, 2015; Grady et al., 2016; Setton et al., 2021; Spreng et al., 2016). The consistency of these network differences during both resting-state and task-based conditions aligns with extant evidence showing that resting-state connectivity represents an intrinsic functional architecture that constrains task-evoked activation and network interactions (Chan et al., 2017; Cole et al., 2014, 2016). Indeed, both YAs and OAs exhibit strong correlations of functional connectivity between rest and task, although OAs may have less consistent network organizations due to reduced segregation at rest that is further exacerbated during task performance (Hughes et al., 2020). The reliability of resting-state fMRI, as well as the relative simplicity of this method compared to more complex task-based paradigms, has proved to be a valuable method for understanding age differences in the brain's functional architecture (Chan et al., 2014; Ferreira & Busatto, 2013; Setton et al., 2021).

Age differences in the functional architecture of the brain are particularly evident in DN connectivity, where reduced intra-network connections have been shown to accompany enhanced inter-network connections with the FPCN (Setton et al., 2021; Spreng & Turner, 2019) and DAN (Spreng et al., 2016). According to the default-executive coupling hypothesis of aging (DECHA; Turner & Spreng, 2015), these changes in neural communication facilitate changing cognitive styles in OAs, such as increased reliance of goal-directed cognition on semantic knowledge and autobiographical experience (Brashier et al., 2017; Spreng et al., 2018; Spreng & Schacter, 2012; Spreng & Turner, 2019). Given the contribution of DN connectivity to moral reasoning, we hypothesize that enhanced resting-state coupling of the DN with executive control and attention networks also predicts differences in utilitarian and deontological tendencies between YAs and OAs. That is, reduced segregation of the DN and enhanced integration with other networks may reflect an intrinsic network architecture underlying the behavioral tendency for OAs to deliberate less on the overall value of utilitarian decisions and instead defer to a semantically represented moral code. Evidence for such an effect would suggest that age differences in neural network connectivity correspond with differences in moral decision-making that accompany a less fluid, and more crystallized, cognitive style in OAs. A similar model was recently proposed to account for age differences in financial decision bias. Enhanced inter-network connectivity of the DN (as proposed by DECHA), coupled with structural and functional decline of the prefrontal cortex, may facilitate financial decision-making biases in OAs by increasing reliance on subjective, experienced-based mental representations and weakening cognitive control processes (McCormick et al., 2019). Whether a related neurobiological process underlies shifts in moral reasoning remains unexplored.

Thus, a second aim of the current study is to evaluate resting-state functional connectivity in YAs and OAs in order to determine the degree to which intra- and inter-network connectivity of the DN is associated with age-related differences in moral decision-making. In our study, participants made moral decisions in sixteen hypothetical moral dilemmas about the extent to which they would engage in a certain action through an online survey; in a separate session, all participants completed two 10-minute resting-state multi-echo fMRI scans. Based on the aforementioned findings (McNair et al., 2019), we expected OAs to make more deontological moral decisions than YAs, but only when the deontological response is considered more intuitive (Kahane et al., 2012). Additionally, we also expected that, relative to YAs, OAs would exhibit reduced segregation among networks as indicated by both decreased intra-network connectivity and increased inter-network connectivity. Finally, we expected that these differences in network architecture, particularly for the default, dorsal attention, and executive control networks, would predict age differences in deontological moral decisions.

Methods

Participants

Participants were recruited from the greater Ithaca, NY area through flyers, word of mouth, a local community email list-serv, and from a database of OAs who had previously participated in studies at Cornell University as part of a larger ongoing project. Participants were screened to rule out individuals with a history of neurological or other medical illness known to impact cognition, acute or chronic psychiatric illness, those undergoing current or recent treatment with psychotropic medication, and those who had experienced significant changes to health status within 3 months of the eligibility interview. YAs and OAs were screened for depressive symptoms using the Beck Depression Inventory-II (BDI-II; Beck et al., 1996) or the Geriatric Depression Scale (GDS; Yesavage et al., 1982), respectively. Those who scored at or above the range for “moderate depression” (BDI-II > 27/63 or GDS > 19/30) were not included. Participants were also administered the Mini-Mental State Examination (MMSE; Folstein et al., 1975) to rule out mild cognitive impairment or sub-clinical dementia. Participants with MMSE scores below 27/30 were excluded if fluid cognition scores (Gershon et al., 2013) also fell below the age-adjusted 25th national percentile. The final sample included 117 YAs (M_{age} = 22.11 years, SD = 3.06, age range = [18, 34]; 68 female, 49 male) and 82 OAs (M_{age} = 67.54 years, SD = 5.74, age range = [60, 83]; 45 female, 37 male; see **Table 2**). All participants were right-handed with normal or corrected-to-normal vision. Procedures were administered in compliance with the Institutional Review Board at Cornell University and all participants provided written informed consent.

Table 2. Group means and standard deviations (in parentheses) for demographics and psychometric scores.

	Younger Adults	**Older Adults**
Number of participants	117	82
Age in years	22.11 (3.06)	67.54 (5.74)
Gender (female/male) $^{n.s.}$	68/49	45/37
Years of education***	15.14 (1.86)	17.74 (2.98)
Race***	75 White 23 Asian 7 Black or African American 5 Other 2 White & American Indian or Alaska Native 2 White & Asian 1 White & Asian & Other 2 NA's	79 White 1 Black or African American 1 Other 1 NA
Ethnicity*	96 Not Hispanic or Latino 15 Hispanic or Latino 6 NA’s	77 Not Hispanic or Latino 1 Hispanic or Latino 4 NA's
Mini-Mental State Exam***	29.15 (1.08)	28.46 (1.25)
NIH Fluid Cognition National Percentile***	66.22 (27.31)	44.86 (20.88)
NIH Crystallized Cognition National Percentile***	90.17 (13.79)	94.49 (10.97)
Behavioral Inhibition System (BIS) scale***	21.97 (3.51)	19.80 (3.60)

Significance annotation, $^{n.s.}$ $p > .05$ * $p < .05$, ** $p < .01$, *** $p < .001$, unadjusted; Chi-squared test with Yates’ continuity correction for *Gender*, *Race* and *Ethnicity*, and Wilcoxon rank sum test with continuity correction for other measures.

