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Neurocognitive determinants of theory of mind across the adult lifespan

Rémi Laillier, Armelle Viard, Marie Caillaud, Harmony Duclos, Alexandre Bejanin, Vincent de La Sayette, Francis Eustache, Béatrice Desgranges, Mickaël Laisney*

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ARTICLE INFO	A B S T R A C T
Keywords: Aging Theory of mind MASC Mediation analysis Structural MRI	Although theory of mind (ToM) has been extensively explored in aging, few studies have used the same tool to simultaneously assess and compare its cognitive and affective components. When we administered the Movie for Assessment of Social Cognition, a dynamic sequence of social scenes, to 60 healthy participants (20–75 years), we observed no different age-related decreases in both cognitive and affective ToM. While each component was associated with cognitive measures (i.e., episodic memory and processing speed were predictive of cognitive ToM, and recognition of facial emotion expressions and inhibition were predictive of affective ToM), mediation analyses showed that these measures only mediated the effect of age on affective ToM. Voxelwise regressions with grey-matter volume showed that the components partly rely on the same neural substrates, reflecting either ToM per se or other cognitive processes elicited by this multi-determinant task. We discuss the specific substrates of each ToM component, emphasising the importance of considering the impact of other aspects of cognition, present in more ecological situations, on ToM functioning.

1. Introduction

1.1. Cognitive and affective ToM in aging

Aging can be accompanied by reduced social participation (Carstensen, Fung, & Charles, 2003) arising from difficulty relating to others or poor communication (Pinto & Neri, 2017), that increase the risk of poor health-related quality of life (Wilkie et al., 2016). These changes may be linked to modifications in theory of mind (ToM), namely the ability to attribute mental states to ourselves and to others in order to explain and predict behaviour (Premack & Woodruff, 1978). Reduced mental states understanding in later adulthood has been identified as a partial mediator of fewer social activities compared to youngers (Bailey, Henry, & Von Hippel, 2008), and was associated with diminished self-reported social skills (Yeh, 2013) and close social network size (Radecki, Cox, & MacPherson, 2019). ToM is usually divided into cognitive (referring to beliefs, thoughts, and intentions) and affective (referring to emotions and feelings) components (Brothers & Ring, 1992). Data from the literature consistently indicate that cognitive ToM abilities decrease in old age, regardless of the tasks used (Charlton, Barrick, Markus, & Morris, 2009; Phillips et al., 2011; Sullivan & Ruffman, 2004) while results regarding affective ToM abilities are less consensual. Assessing both cognitive and affective ToM, three studies found that both components were affected by aging (Duval, Piolino, Bejanin, Eustache, & Desgranges, 2011; Fischer, O'Rourke, & Loken Thornton, 2016; Rakoczy, Harder-Kasten, & Sturm, 2011), while three others only reported age-related effects for cognitive ToM (Bottiroli, Cavallini, Ceccato, Vecchi, & Lecce, 2016; Li et al., 2013; Wang & Su, 2013). These conflicting results may be due to several methodological issues.

First, the tasks used involved different degrees of complexity and processes. The Reading the Mind in the Eyes (RME) test (Baron-Cohen, Wheelwright, & Jolliffe, 1997) mainly relies on decoding processes while the faux-pas task (Stone, Baron-Cohen, & Knight, 1998) rather depends on reasoning abilities. Second, task used verbal and/or visual supports. According to Slessor, Phillips, & Bull (2007), the effects of aging on affective ToM are only observed with visual ToM tasks that mostly rely on decoding abilities (e.g., emotion attribution from faces for instance). Verbal tasks, which require more reasoning abilities, may be less affected, as vocabulary tends to increase in late adulthood (Verhaeghen, 2003). Only two studies have used a single task, namely the faux-pas task (Bottiroli et al., 2016) or a ToM stories task (Wang & Su, 2013), both verbal tasks, to assess cognitive and affective ToM and failed to find an effect of age on affective ToM abilities. In addition, the

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static or dynamic nature of the tasks can have an impact on ToM performances. Older adults' difficulties are less pronounced with dynamic tasks than with static ones, and dynamic conditions typically improve performances at all ages (Krendl & Ambady, 2010) but are more likely to reflect our abilities in real-time situations.

Most of the traditional tests are poor models of the world, because of their decontextualized nature (Baez, García, & Ibanez, 2016; Burgess, Alderman, Volle, Benoit, & Gilbert, 2009). Social interactions naturally occur in context-rich settings that modulate different levels of cognition, from basic perception to interpersonal domains (Ibañez & Manes, 2012). More specifically, decoding abilities have been found to be sensitive to contextual modulations, particularly in aging, affecting the recognition of emotion from faces (Noh & Isaacowitz, 2013), body posture or gestures (Aviezer, Bentin, Dudarev, & Hassin, 2011; Montepare, Koff, Zaitchik, & Albert, 1999), and gaze behavior (Chaby, Hupont, Avril, Luherne-du Boullay, & Chetouani, 2017; Slessor et al., 2014; Ziaei et al., 2016). When it comes to identifying facial expressions or rating the feelings of characters in social interactions, older adults may benefit from the context either more or less than their younger counterparts, depending on its congruent or incongruent nature (Noh & Isaacowitz, 2013; Sze, Goodkind, Gyurak, & Levenson, 2012).

