Multiple routes of communication within the amygdala-mPFC network: A comparative approach in humans and macaques

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ARTICLE INFO

ABSTRACT

The network formed by the amygdala (AMG) and the medial Prefrontal Cortex (mPFC), at the interface between our internal and external environment, has been shown to support some important aspects of behavioral adaptation. Whether and how the anatomo-functional organization of this network evolved across primates remains unclear. Here, we compared AMG nuclei morphological characteristics and their functional connectivity with the mPFC in humans and macaques to identify potential homologies and differences between these species. Based on selected studies, we highlight two subsystems within the AMG-mPFC circuits, likely involved in distinct temporal dynamics of integration during behavioral adaptation. We also show that whereas the mPFC displays a large expansion but a preserved intrinsic anatomo-functional organization, the AMG displays a volume reduction and morphological changes related to specific nuclei. We discuss potential commonalities and differences in the dialogue between AMG nuclei and mPFC in humans and macaques based on available data.

1. Introduction

From the exploration of the environment to the regulation of mood and decision making, the amygdala (AMG) and its dynamic interactions with the medial prefrontal cortex (mPFC) encompass a wide range of functions that support behavioral adaptation in primates (see for review Gangopadhyay et al., 2021; Murray and Fellows, 2021). These interactions are thought to allows us to react to relevant salient information from our environment and to regulate, control, and adjust these reactions when necessary (Kim et al., 2011b). Accordingly, clinical studies in humans (Johnstone et al., 2007; Price and Drevets, 2010; Likhtik and Paz, 2015; Mukherjee et al., 2016; Dong et al., 2019; Paul et al., 2019; Li et al., 2021) and lesion studies in the most studied model of the human brain, *i.e.* the macaque rhesus (Málková et al., 1997; Bechara et al., 1999; Rudebeck et al., 2013; Wellman et al., 2016; Elorette et al., 2020; Taswell et al., 2021), have shown that such behavioral adaptation abilities depend, at least in part, on the integrity of this network. In particular, a dysregulation of the top-down control of the mPFC onto the AMG, present in a wide range of pathologies, leads to inappropriate and maladaptive behavioral reactions (Johnstone et al., 2007; Dong et al., 2019).

Over the course of primate evolution, behavioral adaptation has evolved to permit the proper navigation of each species in their respective ecological niches. In humans, this ability reaches its highest level of complexity to face highly complex environments and social interactions (Henke-von der Malsburg et al., 2020). However, whether and how the anatomo-functional interactions of this AMG-mPFC network change in the primate order to subserve behavioral adaptation with increasing complexity is still currently poorly understood. In the present review article, we aimed at providing insights toward that question by identifying, in humans and macaques, homologies and differences of the morphological characteristics of the AMG nuclei and their functional connectivity with the mPFC, two aspects that are often considered separately. Regarding the functional organization of these networks, we deliberately focus on resting-state functional Magnetic Resonance Imaging (rs-fMRI), a powerful tool increasingly used to study functional networks in comparative neuroscience. By doing so, we sought to identify the potential relationships between anatomical and functional organizations in AMG-mPFC circuitries across species, despite their difference in spatial resolution.

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Abbreviations:

AB	accessory basal nucleus
ACC	anterior cingulate cortex
AMG	amygdala
B	basal nucleus
CE	central nucleus
CM	centromedial subdivision
DTI	diffusion tensor imaging
DWI	diffusion weighting imaging
FC	functional connectivity
LA	lateral nucleus
LB	laterobasal subdivision
MCC	midcingulate cortex
ME	medial nucleus
mPFC	medial prefrontal cortex
NHP	non-human primates
rs-fMRI	resting-state functional MRI
vmPFC	ventro-medial prefrontal cortex