Data Collection Procedures

As mentioned, the final sample of YAs and OAs reported in this study completed the behavioral tasks and resting-state fMRI scans as part of a larger ongoing project. Participants completed the moral decision-making task online. The median time between the moral decision-making task and the resting-state fMRI scan was 30.5 days. Participants also completed the Behavioral Inhibition System (BIS) scale (Carver & White, 1994) through an online survey and the NIH Cognition Toolbox (Weintraub et al., 2014) in a laboratory session prior to the scanning session.

Moral decision-making task

Recent moral research studies have shown that certain moral dilemmas are more likely than others to induce a deontological or utilitarian response. A *deontological intuitive* (DI) dilemma vignette tends to induce moral decisions more in line with deontology, while a *utilitarian intuitive* (UI) dilemma vignette tends to induce moral decisions that are more in line with utilitarianism (see **Table 1**; Kahane, 2014; Kahane et al., 2012). Participants read a collection of these moral dilemma vignettes, which included 8 DI dilemmas and 8 UI dilemmas from Kahane et al. (2012), and indicated the degree to which they believed that they should perform an action proposed in each scenario on a scale of 0-6 (0 = *I don't believe that I should*; 6 = *I strongly believe that I should*; see **Table S1** for the complete list of vignettes). The proposed action was, in some vignettes, deontological, and in others, utilitarian. To allow for cross-vignette comparison, we reverse-coded the ratings of certain vignettes to obtain a *moral decision index* for each moral dilemma, with a higher index indicating a more utilitarian choice. In other words, for each DI dilemma where intuition was biased towards a deontological moral decision, a higher index reflected a disposition that was more utilitarian and, thus, less intuitive (or more counterintuitive); for UI dilemmas where intuition was biased towards a utilitarian moral decision, a higher index reflected a disposition that was more utilitarian and, thus, more intuitive. For simplicity, we refer to deontological moral decisions in DI dilemmas as "deontological-intuitive" and utilitarian moral decisions in UI dilemmas as "utilitarian-intuitive" (see **Table 1**).

Resting-state fMRI scan

Imaging data were acquired on a 3T GE Discovery MR750 scanner (General Electric, Milwaukee, United States) with a 32-channel receive-only phased-array head coil at the Cornell Magnetic Resonance Imaging Facility in Ithaca, NY. Anatomical scans were acquired during one

5 min 25 s run with 2 × acceleration with sensitivity encoding using a T1-weighted volumetric MRI magnetization-prepared rapid gradient echo (TR = 2530 ms; TE = 3.4 ms; TI = 1100 ms; FA = 7°; 1.0 mm isotropic voxels, 176 slices). Two 10 min 6 s resting-state fMRI scans were acquired using a multi-echo echo planar imaging (ME-EPI) sequence with online reconstruction (TR = 3000 ms; TEs = 13.7, 30, 47 ms; FA = 83°; matrix size = 72 × 72; FOV = 210 mm; 46 axial slices; 3.0 mm isotropic voxels; slice order = inferior-superior interleaved; 2.5 × acceleration with sensitivity encoding). Participants were instructed to lay still with their eyes open, breathing and blinking normally in the darkened scanner bay.

Processing. For a comprehensive review of the processing pipeline, including individualized parcellation methods (see below), readers are directed to Setton et al. (2021). Anatomical images were skull stripped using the default parameters in FSL BET (Smith, 2002). Brain-extracted anatomical and functional images were submitted to multi-echo independent components analysis (ME-ICA; version 3.2 beta; https://github.com/ME-ICA/me-ica; Kundu et al., 2012, 2013). ME-ICA relies on the TE-dependence model of BOLD signal to better approximate T2* in every voxel and differentiate BOLD signal from non-BOLD sources of noise. Prior to TE-dependent denoising, time series data were minimally pre-processed: the first 4 volumes were discarded, matrices were computed for de-obliquing, motion correction, and anatomical-functional coregistration, and each TE was brought into spatial alignment. Anatomical-functional coregistration was driven by the T2* map which delineates gray matter and cerebrospinal fluid compartments more precisely than raw EPI images (Kundu et al., 2017; Speck et al., 2001). This is a critical consideration in aging research given that structural changes, such as enlarged ventricles and greater subarachnoid space, blur the boundary between them. TEs were then optimally combined and de-noised.

Post-processing quality assessment was performed on the de-noised time series in native space to identify and exclude participants with unsuccessful coregistration, residual noise (in-scanner motion >3 mm coupled with de-noised time series showing DVARS >1; Power et al., 2012), poor temporal signal to noise ratio (tSNR; < 50), or fewer than 10 retained BOLD-like components. The de-noised ICA coefficient sets in native space, optimized for functional connectivity analyses (Kundu et al., 2013), were used in subsequent steps. We refer to these as multi-echo functional connectivity (MEFC) data. Computing functional connectivity with approximately independent coefficients rendered global signal regression unnecessary (Spreng et al., 2019).

Resting-State Functional Connectivity (RSFC) Parcellation. Whole brain RSFC matrices were initialized with the 200-parcel Schaefer atlas (Schaefer et al., 2018), corresponding to 7 RSFC-defined networks (Yeo et al., 2011). Participant-specific functional connectomes were then computed with the Group Prior Individual Parcellation algorithm (GPIP; Chong et al., 2017; Mwilambwe-Tshilobo et al., 2019; Setton et al., 2021). To do so, MEFC data were mapped to a common cortical surface for each participant using FreeSurfer (Fischl, 2012). To maximize alignment between intensity gradients of structural and functional data (Greve & Fischl, 2009), MEFC data were first linearly registered to the T1-weighted image by run. The inverse of this registration was used to project the T1-weighted image to native space and resample the MEFC data onto a cortical surface (fsaverage5) with trilinear volume-to-surface interpolation. Once on the surface, runs were concatenated and MEFC data at each vertex were normalized to zero mean and unit variance. We generated subject-specific functional parcellations to examine individual differences in functional brain network organization with a group sparsity prior approach (GPIP; Chong et al., 2017). Relative to group-based parcellations, GPIP has been shown to improve homogeneity of resting activity within parcels and delineation between regions of functional specialization (Chong et al., 2017). This approach therefore enables a more accurate estimation of subject-specific individual functional areas (Chong et al., 2017), and may be better suited to detect RSFC associations with behavior (Kong et al., 2021; Mwilambwe-Tshilobo et al., 2019). We extracted the resulting MEFC data from each parcel and computed the Pearson correlation between each pair, resulting in a 200 × 200 functional connectivity matrix (Ge et al., 2017). The canonical Fisher's r-to-z transformation was then applied to account for variation in MEFC data degrees of freedom, or the number of de-noised ICA coefficients, across individuals (Kundu et al., 2013).