1.2. Impact of non-social cognitive functions on ToM performances

ToM decrease in aging may also be related to modifications in general cognitive functioning. Studies in aging have reported either the presence (Bailey et al., 2008; Phillips et al., 2011) or the absence (Cavallini, Lecce, Bottiroli, Palladino, & Pagnin, 2013; Duval et al., 2011) of links between ToM, executive factors and other cognitive functions. Methodological features, such as tasks or statistical methods, probably contribute to this discrepancy (Sandoz, Démonet, & Fossard, 2014). Mediation analyses seem to constitute a relevant means of unravelling how cognitive functions modulate ToM skills. Both direct (Wang & Su, 2013) and executive-mediated (Bailey & Henry, 2008; Duval et al., 2011; Li et al., 2013; Rakoczy et al., 2011) effects of age on ToM performances have been reported. While performances on verbal ToM tasks are at least partially predicted by working memory abilities and executive functions, ToM measures obtained using visual paradigms may best be predicted by emotion recognition abilities (Moran, 2013) as shown in two studies conducted in schizophrenia, bipolar disorder (Baez et al., 2013) and Asperger syndrome (Baez et al., 2012) using The Awareness of Social Inference Test (McDonald, Flanagan, Rollins, & Kinch, 2003). However, most of studies including those related to aging employed paradigms assessing social cognition abilities in isolation (Schilbach et al., 2013). In daily-life, social situations requiring ToM also require a wide range of other non-social cognitive processes whose links should be investigated under comparable conditions. Working memory is requested to maintain and manipulate available cues at short-term while episodic memory is necessary to recollect at long-term relevant information relative to the context and persons socially engaged. Mental flexibility could be useful by switching between different types of information or activities, such as the capacity to follow the progression of a social exchange and the ability to infer mental states. Inhibition is needed to inhibit our own perspective and construct a representation of other's mental state. Finally, social interactions are time constraint and thus also rely on processing speed.

1.3. Neural substrates of ToM and associated age effect

The neuroanatomical modelling of ToM functioning described by Abu-Akel and Shamay-Tsoory (2011) suggests that its cognitive and affective components are underpinned by both shared and specific brain networks. A functional magnetic resonance imaging (fMRI) metaanalysis found that the middle prefrontal cortex and temporoparietal junction are key areas for ToM processes, independently of the task (Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). In addition to this core network, different regions such as the precuneus, temporal lobes and inferior frontal cortices appear to be involved, depending on which task is used. The anterior temporal lobes and amygdala have also been associated with this network (Frith & Frith, 2006; Mar, 2011), albeit less frequently. Interestingly, some of the brain regions associated with ToM have also been found to be sensitive to aging. It is the prefrontal regions that mainly appear to be affected, along with the parietal and temporal cortices (Kalpouzos et al., 2009; Terribilli et al., 2011). To our knowledge, neuroanatomical substrates of ToM have however not been studied using an ecological ToM task.

1.4. Objectives

The main aim of our study was to grasp the evolution of cognitive and affective ToM abilities across adult-lifespan through a single evaluation that reenact daily-life conditions under which they occur. To this end, we used the Movie for the Assessment of Social Cognition (MASC; Dziobek et al., 2006) that assesses both cognitive and affective ToM using a 45 min. dynamic sequence of scenes involving social interactions between 4 characters. A further objective was to identify the non-social cognitive determinants associated to the age-related effects on each ToM component and to assess the extent to which ToM decrease can be explained by the decline of these cognitive functions using mediation analyses. Finally, we sought to describe age-related neuroanatomical substrates of cognitive and affective ToM performances using voxel-wise analyses, including notably the weight of other cognitive functions we found linked to.

2. Materials and methods

2.1. Population

Sixty healthy individuals (31 women) aged 20–75 years (M = 42.42, SD = 17.13) were included in the study. The experiment was approved by the regional ethics committee (CPP Nord-Ouest III), and all participants gave their written informed consent. All participants underwent a neuropsychological assessment and neuroimaging acquisitions. They were all native French speakers and had a minimum level of education equivalent to the French primary school certificate, obtained after 7 years of primary education ($M = 13.1 \pm 2.4$). None of the participants had a history of alcoholism, neurological (head injury, trauma, epilepsy, depression, etc.) or psychiatric problems. Their scores on the Mattis Dementia Rating Scale (Mattis, 1988) were all within the normal range for their age and education level.

2.2. Assessment of affective and cognitive ToM in a social context

The cognitive and affective components of ToM were both measured with the MASC (Dziobek et al., 2006), translated into French at the Sainte-Justine University Hospital (Montreal). The MASC is a computerized test intended to replicate real-life demands on mind-reading abilities, and relies on the comprehension of many concepts related to ToM, including false belief, double bluff, mistakes, irony and white lies. Participants watch a 15-minute movie focusing on the meeting of four characters (two women and two men) at a dinner party. The movie is stopped at 46 points in the plot to ask 4-choice questions about the mental state of one of the characters. Items include verbal and nonverbal content from which mental states have to be inferred on the basis of visual cues such as facial expressions, gestures and body language. The test takes approximately 45 min to complete. The MASC is a reliable and sensitive tool for detecting subtle ToM impairments, as shown by studies conducted among participants with different psychiatric disorders (Buhlmann, Wacker, & Dziobek, 2015; Dziobek et al., 2006; Fretland et al., 2015; Montag et al., 2010; Sharp et al., 2011; Wolkenstein, Schönenberg, Schirm, & Hautzinger, 2011) or

neurodegenerative diseases (Kraemer et al., 2013), whilst avoiding a ceiling effect in healthy controls. This could allow for relevant comparisons of cognitive and affective ToM in participants of different ages. According to Montag et al. (2010), 17 items require the inference of cognitive mental states (cognitive ToM performance) and 18 items require the inference of affective mental states (affective ToM performance). Six items (control questions) require nonsocial inferences to be drawn from clues given in the movie (e.g., inferring the weather from the clothing worn by the characters). Owing to the different numbers of items for each condition, analysis is based on percentages of correct cognitive and affective answers.