First, although the frontal cortex displays an increase of volume from the last common ancestor of humans and old-world monkeys to humans (Semendeferi et al., 2002; Smaers et al. 2011, 2017; Barrett et al., 2020), a large body of evidences point towards a preserved anatomo-functional organization of the mPFC (Petrides and Pandya, 2002; Petrides et al., 2012; Neubert et al., 2015; Procyk et al., 2016; Amiez et al., 2019). Specifically, the mPFC is composed of several regions arranged on the medial part of the brain along the corpus callosum (Fig. 1B). A similar topographical organization can be found along the anterior/ventral-postero/dorsal axis in both macaques and humans, including the ventromedial prefrontal cortex (vmPFC), the anterior cingulate cortex (ACC), the anterior midcingulate cortex (aMCC), and the posterior mid-cingulate cortex (pMCC) (Procyk et al., 2016; Vogt, 2016; Lopez-Persem et al., 2019). From vmPFC to MCC in both macaques and humans, the literature points toward a functional organization sustaining different aspects of behavioral adaptation, *i.e.,* from the evaluation of both our internal and external environment, the evaluation and update of our goals, to the evaluation of our decisions and of their outcomes (Quilodran et al., 2008; Grabenhorst and Rolls, 2011; Amiez et al., 2012; Boorman et al., 2013; Scholl et al., 2015; Procyk et al., 2016; Wittmann et al., 2016; Juechems et al., 2019). Comparatively, as detailed more thoroughly below, the AMG displays the reverse pattern, *i.e.,* a decreased brain occupation volume from the last common ancestor of humans and old-world monkeys to humans that is accompanied by morphological changes of the nuclei forming the AMG (Barger et al. 2007, 2014; Chareyron et al., 2011).

2. Morphological comparison of the amygdala nuclei volumes in primates

In both macaques and humans, the AMG is an almond-shaped structure nested deep in the medial temporal lobe of the brain, and composed of an ensemble of nuclei displaying distinct anatomical and connectivity features (see details in next sections) (Stephan et al., 1987; Aggleton, 2000; Amunts et al., 2005). In primates, AMG nuclei are broadly parcellated into a deep and a superficial group. The deep group is composed of the lateral (LA), basal (B) and accessory basal (AB) nuclei (Aggleton, 2000). In the literature, the latter two nuclei are also found under the abbreviations BL and BM, respectively. LA nucleus is situated on the lateral part of the AMG complex and is ventrally and caudally bounded by the temporal horn of the lateral ventricle (red, Fig. 1A). B nucleus (blue, Fig. 1A) is bounded laterally by LA and medially by AB

nucleus (purple, Fig. 1A). The superficial group is composed of the medial (ME) and cortical nuclei (CO), while excluding the central (CE) nucleus. The CE nucleus, also part of the extended AMG (Fox and Shackman, 2019; Holley and Fox, 2022), lies dorsally and caudally within the AMG complex above the AB nucleus (yellow, Fig. 1A). All these AMG nuclei are strongly interconnected, creating a micro-circuit within the AMG itself, where LA is considered as a sensory gateway, receiving inputs from sensory association cortices, then the flux of information circulates to the other AMG nuclei. Therein, as discussed below, B and AB are more heavily connected to mPFC while CE is connected to autonomic centers nuclei (Aggleton, 2000), and the amygdalar inhibitory intercalated masses contribute to regulatory processes within the AMG (Royer et al., 1999).

The first question we addressed here is whether and how AMG main nuclei, LA, B, AB and CE, have evolved after the split of humans and macaques from their last common ancestor. In that goal, we gathered studies that have examined the volume of AMG and AMG main nuclei in humans and rhesus macaques (see Fig. 2, Table S1 and methods in supplementary material for the studies selected and associated references). As an intermediate specie between humans and macaques, we selected studies including chimpanzees (great apes) to understand whether any changes between humans and macaques are proper to the "homo" genus or to the Hominidae family (comprising great apes and humans' *genii*) (Pozzi et al., 2014). In the 3 species, we only considered *ex-vivo* stereological studies that specifically reported the volume of the whole AMG and AMG main nuclei. We excluded MRI volumetry studies given the lack of consensus and precision in particular regarding the identification of AMG nuclei on MRI images. Note that potential lateralization, sex and age effects were not assessed because 1) several studies reported non-significant volume variations across hemispheres (Brabec et al., 2010; Kedo et al., 2018), and 2) most studies included only one hemisphere. We first created forest plots comprising each of the selected studies for the whole AMG (AMG, Fig. 2A) and its nuclei separately: LA (Fig. 2B), B (Fig. 2C), AB (Fig. 2D) and CE (Fig. 2E).