We focused on DN connectivity patterns, including inter-network connections of the DN with the other large-scale distributed networks (e.g., FPCN, DAN, and SN; see **Figure 1a**). Past research has identified two functional cores within the DN, the medial prefrontal cortex (mPFC) in the anterior medial portion of the DN (amDN), and the precuneus and posterior cingulate cortex (precuneus/PCC) in the posterior medial part of the DN (pmDN) (Buckner et al., 2008; Fransson & Marrelec, 2008; Utevsky et al., 2014). Although age-related activity differences in the DN have been reported for the network as a whole (Damoiseaux et al., 2008; Grady et al., 2006; Persson et al., 2007), there is also divergence between the functional cores of the DN and the network at large in terms of connectivity patterns (Grady et al., 2010; Utevsky et al., 2014). Accordingly, in addition to treating the DN as a whole, homogeneous network, we also assessed how amDN and pmDN individually coupled with executive control networks. To this end, we visually inspected the Schaefer parcellation scheme and assigned medial parcels of the DN to anterior and posterior subregions (see **Figure 1b** and **Figure S1**).

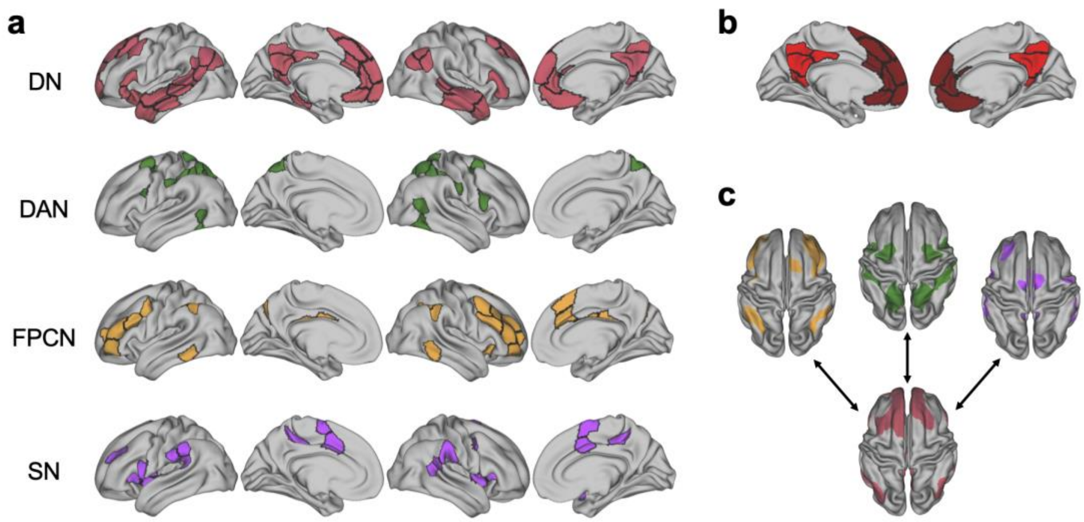

Figure 1. Resting-state functional connectivity (RSFC) network analysis. **a,** primary networks and corresponding nodes assessed in the current study, including the default network (DN; red), dorsal attention network (DAN; green), frontoparietal control network (FPCN; orange), and salience network (SN; magenta). **b,** nodes assigned to the posterior-medial (scarlet) and the anterior-medial (maroon) DN. **c,** assessments of inter-network connectivity focused on DN coupling strength with executive control and attention networks. We also evaluated whole-brain network segregation of the DN (see **Methods**).

For each participant, we computed three types of network connectivity measures: 1) intra-network connectivity levels, 2) inter-network connectivity levels, and 3) a segregation index per network of interest. The intra-network connectivity level of a selected network (e.g., *intra-DN*) was obtained by averaging the Fisher-transformed correlation coefficients between all pairs of nodes of that network. The inter-network connectivity of two selected networks (e.g., *DN-FPCN*) was obtained by averaging the Fisher-transformed correlation coefficients between all pairs of nodes, wherein one node belonged to one network and the other node belonged to the other network. Finally, the segregation index of a selected network was computed as $(\overline{Z_{intra}} -$

$\overline{Z_{inter}})/\ \overline{Z_{intra}}$, where $\overline{Z_{intra}}$ stands for the intra-network connectivity level of the selected network and $\overline{Z_{inter}}$ stands for the averaged inter-network connectivity levels between the selected network and all other networks (Chan et al., 2014). As such, a higher segregation index of a network indicates more connections within the given network than with other networks. For this calculation we included all seven networks originally defined by Yeo et al. (2011).

Analytic strategy

We first examined the relationship between age group and moral decision-making by fitting linear mixed-effects models (LMMs) to predict participants' moral decision index (0 to 6) on each dilemma using the 'lme4' package (Bates et al., 2015) in R (R Core Team, 2020). Categorical variables including age group (YA = -0.5, OA = 0.5) and dilemma vignette category (DI = -0.5, UI = 0.5) were coded using deviation coding in order to characterize the main effect of each predictor in cases of interaction. We applied stepwise hierarchical regressions to examine if independent variables, including age group, dilemma vignette category, gender, BIS scale, fluid cognition national percentile, and crystallized cognition national percentile, accounted for a proportion of variation in participants' moral decision index. The maximal feasible random effects structure was then determined using the 'buildmer' package (Voeten, 2021) in R (see **Table S2** for model comparisons). The 'emmeans' package (Lenth, 2020) in R was used to compute the estimated marginal means and visualize interactions. In all LMMs, significance for fixed effects was assessed using Satterthwaite approximations to degrees of freedom (Satterthwaite, 1941), and 95% confidence intervals around beta-values were computed using parametric bootstrapping with 1,000 simulations. Family-wise error (FWE) rate was controlled using the Bonferroni method in each analysis step.

Second, we examined the relationship between age group and DN-connectivity by running separate linear regressions for each connectivity measure with a predictor of age group. Following recent findings (Ritchie et al., 2018; Weis et al., 2020), we controlled for gender as a covariate of no interest in all regression models that included resting-state connectivity as either the dependent variable or a predictor.