2.3. Assessment of dynamic facial emotion recognition

We administered a 50-item facial emotion recognition task based on the dynamic condition of the Amsterdam Dynamic Facial Expression Set (van der Schalk, Hawk, Fischer, & Doosje, 2011). This task features 10 different emotions (joy, pride, surprise, anger, fear, disgust, sadness, disdain, embarrassment and neutral), each assessed with five multiplechoice items in which participants have to choose the right emotion from a printed list of the task's 10 emotions. The total score (/50) was taken into account in the analyses described below.

2.4. Complementary neuropsychological assessment

We undertook five complementary neuropsychological measures of processing speed and attentional capacities, flexibility, inhibition, working memory, and episodic memory which are known to undergo age-related changes. As described above, such abilities are essential in social situations in which ToM occur. Standardized psychometric tests with time constraint designed to avoid floor and ceiling effects in healthy subjects including youngest have been selected. In order to limit collinearity among variables in further analyses, we voluntarily restricted the number of neuropsychological measures selecting only one measure for each of the cognitive function. Processing speed and attentional capacities were explored with the Digit-Symbol-Coding test of the Wechsler Adult Intelligence Scale (WAIS-III; Wechsler, 2000). Regarding executive functioning, mental flexibility was assessed with the Trail Making Test, and inhibition with the Stroop test (Godefroy & Groupe de réflexion sur l'évaluation des fonctions exécutives., 2008). The difference in reaction times between the TMT B and A conditions was taken as a measure of flexibility, and the reaction time in the interference condition of the Stroop test as a measure of inhibition. The number of recalled series in the letter-number sequencing task (WAIS-III, Wechsler, 2000) was used as a measure of working memory. Finally, episodic memory was assessed with the 12-word delayed recall score of the French version of the Hopkins Verbal Learning Test (Rieu, Bachoud-Lévi, Laurent, Jurion, & Dalla Barba, 2006).

2.5. MRI data acquisition

All anatomical images were acquired using a Philips (Eindhoven, The Netherlands) Achieva 3.0 T scanner at the CYCERON centre (Caen, France). High-resolution T1-weighted anatomical volumes were acquired using a three-dimensional fast field echo sequence (sagittal, SENSE factor = 2, time of repetition = 20 ms, time of echo = 4.6 ms, flip angle = 10°, 180 slices, no gap, slice thickness = 1 mm, voxel size $1.5 \times 1.5 \times 1.5$ mm, field of view = 256×256 mm², in-plane resolution = 1×1 mm²). Participants were equipped with earplugs and their head was stabilized with foam pads to minimize head motion.

2.6. Behavioral data analyses

$2.6.1. \ \ \text{Analyses of age-related cognitive and affective ToM performances}$

We ran an analysis of covariance (ANCOVA), using a homogeneityof-slopes model, on cognitive and affective ToM performances, with type of ToM (cognitive vs. affective) as a within-participants factor and age as a covariate. We tested the interaction between age and type of ToM.

2.6.2. Mediation analyses of cognitive and affective ToM performances

In order to determine whether age-related ToM performances were linked to other cognitive functions, we first calculated Pearson correlation coefficients between (i) age and both ToM performances, (ii) age and the six complementary cognitive measures and (iii) ToM performances and the complementary measures including the facial emotion recognition score for affective ToM. Years of education were included as a covariate in the correlation matrix.

We then ran forward stepwise regressions to identify the best predictors of ToM performances among the cognitive measures that might affect them. Stepwise regressions provide the advantage of reducing potential collinearity, by limiting the number of explanatory variables, ranked by their partial coefficient correlations (Hocking, 1976). We performed this procedure separately for cognitive and affective ToM performances, as their respective explanatory factors could differ according to the specific cognitive demand they involve. In addition, we calculated variance inflation factors (VIF) relative to each of the variables entered in both stepwise regression models. None of the variables showed collinearity effect that would have been detrimental to our analyses, all VIF values being lower than 2. Analyses were stopped when introducing a new predictor no longer had a significant impact on the variance analyses of each ToM performance.

Finally, we carried out mediation analyses to determine whether the effect of age on ToM performances was mediated by other cognitive functions. According to the Baron and Kenny procedure (Baron & Kenny, 1986), four conditions had to be met to demonstrate a mediation effect: (i) significant association between age and ToM performance; (ii) significant association between age and complementary cognitive measures; (iii) significant association between ToM performance and complementary cognitive measures; and (iv) substantial weakening of the relation between age and ToM performance after inclusion of complementary cognitive measures in the model. In other words, it had to account for a significant proportion of the variance in ToM performance. If the relationship in the last analysis decreased but remained significant, the mediation might be either partial or inexistent. If it became non-significant, the mediation would be complete. All analyses were performed using Statistical Software (Foundation for Statistical Computing, Vienna, Austria). Mediation analyses were performed using the R mediation package (Tingley, Yamamoto, Hirose, Keele, & Imai, 2014), a package for causal mediation analysis. The mediate function allows to estimate different outcome measures such as the average causal mediation effects (ACME) and the average direct effects (ADE) for which quasi-Bayesian Monte Carlo confidence intervals (CI) are obtained in order to take into account uncertainty estimates. The bootstrapping method with bias-corrected CI is used to validate the significance of the mediation when it exists (1000 bootstrap resamples). The 95% CI obtained with this method must not contain zero for there to be a significant effect of mediation. The significant threshold was set at p = 0.05.