Results showed that the absolute AMG volume is higher in humans (mean across studies, blue dotted line, 1285.7 ± 294.1 mm^3), compared to chimpanzees (green dotted line, 754.4 ± 137 mm^3, 1.8 times smaller than humans), and macaques (brown dotted line, 202.5 ± 51.9 mm^3, 6 times smaller than humans). When accounting for differential brain size between species using telencephalic absolute volume as a reference (Semendeferi et al., 1997: humans ($1\,125\,492$ mm^3), chimpanzees ($305\,521$ mm^3), and macaques ($62\,737$ mm^3)), we identified that the volume occupied by the AMG in the whole brain is 0.11%, 0.24%, and 0.34% in human, chimpanzee, and macaque brains, respectively. In other words, although the absolute volume of the AMG increased in humans compared to the other species, the percentage of volume it represents in the whole brain decreased compared to the other species.

Importantly, among the AMG nuclei, the LA displays the largest expansion relative to the other nuclei in humans, compared to chimpanzees and macaques (Fig. 2B and F). It represents 34% of the whole AMG volume in humans whereas it represents 20% and 21% in chimpanzees and macaques, respectively. These results are in agreement with previous findings that either compared humans and great apes or humans and macaques (Barger et al., 2007; Chareyron et al., 2011) suggesting that the expansion of LA appeared after the split of humans and chimpanzees from their last common ancestor. In the next sections, we will successively summarize the current state of knowledge regarding the anatomical and functional relationships of the different AMG nuclei in humans and macaques before discussing the potential functional significance of the expansion of the LA nucleus in humans (see last section).

3. Amygdala and medial prefrontal cortex anatomical connections in humans and macaques

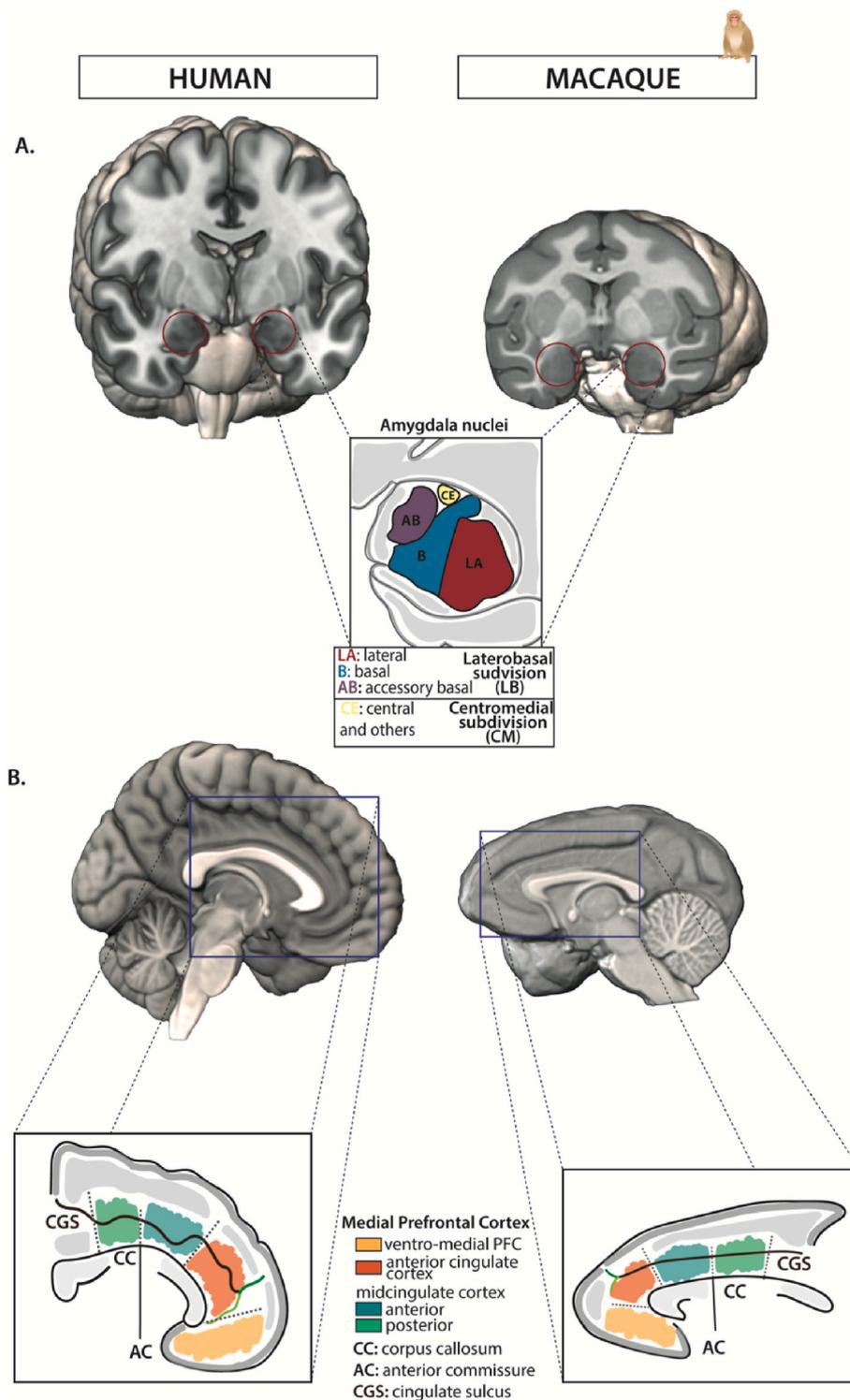Pioneer lesion studies in macaques showed causal evidences of