Third, we examined the relationship between moral decision index and DN-connectivity. Separately for DI and UI dilemmas, we fitted LMMs that used a single connectivity measure to predict participants' moral decisions, controlling for dilemma vignettes and individual participants as random intercepts. Upon identifying network measures that were associated with moral decision-making styles, we further investigated whether those DN-connectivity measures predicted participants' moral decisions while controlling for the effect of age group.

Finally, as an exploratory analysis, we examined the extent to which the selected DN-connectivity measures potentially account for differences in moral decisions of YAs and OAs through mediation (Baron & Kenny, 1986). The nonparametric bias-corrected and accelerated (BCa) confidence intervals (DiCiccio & Efron, 1996) of the indirect effects were computed using the 'coxed' package (Kropko & Harden, 2020) in R with 10,000 bootstrapped samples and significance levels were estimated using BCa intervals with different confidence levels α.

Results

OAs made more deontological-intuitive moral decisions than YAs

Model comparisons indicated a best fixed effects structure that included age group, dilemma vignette category, and their interaction, and a maximal feasible random effects structure that included a random intercept for each participant and each dilemma vignette as well as a random slope of category for each participant and a random slope of age group for each dilemma vignette (see **Table S2**). As expected, dilemma category had a significant effect on moral decisions, with all participants making more utilitarian moral decisions (i.e., higher moral decision index) in UI dilemmas than in DI dilemmas (b = 2.67, SE = 0.37, df = 15, t = 7.28, p < .0001, 95% CI = [1.95, 3.43]; see **Figure S2** and **Table S3**). In regard to age effects, OAs' moral decisions were more deontological than YAs' overall (b = -0.37, SE = 0.16, df = 21, t = -2.26, p =

.0345, 95% CI = [-0.72, -0.04]); however, this effect was qualified by a significant interaction of dilemma category and age group (b = 1.19, SE = 0.32, df = 18, t = 3.75, p = .0015, 95% CI = [0.56, 1.82]). This interaction of dilemma category and age group was due to OAs making more deontological-intuitive moral decisions relative to YAs ($EMM_{DI, OA-YA}$ = -0.97, SE = 0.24, df = 24, t = -4.01, p = .0005, 95% CI = [-1.46, -0.47]), whereas age groups did not differ in their decisions in UI dilemmas ($EMM_{UI, OA-YA}$ = 0.22, SE = 0.22, df = 16, t = 1.03, p = .3185, 95% CI = [-0.24, 0.68]; see **Figure 2** and **Table S3**). Because the difference in moral decision-making between YAs and OAs was only found for DI dilemmas but not for UI dilemmas, subsequent analyses separated the two dilemma categories.

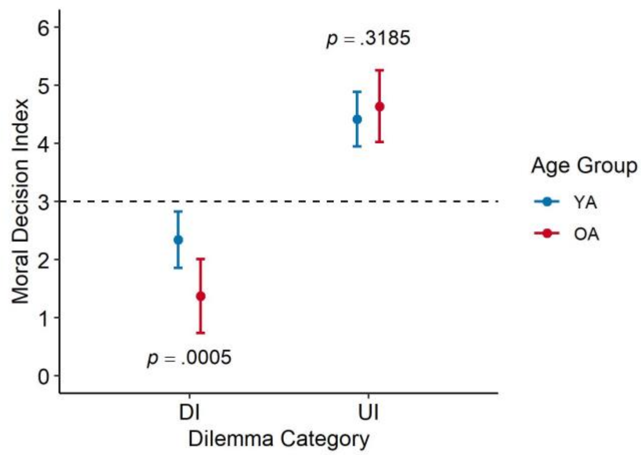

Figure 2. Estimated marginal means of moral dilemma index (0-6) by *dilemma category* (DI / UI) and *age group* (YA / OA). A lower moral decision index indicates a more deontological moral decision, and a higher index indicates a more utilitarian moral decision. A difference in moral decisions between YAs (blue) and OAs (red) was found for DI dilemmas but not for UI dilemmas. Error bars indicate 95% confidence intervals.

OAs exhibited greater inter-network connectivity and lower network segregation

We next assessed differences in connectivity measures between YAs and OAs, focusing on the DN and executive control and attention networks. Compared to YAs, OAs exhibited decreased connectivity levels within the DN (b = -0.17, SE = 0.05, t = -3.44, p = .0007, FWE-corrected p = .0099, 95% CI = [-0.27, -0.07]), as well as increased inter-network connectivity levels with the DAN (b = 0.23, SE = 0.04, t = 5.17, p < .0001, FWE-corrected p < .0001, 95% CI = [0.14, 0.32]) and SN (b = 0.18, SE = 0.05, t = 3.50, p = .0006, FWE-corrected p = .0081, 95% CI = [0.08, 0.28]). The connectivity level between DN and FPCN was also greater in OAs than in YAs, although this effect did not survive FWE rate correction (b = 0.08, SE = 0.04, t = 1.98, p = .0488, FWE-corrected p = .6836, 95% CI = [0.00, 0.16]; see **Figure 3** and **Table S4**; see also **Figure S3**). These results generally held for the core midline regions of the DN as well: OAs showed greater inter-network connectivity levels of amDN-DAN (b = 0.23, SE = 0.05, t = 4.79, p < .0001, FWE-corrected p < .0001, 95% CI = [0.13, 0.32]), pmDN-DAN (b = 0.24, SE = 0.06, t = 4.22, p < .0001, FWE-corrected p = .0005, 95% CI = [0.13, 0.36]), and pmDN-SN (b = 0.30, SE = 0.07, t = 4.32, p < .0001, FWE-corrected p = .0003, 95% CI = [0.16, 0.44]). Finally, OAs showed lower segregation indices of DN (DN_{seg}; b = -0.16, SE = 0.02, t = -7.18, p < .0001, FWE-corrected p < .0001, 95% CI = [-0.21, -0.12]), amDN (amDN_{seg}; b = -0.08, SE = 0.01, t = -6.09, p < .0001, FWE-corrected p < .0001, 95% CI = [-0.11, -0.05]), and pmDN ($pmDN_{seg}$; b = -0.10, SE = 0.01, t = -6.38, p < .0001, FWE-corrected p < .0001, 95% CI = [-0.12, -0.07]), suggesting that the DN was generally more functionally integrated with other networks in OAs than in YAs.