2.7. Structural neuroimaging analysis

2.7.1. Anatomical MRI data preprocessing

The T1-weighted structural image preprocessing steps included segmentation and spatial normalization to the Montreal Neurological Institute (MNI) template, using the Computational Anatomy Toolbox (CAT12) in SPM12. The normalized grey-matter images were modulated by the Jacobian determinants, correcting for the effects of nonlinear warping only, and smoothed with an 8-mm Gaussian filter.

2.7.2. Neuroimaging analysis

First, we ran a voxelwise analysis of the effect of age on volume

across the 60 participants using SPM12. The results of this analysis were used as a mask for subsequent analyses between T1-weighted MRI images, ToM performances and complementary cognitive measures. This allowed us to restrict these analyses to clusters for which a significant age effect had been detected. Years of education was used as a nuisance covariate in the analysis, as it was correlated with age. Results were considered significant at a threshold of p = 0.05, FWE-corrected for multiple comparisons, with a cluster extent of k > 100.

Second, we performed regressions to identify brain regions related to either cognitive or affective ToM performances in all subjects. To further highlight specific age-related regions associated with ToM, we calculated an additional model with the complementary cognitive measures that (at least partially) mediated the effect of age on ToM performances as covariates. Regions that no longer appeared in the model after entering these covariates were assumed to be linked to them. Conversely, if brain regions remained correlated with ToM performances, we concluded that these regions were associated with these performances per se. Results were considered significant at a threshold of p = 0.001 uncorrected for multiple comparisons, with a cluster extent of k > 100.

3. Results

3.1. Behavioral results

Age-related cognitive and affective ToM performances are reported in Fig. 1 (both performances follow the normal distribution according to Kolmogorov-Smirnov test). The ANCOVA with type of ToM (affective, cognitive) as a within-participants factor and age as a covariate revealed a main effect of age, F(1, 116) = 60.07, p < .001, $\eta^2 = 0.34$, no main effect of type of ToM, F(1, 116) = 0.004, p = .95, $\eta^2 < 0.001$, and no age × type of ToM interaction, F(1, 116) = 1.13, p = .29, $\eta^2 = 0.01$. Results for the homogeneity-of-slopes model, with type of ToM (cognitive, affective) as a within-participants factor and age as a covariate, thus indicated that the cognitive and affective performance slopes across age did no differ significantly. No age effect was found for control items.

3.2. Cognitive functions subtending the age-related decline in ToM

3.2.1. Correlation analyses

Results of the Pearson correlation analyses between age, education level, cognitive and affective ToM performances, complementary cognitive measures (processing speed/attention, inhibition, flexibility, working memory, and episodic memory) and facial emotion recognition are set out in Table A.

First, age was correlated with all measures. Cognitive ToM performances were correlated with all measures, except for education level and working memory, while affective ToM performances were



Fig. 1. Cognitive and affective MASC performances across the adult lifespan.

correlated with all measures. Correlations between age and education level, cognitive ToM and working memory, affective ToM and education level, and both ToM components and flexibility ceased to be significant after Bonferroni correction. We nonetheless decided to keep education level, working memory and flexibility in the subsequent analyses for both cognitive and affective ToM performances, as links between age-related changes in ToM, education level and cognitive processing have been well described (Li et al., 2013). Their inclusion did not affect the results of the other statistical analyses, and even enhanced the statistical power of the forward stepwise regressions, by increasing the number of predictors taken into account in the analyses.

3.2.2. Forward stepwise regression analysis

Forward stepwise regressions were performed using years of education, processing speed/attention, inhibition, flexibility, and working and episodic memory measures as predictors of cognitive and affective ToM performances (Table B). In addition, the facial emotion recognition measure was included in the affective ToM performance analysis. Results in Table B show that the best predictors were (i) episodic memory and speed of processing/attentional measures for cognitive ToM performances, and (ii) facial emotion recognition and inhibition measures for affective ToM performances.

3.2.3. Mediation analyses

We ran mediation analyses for cognitive and affective ToM performances, entering separately the best predictors as revealed by the forward stepwise regression analyses. Results are reported in Fig. 2. The relation between age and cognitive ToM performances remained unchanged when predictors were included in the model A $(Es_{(ACME(A))} = -0.012, CI_{(ACME(A))} = [-0.0329, 0.0072], p = .22)$ and B $(Es_{(ACME(B))} = -0.002, CI_{(ACME(B))} = [-0.0260, 0.0022], p = .84),$ and analyses confirm a direct effect of age $(Es_{(ADE(A))} = -0.081)$, $CI_{(ADE(A))} = [-0.1150, -0.0453], p < .001; Es_{(ADE(B))} = - 0.090,$ $CI_{(ADE(B))} = [-0.1291, -0.0491], p < .001).$ Conversely, we found significant mediations after bootstrapping by both inhibition $(\text{Es}_{(\text{ACME(C)})} = -0.019, \text{CI}_{(\text{ACME(C)})} = [-0.0387, -0.0053], p < .001)$ emotion recognition and facial $(Es_{(ACME(D))} = -0.044,$ $CI_{(ACME(D))} = [-0.0801, -0.0177], p < .001)$ measures for affective ToM performances in model C and D (indirect effect). However, whereas relashionship between age and affective ToM performance disappeared in the model D, it remained significant in the model C despite the mediation, indicating partial mediation.