Fig. 1. Amygdala and medial prefrontal cortex organization in humans and macaques. Human brain sections, from the MNI averaged ICBM152 brain, are displayed in the left column. Macaque rhesus brain sections, from the NMT macaque atlas, are displayed in the right column. **A.** The amygdala (AMG) is outlined (red circle) on the coronal sections of both species. A schematic representation of the AMG main nuclei subdivisions are represented in the center of the figure: Lateral (LA, in red), Basal (B or BL, in blue), Accessory Basal (AB or BM, in purple), and Central (CE, in yellow) nuclei. **B.** The mPFC organization is displayed on sagittal sections in both species. The mPFC encompasses the ventro-medial Prefrontal Cortex (vmPFC, which includes area 25, and parts of area 14m, 10m, and 32, yellow area), the Anterior Cingulate Cortex (ACC, *i.e.,* which includes areas 32 and 24 abc, orange area), the anterior and posterior Mid-Cingulate Cortex (MCC, which includes areas 24a'b'c', 32', anterior MCC: teal area, posterior MCC: green area). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

bidirectional anatomical connections between AMG and mPFC: 1) broad lesions of AB and LA nuclei induce an axonal degeneration in the rostral cingulate cortex, and, 2) reciprocally, lesions in various areas of the cingulate cortex and vmPFC are associated with degenerated cells in B nucleus (Pandya et al., 1973; Nauta, 1993). Tracers' studies in NHP further refined the topological organization of the anatomical connections between AMG and mPFC. First, they demonstrate that these connections are strictly ipsilateral. Second, AMG efferent fibers preferentially terminate in the deep layer II and I of mPFC regions while mPFC efferences towards AMG arose mainly from layer V (Jacobson and Trojanowski, 1975; Aggleton et al., 1980; Porrino et al., 1981; Amaral and Price, 1984; Vogt and Pandya, 1987; Barbas and de Olmos, 1990; Carmichael and Price, 1995; Stefanacci and Amaral, 2000; Ghashghaei and Barbas, 2002; Ghashghaei et al., 2007; Morecraft et al., 2007; Cho et al., 2013; Zikopoulos et al., 2017; Kim et al., 2018; Sharma et al., 2020; Calderazzo et al., 2021; Kelly et al., 2021). In addition, mPFC projections toward the AMG are denser compared to AMG projections toward mPFC, qualifying the mPFC as a "sender" region (Fig. 3A) (Ghashghaei et al., 2007). These connections display a peculiar rostro-caudal organization from low to high density in mPFC regions
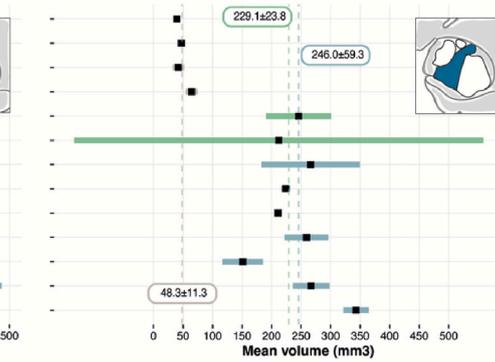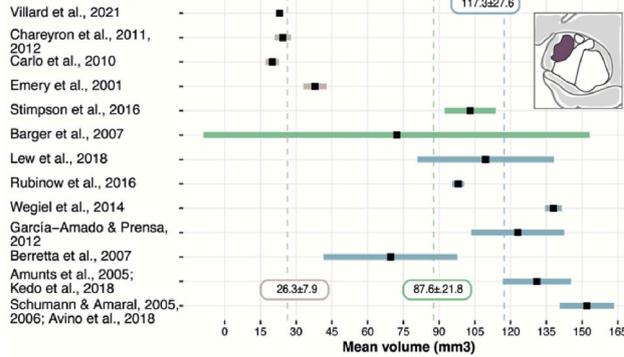
A. Amygdala absolute volume
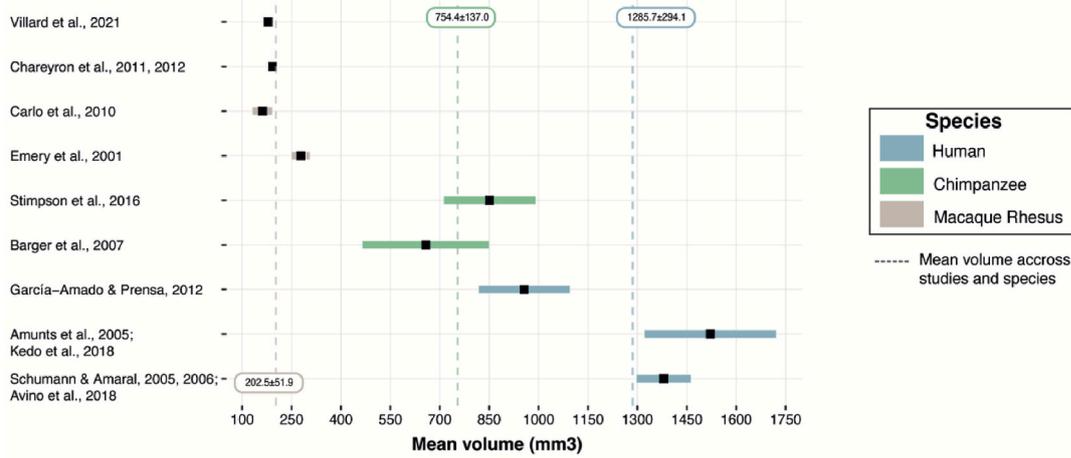
B. Lateral nucleus absolute volume
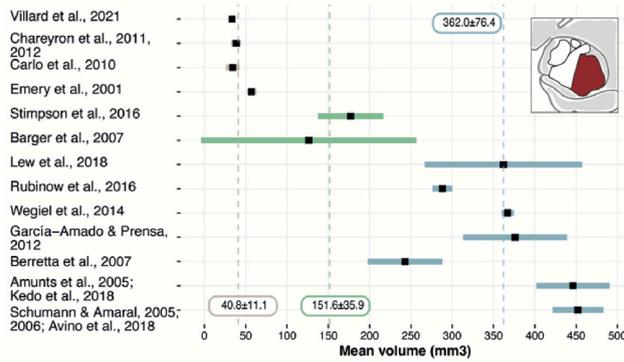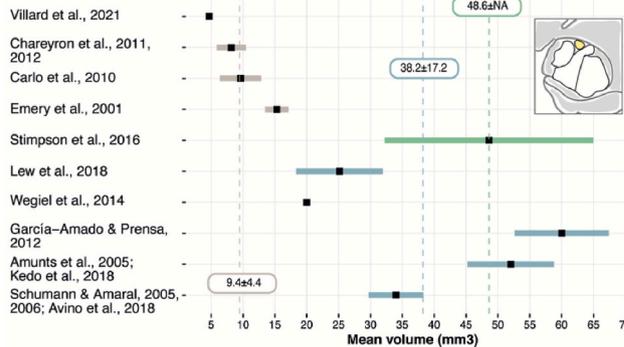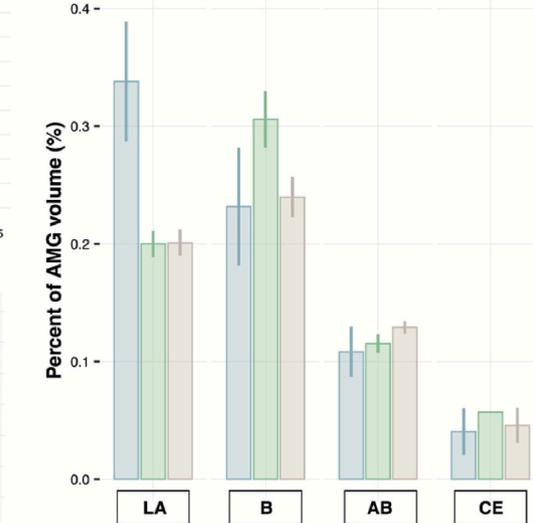