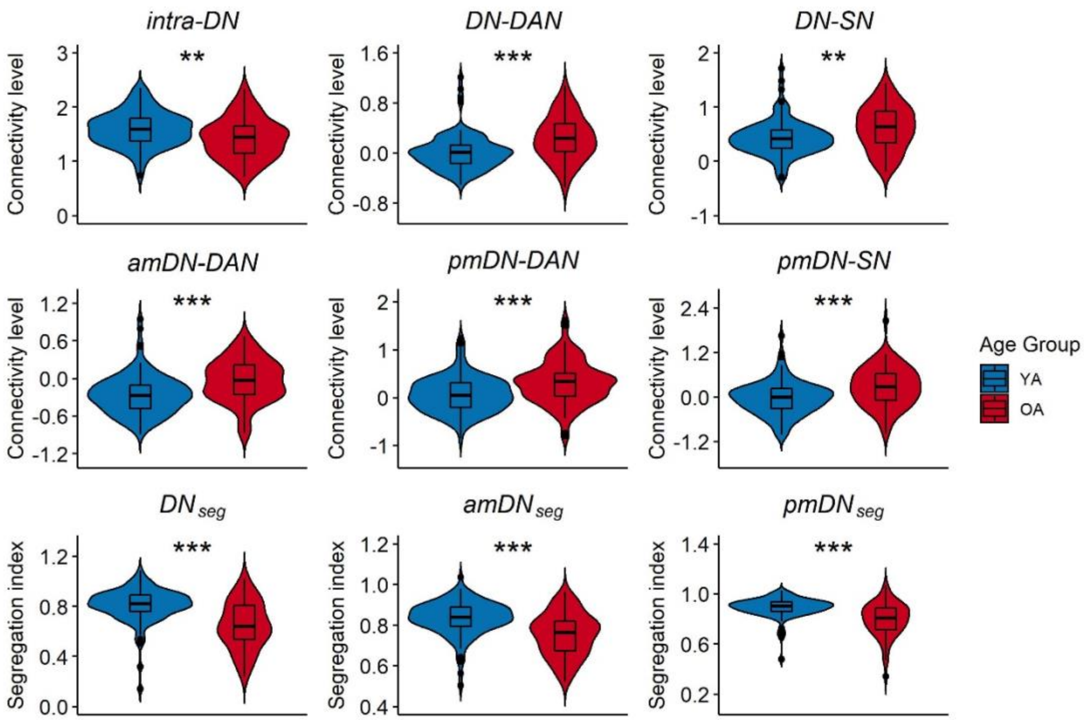

Figure 3. Violin plots of connectivity measures of the default and executive control networks. OAs (red) compared to YAs (blue) showed lower intra-network connectivity levels and higher inter-network connectivity levels, as well as lower functional segregation of DN regions. Connectivity is represented as Fisher's z-transformed correlational coefficients. *DN*, default network; *amDN*, anterior-medial DN; *pmDN*, posterior-medial DN; *FPCN*, frontoparietal control network; *DAN*, dorsal attention network; *SN*, salience network; *intra-Network*, connectivity level within *Network*; *Network A-Network B*, connectivity level between *Network A* and *Network B*; $Network_{seg}$, segregation index of *Network*. Significance annotation, * $p < .05$, ** $p < .01$, *** $p < .001$, FWE-corrected.

DN connectivity and segregation were associated with deontological-intuitive moral decision-making

In all participants, moral decision index in DI dilemmas was associated with the inter-network connectivity of pmDN-DAN ($b = -0.69$, $SE = 0.18$, $t = -3.72$, $p = .0003$, FWE-corrected *p* = .0037, 95% CI = [-1.05, -0.33]) and pmDN-SN (*b* = -0.47, *SE* = 0.16, *t* = -3.05, *p* = .0026, FWE-corrected *p* = .0364, 95% CI = [-0.78, -0.17]), as well as the segregation index of pmDN ($pmDN_{seg}$; *b* = 3.00, *SE* = 0.67, *t* = 4.48, *p* < .0001, FWE-corrected *p* = .0002, 95% CI = [1.69, 4.31]) and that of the whole DN (DN_{seg}; *b* = 1.48, *SE* = 0.44, *t* = 3.38, *p* = .0009, FWE-corrected *p* = .0124, 95% CI = [0.62, 2.34]). The associations between all other connectivity measures and moral decision index did not survive FWE correction (see **Table S5**). As such, these four connectivity measures (*pmDN-DAN*, *pmDN-SN*, DN_{seg}, and $pmDN_{seg}$) showed divergence in RSFC levels between YAs and OAs (see **Figure 3**) and, importantly, were also predictive of deontological-intuitive moral decision-making.

To evaluate the strength of these associations above and beyond the effect of age, we next assessed models with both age group and connectivity measures as predictors of moral decision index. The effect of age group remained significant in all four LMMs, with OAs' decisions being more deontological-intuitive than those of YAs (*b*s < -0.83, *t*s < -5.24, *p*s < .0001, FWE-corrected *p*s < .0001; see **Table S5**). Additionally, more deontological-intuitive moral decisions were associated with a higher *pmDN-DAN* (*b* = -0.39, *SE* = 0.18, *t* = -2.16, *p* = .0321, FWE-corrected *p* = .1285, 95% CI = [-0.73, -0.01]) and lower $pmDN_{seg}$ (*b* = 1.51, *SE* = 0.69, *t* = 2.18, *p* = .0306, FWE-corrected *p* = .1222, 95% CI = [0.15, 2.88]; see **Figure 4**), although neither pmDN-related effects survived an additional conservative Bonferroni FWE correction for multiple comparisons (four LMMs). For both *pmDN-DAN* and $pmDN_{seg}$, we also fitted LMMs that additionally included the interaction term of age group and either connectivity measure, all of which confirmed the significant main effects of both pmDN-related connectivity measures (*p*s < .04) and no modulation by age group (*p*s > .55). Finally, we found no evidence for any connectivity measure reliably predicting participant's moral decisions in UI dilemmas (see **Table S5**).