3.3. Neuroimaging results

3.3.1. Negative correlations between grey-matter volume and age

Table C shows brain regions in which grey matter was significantly and negatively correlated with age. These correlations mainly concerned the frontal (left frontal superior medial, right middle frontal, anterior cingulum, orbitofrontal) and temporal (bilateral middle temporal, temporal pole and right Heschl's gyrus) cortices, extending to parietal areas (right parietal inferior, supramarginal and angular), subcortical areas (right thalamus, caudate and left putamen, and bilateral insula), and the cerebellum (left Lobule VI and Crus I). The results of this analysis were used as a mask for the following voxelwise analyses, in order to restrict analyses to clusters with a significant agerelated effect.

3.3.2. Positive correlations between grey-matter volume and ToM performances

Among the age-related regions, cognitive ToM performances were mainly correlated with the right and left middle frontal, right superior and inferior frontal gyri, right temporoparietal junction, bilateral superior temporal pole, and left cerebellar Lobule VI (Table D). A similar pattern of results was found for affective ToM performances, with correlations observed mainly in the right medial, inferior and superior



Effect with mediator

Fig. 2. Mediation analyses of age-related cognitive and affective ToM performances. *Note.* Coefficients correspond to the beta weights. ns = nonsignificant. * p < .05. ** p < .01 *** p < .001.



Fig. 3. Right temporoparietal junction (A), right temporal pole (B) and medial prefrontal clusters (C) identified by the voxelwise multiple regression between greymatter volume and cognitive ToM performances when episodic memory and processing speed/attention were regressed out (p < .001 uncorrected, k > 100).

frontal regions, right temporoparietal areas, and left cerebellum (Table D).

(Fig. 3). A second analysis revealed that no region remained correlated with affective ToM performance when facial emotion recognition and inhibition measures had been taken into account.

3.3.3. Positive correlations between grey-matter volume and ToM performances with covariates

We ran analyses searching for positive correlations in order to explore links between structural imaging and cognitive mediation analyses. Given that no complete mediation was found for cognitive ToM performances, we included predictors in order to consider the influence of regions that were correlated with them. Table E lists the brain areas correlated with cognitive ToM performance, after introducing episodic memory and processing speed/attention measures as nuisance covariates. After these predictors had been taken into account in the voxelwise multiple regression, the right temporoparietal junction, right temporal pole, parahippocampal regions and medial prefrontal regions were still correlated with age-related cognitive ToM performances

4. Discussion

The MASC revealed age-related declines both in cognitive and affective ToM performances that are predicted by different cognitive measures. Whereas age had a direct effect on cognitive ToM, its effect on affective ToM was respectively fully and partially mediated by facial emotion recognition and inhibition abilities. Cognitive and affective ToM performances are partly related to common brain regions. When cognitive/affective predictors were taken into account, several brain regions remained associated with cognitive ToM performance, but no region remained related to affective ToM, reflecting the complete cognitive mediation.

4.1. Decrease in cognitive and affective ToM abilities across the adult lifespan and common substrates

We assessed both cognitive and affective ToM abilities using a single dynamic task that featured a combination of verbal and visual content in a social context, in order to conduct the most representative assessment possible of daily life social interactions. The MASC revealed that the two ToM components were sensitive to aging, with no significant differences in the slope of decrease. This could suggest an equivalent decline in ToM performances. Our results differed from those of other studies that assessed both components and only reported a decrease in cognitive ToM using a single verbal task (Bottiroli et al., 2016; Wang & Su, 2006). Whereas affective ToM decreases have only been identified with visual tasks, our results may be the consequence of the use of both modalities in the MASC.

One of our main aims was to identify the cognitive determinants of the age-related decline in ToM performance. Our results fit with those of previous studies showing correlations between ToM and executive functioning (Bailey & Henry, 2008), episodic memory (Castelli et al., 2011; German & Hehman, 2006), and processing speed (Li et al., 2013; Rakoczy et al., 2011). However, the forward stepwise regressions on cognitive and affective ToM performances indicated that a large proportion of the variance remained unexplained. This could be attributed to specific ToM processes, as well as to the influence of other cognitive processes that were not taken into account, and to age.

Correlations between age-sensitive brain areas and ToM performances revealed broadly similar patterns for cognitive and affective components and support the notion of a shared neural basis. The involvement of the temporoparietal junction, particularly on the right side (Saxe, Moran, Scholz, & Gabrieli, 2006), fits with its core role in ToM (Uddin, Molnar-Szakacs, Zaidel, & Iacoboni, 2006). We also found an involvement of left temporoparietal junction which has been found involved in low social perception but also particularly to higher-level social reasoning, such reasoning about beliefs of others (Samson, Apperly, Chiavarino, & Humphreys, 2004).