C. Basal nucleus absolute volume

D. Accessory Basal nucleus absolute volume

F. Relative volume occupied by each nucleus in the whole amygdala (percentage)

E. Central nucleus absolute volume

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Fig. 2. **Volumetric analysis of whole amygdala and amygdala nuclei (LA, B, AB, and CE) in primates.** Humans in blue and non-human primates (chimpanzees and macaques) in green and brown, respectively. The analysis was performed exclusively on ex-vivo stereological studies in which we extracted mean volumes, standard deviations and sample size. The majority of studies either include only one hemisphere or did not specify; for the few studies indicating AMG volumes in both hemispheres, we calculated the average volume across hemispheres. **A.** Forest plots displaying the mean volume of the whole AMG in each selected study (black square) and 95% confidence interval around the mean (wide line) for each specie. Mean ± sd volume across species and studies are represented by dashed vertical lines and displayed in rectangles. **B.C.D.E.** Mean absolute volumes of LA (B), B (C), AB (D) and CE (E) nuclei across studies and species. Note that the studies included in C are those included in B. **F.** Because the absolute volume cannot be used to compare the 3 primate species, we calculated the percentage of volume occupied by each nucleus in the whole AMG volume (volume nuclei/volume AMG*100) in each study indicating the volume of the whole AMG. Results are displayed on a bar plot representing the relative volume of LA, B/BL, AB/BM and CE within the AMG for each species (error bars represent interstudy variability). The LA nucleus displays a large expansion in humans compared to macaques and chimpanzees. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

along the corpus callosum: the connection density is stronger between the most caudal part of vmPFC (area 25), then decreases rostrally in ACC (area 32), and increases with MCC regions (area 24; Fig. 3A) (Ghashghaei et al., 2007; Sharma et al., 2020; Calderazzo et al., 2021).