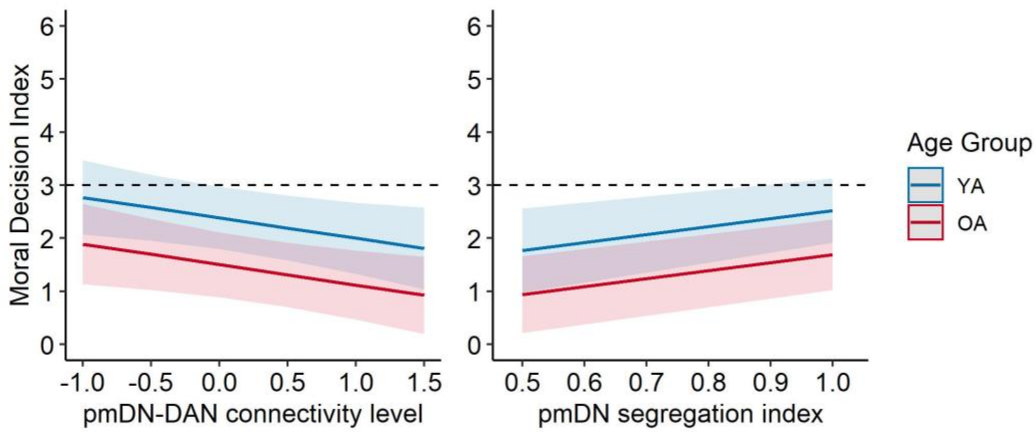

Figure 4. Estimated moral decision index in DI dilemmas for YAs and OAs with different levels of pmDN-DAN connectivity and pmDN segregation. In DI dilemmas, a lower moral decision index indicates a more deontological and more intuitive moral decision. Shaded bands indicate 95% confidence intervals.

Preliminary mediation analysis

The findings presented thus far demonstrate statistically independent associations of age group and inter-network functional connectivity with moral decisions on DI dilemmas, which satisfy the three conditions necessary to test an indirect effect (Baron & Kenny, 1986; Madden et al., 2008): age-related differences in moral decision-making, age-related differences in inter-network neural connectivity, and inter-network connectivity that significantly accounts for variance in moral decision-making after including age group in the regression model. Given these results, it is possible that age group may indirectly associate with the moral decision index via inter-network connectivity. However, readers are reminded that the cross-sectional nature of our study precludes proper causal interpretation, and therefore we only present this mediation analysis as a preliminary assessment that warrants future examination in a longitudinal sample. Using 10,000 bootstrapped samples, we found that the tendency of OAs to make more deontological-intuitive moral decisions was associated with decreased $pmDN_{seg}$ (indirect effect =

-0.14, p = .0284, 95% BCa CI = [-0.31, -0.01]) and increased *pmDN-DAN* (indirect effect = -0.09, p = .0336, 95% BCa CI = [-0.25, -0.01]) among OAs (see **Figure 5** and **Table 3**; see also **Figure S4** and **Table S6**). Finally, we conducted the same mediation analysis while statistically controlling for different covariates such as *Gender* and BIS scale, but we found little difference in results (see **Table S6**).

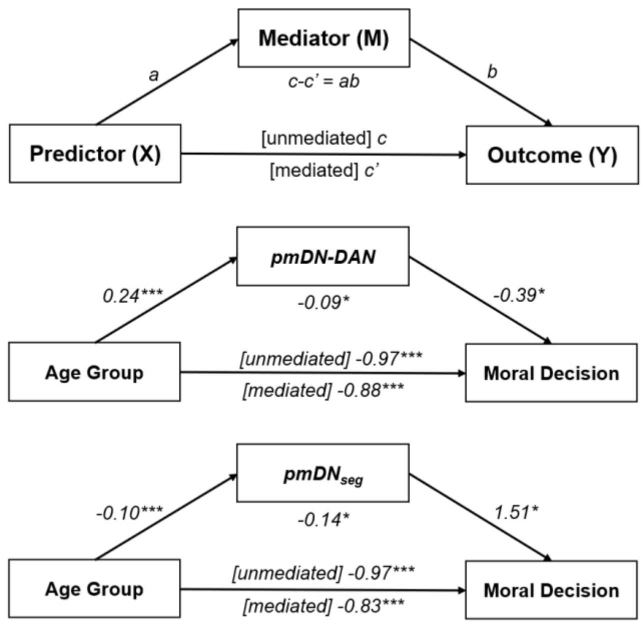

Figure 5. Mediation analysis. Both pmDN-DAN connectivity (middle) and pmDN functional segregation (bottom) associate with age-related differences in deontological-intuitive moral decision-making. Significance levels were estimated using bias-corrected and accelerated (BCa) intervals with different confidence levels α (see **Figure S4**). Significance annotation, * $p < .05$, ** $p < .01$, *** $p < .001$.

Table 3. The indirect effect of age group on moral decision index via pmDN-DAN connectivity and pmDN segregation

Mediator	Effect	Estimate	*p*	95% BCa CI
pmDN-DAN	*a*b*	-0.09	.0336	[-0.25, -0.01]
	PM	0.09	.0300	[0.01, 0.27]
$pmDN_{seg}$	*a*b*	-0.14	.0284	[-0.31, -0.01]
	PM	0.15	.0251	[0.02, 0.34]

Note. See **Figure 5** for mediation models. Effect estimates were computed using results from our previous analysis steps. *p* values and 95% CIs were estimated using the nonparametric bias-corrected and accelerated (BCa) confidence intervals with 10,000 bootstrapped samples (see **Figure S4**). *PM*, proportion mediated, calculated as $PM = a*b / c$.

Discussion

Until now, it was unclear whether and how differences in intuitive moral decision-making between YAs and OAs are associated with the functional architecture of the brain. Consistent with previous findings (e.g., McNair et al., 2019), we show here that OAs tend to make more deontological decisions than YAs, but we also find that this difference only occurs for deontological intuitive (DI) moral dilemmas, while no difference was found for utilitarian intuitive (UI) dilemmas. Additionally, we also found that this behavioral effect is predicted by lower whole-brain segregation of the DN. To our knowledge, the present study provides the first evaluation of differential network connectivity associated with differences in moral decision-making in YAs and OAs, thereby expanding our understanding of the diversity of neurocognitive changes that accompany aging.

To examine how normal aging may contribute to changes in moral cognition, we assessed nearly two hundred YAs and OAs on a diverse set of hypothetical moral dilemmas. We found that, across all dilemmas, OAs tended to make moral decisions that are more deontological than those made by YAs, which is consistent with recent findings (McNair et al., 2019). A notable difference is that the moral dilemmas employed in our study had been previously classified by Kahane et al. (2012) as more likely to induce either an intuitive, deontological response or an intuitive, utilitarian response. As such, we were able to explore this age-related bias toward deontological decisions while controlling for the intuitiveness of the moral dilemma. Using this approach, we found that in DI dilemmas, OAs indeed made more deontological decisions than YAs; in UI dilemmas, however, OAs did not differ from YAs in their moral decisions. Interestingly, a previous study of thirty traumatic brain injury patients reported a complementary, dilemma category-modulated pattern of moral decisions: relative to healthy controls, patients' decisions were more utilitarian in DI dilemmas (where the intuitive decision is deontological) and more deontological in UI dilemmas (where the intuitive decision is utilitarian), showing an overall *counterintuitive* tendency (Rowley et al., 2018).