Common brain regions we found in cognitive and affective ToM analyses can also be attributed to other cognitive processes on which ToM relies. Correlations with grey-matter volume in the prefrontal cortex may thus reflect an overlap between ToM and executive functions, attention or working memory (Stuss & Levine, 2002). More specifically, correlations with dorsomedial prefrontal regions may reflect inhibition abilities (Isoda & Noritake, 2013), such as the ability to inhibit our own perspective, that may contribute to ToM functioning regardless of the mental state to be processed. Functional imaging studies have also highlighted a neuroanatomical overlap of the brain substrates of ToM and episodic memory, including the medial prefrontal cortex, precuneus, posterior cingulate cortex, medial temporal lobe and temporo-parietal junction (Buckner & Carroll, 2007; Spreng, Mar, & Kim, 2009), whose relationships have already been described (see below). Similarly, the temporal pole may contribute to ToM functioning through the involvement of social knowledge (Olson, McCoy, Klobusicky, & Ross, 2013). Regarding the parietal lobe, particularly the angular gyrus, which correlated with both ToM components and overlapped with the temporoparietal junction, it has been shown to be involved in both verbal and nonverbal social cognition tasks (Binder, Desai, Graves, & Conant, 2009; Mar, 2011), supporting access to mental representations and judgment making on contextual associations that could contribute to ToM (Seghier, 2013). Finally, the fusiform gyrus has been reported to be related to face and object perceptions on which ToM abilities may depend, particularly in a task such as the MASC, where numerous cues require perceptual processing. Strong relationships have also been found between both types of ToM performance and the cerebellum, a region related to emotional behaviours and many cognitive domains, including ToM (Overwalle, Baetens, Mariën, & Vandekerckhove, 2014). However, further analyses are needed to clarify the respective degrees of involvement of these regions in ToM,

considering the weight of other cognitive functions that are linked to.

4.2. Specific cognitive determinants of cognitive and affective ToM

The best predictors of cognitive ToM performance were processing speed/attention and episodic memory measures, while affective ToM performance was best predicted by facial emotion recognition and inhibition measures. Results for cognitive ToM predictors were not unexpected. First, the task features required participants to remain attentive and retain information from the beginning to the end of the movie, while responding to questions in quick succession. In the scope of normal aging, this outcome emphasizes the importance to use tasks based on strong time constraint when assessing ToM abilities, as is it the case in daily-life situations. Second, ToM functioning involves recollecting personal experiences in order to understand a character's mental states. ToM and episodic memory are also closely related in terms of their parallel development (Perner, Kloo, & Gornik, 2007) and the extensive functional neuroanatomy they share (Buckner & Carroll, 2007; Spreng et al., 2009). Episodic memory could be critical for adaptive social cognition, with the recollection of previous experiences helping us to project ourselves into a situation concerning another person or imagine their thoughts and feelings, depending on the current context (Buckner & Carroll, 2007; Hassabis et al., 2013).

We did not find any mediation of the age effect on cognitive ToM performances when we included cognitive ToM predictors. While we cannot exclude the possibility that cognitive processes such as nonsocial reasoning abilities that were not assessed here mediate the age effect, it is worth mentioning that executive measures we used were closely related to reasoning abilities. In addition, we did not find any age effect for control items that required nonsocial reasoning (data not shown), suggesting that age had a selective effect on the resolution of ToM items. The lack of mediation may reflect a direct effect of age on cognitive ToM abilities. This result contrasts with those of studies showing that the relationship between age and cognitive ToM is fully mediated by executive functions. These studies used verbal stories (Rakoczy et al., 2011), false beliefs (Bailey & Henry, 2008; Duval et al., 2011) or fauxpas (Bottiroli et al., 2016) tasks that require a strong involvement of executive functions, particularly inhibition (Cavallini et al., 2013). Nor we did obtain a correlation between inhibition and cognitive ToM as it was often been reported for false belief tasks (Duval et al., 2011; Li et al., 2013). By contrast, the MASC contains very few situations involving false-belief reasoning or situations where mental states of characters are not congruent with the social context. Participants have thus less to inhibit their own perspective in order to consider that of the character depicted in the task.

We found that facial emotion recognition measure was the best predictor of affective ToM performances despite the performance also relies verbal contents. Statistical analyses also highlighted the involvement of inhibition in affective ToM even if they did not explain the biggest proportion of the variance. Within the MASC items, the characters' affective mental states that participants had to infer were not necessarily those that they themselves would have in the same situation, and they therefore needed to inhibit their own perspective. The involvement of inhibition could thus reflects high-level cognitive processes needed in most complex situations featured in the MASC where reasoning abilities have to be engaged.

The effect of age on affective ToM performance was totally mediated by facial emotion recognition. Decreased affective ToM performance may therefore be due more to an effect of aging on decoding abilities than to a specific decrease in reasoning abilities. To a lesser extent, we nonetheless also found that inhibition partially mediates affective ToM performance as in previous studies that used visual tasks with inhibition or executive composite scores (Bailey & Henry, 2008; Duval et al., 2011; Rakoczy et al., 2011). Although both facial emotion recognition and inhibition determine affective ToM performance, difficulties faced by older adults are most pronounced when visual

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contents are engaged. Nonetheless, it is possible that, in most cases, affective ToM as assessed with the MASC relies on emotion recognition abilities.

4.3. Specific neural correlates of cognitive and affective ToM performances

Cognitive ToM performances were related to several regions, including the medial and dorsolateral prefrontal cortex, right temporoparietal junction, right temporal pole, and fusiform gyrus. Some of these regions are assumed to be specific to cognitive ToM, such as the dorsolateral prefrontal regions (Kalbe et al., 2010) and right temporoparietal junction, the latter possibly being linked more to the attribution of intentions than to the attribution of emotions (Zaitchik et al., 2010).