Accordingly, one possible explanation of the results in the present study is that OAs were both more *deontological* and more *intuitive* than YAs, such that these two age-related tendencies manifested as OAs' moral decisions being much more deontological than YAs' in DI dilemmas while being no different from YAs' in UI dilemmas. Past research has demonstrated an intuitive response bias for OAs in other decision-making domains (Mikels et al., 2010, 2013; Peters et al., 2008), although our findings are the first to show how this intuitiveness interacts with age differences in moral reasoning. The unbalanced effects we observed across the two dilemma types may have resulted from the more salient nature of DI dilemmas, which generally involve sacrificial scenarios of physical harm, whereas UI dilemmas involve less severe actions and consequences, such as white lies. As with the conclusion from Kahane et al. (2012), our findings suggest that individuals can be deontological for some moral decisions and utilitarian for others, depending on the intuitiveness of the response. Importantly, though, greater sensitivity to negative affect in OAs has been associated with age differences in deontological moral judgments (McNair et al., 2019), which may explain why a primary age effect was observed for the more salient DI dilemmas in the current study. We note that this interpretation may seem at odds with the positivity bias commonly reported among OAs, whereby emotional reactivity to negative stimuli is typically reduced while attention and memory towards positive content is enhanced (Carstensen et al., 2006; Mather, 2016). However, moral scenarios that force participants to make a difficult decision between two negative outcomes may represent a unique context that differentially shapes emotional reactivity (McNair et al., 2019), as both outcomes to the dilemma involve the death or misfortune of at least one individual, and thus there is no option to avoid this negativity and orient attention towards a positive alternative. Indeed, age correlates positively with empathic concern (Hannikainen et al., 2018), and OAs exhibit stronger negative affect than YAs specifically toward death-related content (Katzorreck & Kunzmann, 2018; McNair et al., 2019). We did not collect emotional ratings for the scenarios and thus are unable to determine whether differences in valence or arousal between the DI and UI dilemmas contributed to the observed age effects. Previous findings, however, suggest that affect does influence the moral decision-making process differently in OAs compared to YAs (McNair et al., 2019) and may be responsible for initially triggering intuitive judgments (Kahane et al., 2012).

Of note, the DI dilemmas used in the present study primarily consisted of personal dilemmas—that is, dilemmas in which a harmful action is produced, rather than edited, by the agent. For example, in the trolley dilemma, a personal moral decision would involve pushing a nearby stranger off a bridge to stop the incoming trolley from reaching others. In contrast, an impersonal intervention would involve diverting the trolley onto a separate set of tracks to one person instead of five (Christensen et al., 2014). Our DI dilemmas closely matched with the personal sacrificial dilemmas that have been used in previous aging studies on morality (Hannikainen et al., 2018; McNair et al., 2019), although age effects have also been found with a combination of both personal and impersonal moral dilemmas (Arutyunova et al., 2016). With regard to the UI dilemmas that were mostly non-sacrificial, our findings seemingly diverge from McNair et al. (2019) who assessed both sacrificial and non-sacrificial dilemmas but found no interaction between age and dilemma type. Note, however, that the authors acknowledged further work is needed in this area provided that a combination of sacrificial and non-sacrificial dilemmas, compared to just sacrificial ones, produced a weaker effect of negative affect on the relationship between age and moral judgments, and non-sacrificial dilemmas were also rated as less negative and arousing than sacrificial dilemmas (McNair et al., 2019). The present findings address this need by demonstrating that dilemma type can indeed influence the effect of age on moral reasoning when accounting for the intuitiveness of the response. Our stimulus set was also double in number compared to that of McNair et al. (2019; Experiment 2), and thus may have been more sensitive to differences in dilemma type. Future research should continue to explore how moral intuitiveness, coupled with state affective response and trait characteristics such as emphatic concern, influences the moral decision-making process.

In addition to the moral decision task, we also analyzed resting-state fMRI activity from the same younger and older participants. To our knowledge, very few studies have assessed the link between RSFC and morality (Jung et al., 2016), and here we also provide a novel evaluation of age group differences in such a relationship. Our approach was guided by previous work demonstrating that the functional integration of the DN with the executive and attention networks observed in OAs is associated with their greater reliance on prior knowledge and autobiographical experience during goal-directed cognition (Brashier et al., 2017; Spreng et al., 2018; Spreng & Schacter, 2012; Spreng & Turner, 2019). This neurocognitive shift towards an experience-based decision-making style might also predispose greater reliance on engrained moral codes when making difficult moral decisions, in line with neural evidence of the processing of deontological beliefs as semantic knowledge (Berns et al., 2012). We thus focused on whether reduced segregation of the DN could help explain the more deontological moral decisions observed in OAs for DI dilemmas.

In the current study, we implemented a novel fMRI data acquisition sequence (ME-fMRI) combined with ME-ICA to differentiate neural from non-neural (i.e., noise) sources in the BOLD signal (Kundu et al., 2017). This enhances signal to noise ratios across the cortex, while enabling us to attribute group differences to neural sources, as opposed to systematic differences in non-neural noise between the groups. Further, we used an individualized cortical parcellation approach to identify person-specific network nodes. This approach further ameliorates potential age-group biases in spatial registration to a common template (Setton et al., 2021). These novel approaches enabled us to conduct a comprehensive, cross-sectional assessment of intra-network connections, inter-network connections, and network segregation. Our findings confirmed that OAs exhibit reduced system segregation of the DN, as well as reduced segregation of the anterior medial (mPFC) and the posterior medial (precuneus and PCC) subcomponents of the DN (see **Figure S3** and **Table S5**). Importantly, we found that low pmDN segregation predicted deontological-intuitive moral decisions across age groups. Subsequent preliminary analyses suggest the possibility of an indirect effect of age group on moral decisions via this connectivity measure, as well as inter-network connectivity between pmDN and DAN, although longitudinal and/or intervention-based studies would be needed to properly assess this proposal.