Those findings may reflect either the involvement of ToM per se or other cognitive processes. Thus, the correlation with the right middle frontal gyrus (Brodmann areas, BAs 9 and 46) may point to the involvement of self-perspective inhibition (Le Bouc et al., 2012). Indeed, inhibition measure was not identified as a predictor of cognitive ToM and has not been introduced as covariate in the VBM analysis. Surprisingly, cognitive ToM performances were also linked to orbitofrontal regions (BA 47) that are usually linked to affective ToM. However, their involvement in ToM remains to be clarified, given inconsistent reports (Carrington & Bailey, 2009). In association with other regions, the orbitofrontal cortex may play a role in encoding, maintaining and retrieving social cues, especially in multiple interactions, to ensure appropriate social responses in a changing social context (Ross, LoPresti, Schon, & Stern, 2013). Interestingly, the largest cluster was located in the right temporal pole, which has been found to contribute to ToM functioning by allowing personal and interpersonal information to be integrated, and providing a means of turning personal experiences into social conceptual knowledge (Spreng & Mar, 2012). Thus, it has been suggested that the anterior temporal pole plays a critical role in representing and retrieving social knowledge (Olson et al., 2013; Zahn et al., 2009). The latter could be used to guide the inference of mental states, by permitting access to relevant scripts according to the context (Frith & Frith, 2003) and interpreting the sense of social information, and to understand other social behaviours. Together, these regions may be involved in the integration and retrieval of information linked to our experiences, in both episodic and semantic memory, according to the context in which inferences are made.

Brain substrates relative to affective ToM network seem to be partly different from those of cognitive ToM network, as mentioned in the neuroanatomical modelisation of ToM (Abu-Akel & Shamay-Tsoory, 2011). Regarding affective ToM, the absence of significant correlations after the cognitive data had been included as a covariate fits well with our finding of complete mediation (see above). This finding may be explained by the existence of a brain network common to affective ToM and emotion decoding processes (Mitchell & Phillips, 2015). Brain substrates correlated with emotion recognition ability could thus correspond to the part of affective ToM neuroanatomical network with whom they overlap.

Most affective ToM tasks primarily require mental states to be decoded rather than inferred, owing to decontextualized nature of the stimuli. Affective and cognitive components are classically more associated to decoding and reasoning processes, respectively. Our findings could thus reflect the differential involvement of the two processes rather than differences in two types of ToM. However, affective ToM items of the MASC are supposed to rely on both decoding and reasoning processes. The respective weight of such factors should be further studied. Only few paradigms have been developed to involve decoding and reasoning abilities independently (for affective ToM, see Duclos, Bejanin, Eustache, Desgranges, & Laisney, 2018). The study of those processes imply to create tasks in which both processes lead to different mental attributions. Such paradigms would allow to study their relative influence on mentalizing abilities and how they interact with each other.

5. Limits

It should be noted that the MASC only shows characters who are in their mid-30 s, which may influence older adults' performances. As mentioned by its developers, language use and the appropriateness of certain behaviours may vary across generations, meaning that some of the social interactions featured in the MASC are more easily understood by individuals in the same age group (Dziobek et al., 2006). According to some authors, methods eliciting processes in real time (Redcay et al., 2013), where interactions can be established between socially engaged participants in contextual environments (Baez et al., 2016; García & Ibáñez, 2014; Schilbach et al., 2013), have greater ecological validity. This can constitute a motivational bias, particularly in older people, and have an impact on the cognitive functions engaged while performing the task, compared with a real-life interaction. It should also be noted that our imaging analyses only considered brain regions that are sensitive to aging, even though other regions, such as the amygdala and ventromedial prefrontal regions (Cassidy & Gutchess, 2012), may be involved in cognitive processes that contribute directly or indirectly to ToM functioning. Finally, while we focused here on grey matter neuroanatomical substrates, white matter has also been though to play a crucial impact on social cognition (Wang, Metoki, Alm, & Olson, 2017) and has not been taken into account in our analyses.

6. Conclusion

We found that aging is associated with a decline in both cognitive and affective ToM. Some brain substrates sensitive to aging partly underpin one or both ToM components, as well as other cognitive functions that must be taken into account and which contribute differently to ToM functioning, depending on the nature of the mental states to be processed. This finding underlines the importance of assessing ToM functioning in contextual social situations that are representative of real life, where decoding and reasoning processes act in concert with other cognitive functions such as episodic memory, social knowledge, and self-related processes, according to several models of social cognition functioning (Duclos, Desgranges, Eustache, & Laisney, 2018; Ibañez & Manes, 2012). Further research is needed to explore contextual social cognition networks and associated processes in aging, using fMRI methods that can pinpoint functional networks with specially designed ToM tasks in real time. Such studies shall notably distinguish decoding and reasoning processes regarding cognitive and affective ToM abilities in order to compare them. This could also be relevant to better understand the nature of deficits in clinical settings.

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Declaration of Competing Interest

None.

Appendix A

See Tables A, B, C, D.1, D.2, and E.

Table A

Correlations between age, ToM performances, and complementary cognitive measures.

	Years of education	Processing speed/Attention	Inhibition	Flexibility	Working memory	Episodic memory	Facial emotion recognition
Age	-0.28 (0.03)	-0.63 (< 0.001)*	0.47 (< 0.001)*	0.45 (0.001)*	-0.39 (0.002)*	-0.55 (< 0.001)*	-0.73 (< 0.001)*
Cognitive ToM	0.19 (0.14) ^{ns}	0.41 (0.001)*	-0.43 (0.001)*	-0.38 (0.003)	0.23 (0.074) ^{ns}	0.45 (< 0.001)*	nd
Affective ToM	0.29 (0.02)	0.52 (< 0.001)*	-0.50 (0.001)*	-0.35 (0.008)	0.35 (0.006)	0.42 (0.001)*	0.51 (< 0.001)*

Note. ns = nonsignificant correlation (<math>p > .05); * = significant correlation with a threshold of p = .0025 given by the Bonferroni correction for multiple comparisons; nd = correlation not calculated.

Table B

Forward stepwise regressions for cognitive and affective MASC, with measures of interest as predictors.

	Step	Predictors	R2	F	β	р
Cognitive ToM	1 2	Episodic memory Episodic memory Processing speed / Attention	0.20 0.26	14.39 6.59 4.53	0.45 0.33 0.27	< 0.001 0.013 0.037
Affective ToM	1	Facial emotion recognition	0.37	33.40	0.60	< 0.001
	2	Facial emotion recognition Inhibition	0.42	16.49 4.95	0.47 - 0.26	< 0.001 0.030

Table C

Age-related decrease in grey-matter volume ($p_{FWE} < 0.05$, k > 100).

Label	MNI coordinates			z value	k	Brodmann area
	x	у	Z			
Frontal superior medial L	0	45	24	7.67	8543	9/32
Anterior cingulum R Cerebellum Lobule VI L	-27	-62	-28	7.22	13.731	19/0
Superior temporal pole L	-24	16	-28	6.48	1801	38/48/47
Insula L Inferior frontal / Orbitofrontal L						
Heschl's R Insula R	45	-14	9	6.32	5375	48
Middle temporal L	-54	-58	20	6.04	725	21
Middle temporal R	64	-32	0	5.59	478	21
Middle cingulum R	-8	-24	44	5.47	639	23
Inferior parietal R	44	-42	56	5.42	246	2/40
Supramarginar K	20	4	0	E 96	207	40
Thalamus R Hippocampus R	-28 15	4 -34	2	5.26	230	27
Middle frontal R	50	51	3	5.20	188	46
Caudate R	22	12	12	5.20	154	48
Angular R	57	- 57	36	5.09	298	39

Note. k = number of voxels in the cluster; L = left; R = right.

Table D.1

Brain regions correlated with cognitive MASC performances (p < .001 uncorrected, k > 100).

Label	MNI coordinates			z value	k	Brodmann area
	x	у	Z	_		
Superior temporal pole R Insula B	33	-14	-33	4.47	1392	20/38
Superior temporal R Angular R	52	- 45	22	4.37	1025	42/39
Superior parietal R	32	-72	48	4.24	505	7
Middle frontal R	28	30	42	4.20	5170	9/24
Middle cingulum R						
Superior temporal pole L	-26	12	-28	3.97	286	38
Middle frontal Orbitofrontal L	-26	39	-14	3.93	752	11
Superior frontal R	21	54	38	3.91	292	9
Inferior frontal Triangularis R	44	45	-3	3.89	517	47
Middle temporal L Angular L	- 48	- 58	22	3.84	274	39/41
Caudate R	22	8	18	3.71	340	48
Cerebellum Lobule VI L	-32	-60	-28	3.63	1914	37

Note. k = number of voxels in the cluster; L = left; R = right.

Table D.2

Brain regions correlated with affective MASC performances (p < .001 uncorrected, k > 100).

Label	MNI coordinates			z value	k	Brodmann area
	x	у	z			
Cerebellum Lobule VI L	-36	-66	-24	4.46	2642	19
Cerebellum Crus I						
Inferior frontal	48	15	14	4.42	1019	48
operculum R						
Posterior cingulum L	-3	- 39	27	4.26	4445	23/10
Medial frontal medial						
superior						
Middle temporal pole L	-42	-58	22	4.23	845	39
Angular L						
Supramarginal R	60	-26	28	4.20	1876	48
Superior parietal R	20	-54	72	4.06	152	5
Supramarginal L	- 56	-36	29	4.00	1843	40
Inferior parietal L						
Inferior temporal R	51	3	- 44	3.98	318	20
Precuneus R	9	-60	46	3.97	1168	5
Inferior parietal R	46	-42	56	3.96	182	40
Angular R	54	-64	26	3.92	597	39
Inferior temporal L	- 39	-3	- 34	3.78	163	20
Superior frontal R	26	26	52	3.75	386	8
Putamen L	-24	14	2	3.47	650	48

Note. k = number of voxels in the cluster; L = left; R = right.

Table E

Positive correlations between grey-matter volum	e and cognitive MASC performa	nces with measures of interest as	s covariates ($p < .001$ uncorrected, $k > 1$.00).
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Label	MNI coordinates	MNI coordinates			k	Brodmann area
	x	у	z			
Inferior frontal Orbitofrontal R Middle frontal R	40	42	- 4	3.86	168	47
Superior frontal R	21	54	38	3.85	114	9
Superior temporal pole	33	14	-33	3.78	348	20
R						
Middle frontal L	-26	46	10	3.71	109	47
Fusiform R	30	-32	-21	3.59	126	37
Supramarginal R Superior temporal R	50	- 39	24	3.58	117	48/42

Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.bandc.2019.103588.

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