The posterior medial cortex, a core hub of the DN, has been shown to facilitate internally directed thought and, specifically, the simulation of past and future events (Cavanna & Trimble, 2006; Leech & Sharp, 2014; Xu et al., 2016). Accordingly, this region is commonly implicated in self-referential processing (Northoff et al., 2006), with accumulating evidence suggesting that the posterior medial cortex constitutes a general evaluative or judgment system (Brewer et al., 2013; Qin & Northoff, 2011). Supporting these proposals, the precuneus and/or PCC have consistently shown increased response during the evaluation of moral content (Avram et al., 2013; Eres et al., 2018; Greene et al., 2001; Pujol et al., 2008; Reniers et al., 2012; Sommer et al., 2010), in particular for deontological compared to utilitarian moral decisions (Kahane et al., 2012). Thus, the unique association of this region's resting-state connectivity profile to a deontological response tendency in the present study is in line with past evaluations of neural response during the online evaluation of moral dilemmas.

Our findings suggest that reduced segregation of the posterior DN in OAs, as well as enhanced integration with attentional control networks such as the DAN, predicts a more deontological decision-making process in difficult, morally-laden scenarios. Extant models on moral decision-making posit that deontological thinking resembles a model-free system in reinforcement learning, whereby an action is evaluated based on previously learned outcomes as opposed to a more computationally expensive, forward-looking model-based system that evaluates an action by inferring its possible outcomes (Crockett, 2013; Cushman, 2013; but see Christopoulos et al., 2017). Speculatively, the posterior DN may implement such a model-free approach during moral decision-making, whereby greater integration of the posterior DN with other networks with advancing age configures a dedifferentiated neural profile that biases older adults towards more deontological moral decisions. This interpretation is in agreement with previous research demonstrating significant associations of DN segregation with individual differences in executive function and memory (Geerligs et al., 2015; Spreng & Turner, 2019), although here we suggest that network segregation may also predict differences in moral decision-making.

One limitation of the present study is that with a cross-sectional design, the observed differences in moral decision-making of YAs and OAs might be a generational cohort effect instead of being a consequence of neurocognitive aging per se. This possibility was explored by Hannikainena et al. (2018), whose results from three separate cross-sectional, longitudinal, and time-lag studies suggested a generational shift of younger cohorts toward greater endorsement of instrumental harm (an indication of utilitarian thinking) in salient, sacrificial moral dilemmas. While we fully agree that longitudinal or cross-sequential studies are needed, our results suggest that around 10% of the variance in age-related differences in moral decision-making may be accounted for by concomitant age differences in the functional architecture of the DN. Although any causal interpretations are speculative, our approach was informed by a burgeoning literature demonstrating that the brain’s structure and function is closely coupled with age differences in cognition (Madden et al., 2010, 2020; McCormick et al., 2019; Ruiz-Rizzo et al., 2019; Spreng & Turner, 2019). We thus interpret the present findings as suggesting a predictive relationship between reduced neural segregation and a deontological response bias, which future longitudinal studies will be able to more properly assess as a causal mechanism in aging. Note, however, that even longitudinal assessments are limited in causal inference (Salthouse, 2011) and accounting for age-related changes in cognition will ultimately require integrating both cross-sectional and longitudinal analyses (i.e., cross-sequential design).

Another limitation is that the collection of moral dilemmas employed in the present study conflates the intuitiveness of moral decisions with action tendency: the predefined intuitive response was to not take the proposed action (i.e., inaction) in all but one dilemma (UI-1 *Modified Preventing the Spread*; see **Table S1**). Past research has investigated the interaction of a utilitarian tendency and an action tendency (Crone & Laham, 2017; Dieterich, 2016; Gawronski et al., 2016; van den Bos et al., 2009). In one particular study, university students who were identified as hypersensitive by the BIS scale (Carver & White, 1994) and thus more likely to suppress their own behaviors were more inclined to choose a utilitarian action over a deontological inaction in two sacrificial moral dilemmas (van den Bos et al., 2011; see also Balash & Falkenbach, 2018). To statistically control for the effect of behavioral inhibition, we also included the BIS scale as an additional covariate in our mediation models and found little difference in results (see **Table S6**). Finally, it should be noted that the materials employed here include sacrificial moral dilemmas alone, and thus likely only reflect people's opinions on instrumental harm without regard to impartial beneficence, both of which are essential components of utilitarianism (Everett & Kahane, 2020; Kahane et al., 2015). Future studies will be needed to further clarify possible age-related differences in judgments of impartial beneficence in moral decision-making.

Finally, another limitation is the lack of formal psychometric testing of the UI and DI dilemmas used in the present study. We administered the stimulus set from Kahane et al. (2012) since it provides the only available separation of UI/DI dilemmas in the moral neuropsychology literature. In the original norming of these stimuli, the intuitive response for each dilemma was assigned based on the immediate, unreflective response from a majority of participants (Kahane et al., 2012). Generally, the DI dilemmas consist of extreme, sacrificial scenarios where both outcomes could still lead to the death of at least one individual, whereas UI dilemmas are not sacrificial and contain the option for a less severe consequence than death, such as lying. Whether and how these differences in dilemma content and consequences determine the direction of intuitiveness needs to be further tested. Indeed, other methods may be necessary to confirm the intuitive versus counterintuitive distinction originally proposed by Kahane et al. (2012). For instance, researchers can induce more reflective response styles prior to moral decision-making and evaluate if increased reflection modifies support for the intuitive decisions (for an example, see Paxton et al., 2014). Ultimately, more research is needed to pinpoint how dilemma characteristics and moral context determine the direction of moral intuitiveness, perhaps also by assessing a more diverse set of moral scenarios.

Conclusions

In the current study, we investigated the moral decisions of a large group of YAs and OAs, and tested whether inter-network connectivity of the DN accounts for age-related differences in decision-making styles. We found that OAs, compared to YAs, made more deontological decisions in DI dilemmas but did not differ from YAs in UI dilemmas. In other words, OAs were less likely to endorse instrumental harm or sacrifice for maximal collective utility, specifically when such endorsement was intuitively compelling. This age difference in moral decisions was predicted by enhanced connections between the posterior medial core of the DN and other neural networks, in particular the DAN. These findings suggest that greater DN integration with the rest of the brain can possibly help to account for differences in moral decision-making styles between YAs and OAs.

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