Finally, with their fine-grained spatial resolution, these latter studies also revealed a gradient with a varying density of connections between AMG nuclei and mPFC regions. Specifically, among the AMG nuclei, LA and CE share few direct connections with mPFC (Barbas and de Olmos, 1990; Zikopoulos et al., 2017; Kim et al., 2018; Kelly et al., 2021) as they are mainly connected to sensory association cortices (inferior temporal areas TE and TEO, Superior Temporal Sulcus, etc.) and autonomic centers (hypothalamus or brainstem), respectively (Aggleton, 2000; Stefanacci and Amaral, 2000). By contrast, the B and AB nuclei present the densest reciprocal anatomical connections with mPFC regions. Quantitative histological studies further revealed a differential pattern of efferent connections from these two AMG nuclei (AB and B) toward mPFC regions. the rostral and dorsal mPFC regions, namely ACC and aMCC, receive more projections from B nucleus compared to AB nucleus with a proportional ratio of 90-80% and 10–20%, respectively. Note that pMCC appears to receive sparser projections from the AMG (Morecraft et al., 2007). By contrast, vmPFC receives a similar proportion of projections from both B and AB nuclei (Barbas and de Olmos, 1990; Morecraft et al., 2007; Kim et al., 2018; Sharma et al., 2020), yet, relative to ACC and MCC, its inputs from nucleus AB are denser (Sharma et al., 2020). A similar topographical organization is also present when considering efferences from mPFC toward those AMG nuclei: whereas both MCC and ACC project heavily to B nucleus compared to AB nucleus (Ghashghaei and Barbas, 2002; Ghashghaei et al., 2007; Morecraft et al., 2007; Cho et al., 2013; Zikopoulos et al., 2017; Kelly et al., 2021), vmPFC sends efferences to both B and AB nuclei (Ghashghaei and Barbas, 2002; Ghashghaei et al., 2007; Cho et al., 2013).

Knowledge about the structural connectivity in humans comes from either post-mortem dissection or from non-invasive diffusion MRI performed *in-vivo* or *ex-vivo* (Diffusion tensor imaging -DTI). DTI refers to analytic methods using diffusion weighting imaging (DWI) MRI sequence that provides information about the orientation, the strength and integrity of white fiber tracts at the macroscopic level (Basser and Pierpaoli, 1996). DTI can inform on the orientation and pathway of white fiber tracts and the strength and integrity of fiber tracts (Basser and Pierpaoli, 1996). DTI is an indirect measure with limited spatial resolution and accuracy compared to *ex-vivo* tracer studies in animal studies (Sarwar et al., 2021). Direct comparisons in macaques between anatomical connectivity as estimated with *ex-vivo* tracer studies and DTI studies using at 3T show that these connectivity measures display only moderate correspondances (*e.g.* Grier et al., 2020; Yendiki et al., 2022). This becomes even trickier when considering the intricate structural connectivity pattern of each individual amygdala nucleus with mPFC. However, DTI has the advantage of allowing the comparison of structural connections in both human and non-human primates using the same approach. These studies have shown that the principal white matter tracts connecting AMG with mPFC, *i.e.,* the uncinate fasciculus, the amygdalofugal pathway, and the cingulum, are highly conserved between humans and macaques (Thiebaut de Schotten et al., 2012; Folloni et al., 2019a; Barrett et al., 2020). In addition, Mars et al. (2018)

have developed a connectional blueprint based on the main bundles of white matter tracts that can be anatomically matched across species (*i.e.,* the uncinate fasciculus) to identify homologous brain areas (Mars et al., 2018). In humans, DTI has also been used to delineate the AMG in two subdivisions based on their differential structural connections with other brain regions, i.e. the basolateral and the centromedial subdivision (defined by Amunts et al., 2005 in humans, see next section), coherently with macaque ex-vivo tracer studies (Aggleton, 2000; Solano-Castiella et al., 2010; Bzdok et al., 2013; Balderston et al., 2015). Finally, more recent development in the field provides a finer segmentation of the AMG nuclei at different times during adolescence (Azad et al., 2021). While DTI is a promising tool, future developments using for instance ultra-high-resolution MRI and advances in analytical tools will undoubtedly help overcome the current limitations and hopefully provide more finer-grained cross-species comparisons (Sotiropoulos and Zalesky, 2019; Grier et al., 2022).

In summary, although the literature suggests preserved fiber tracts between macaques and humans at the macroscopic level, differential connectivity profiles between the various AMG nuclei and mPFC regions are observed in macaques at the microscopic level. Importantly, whether these latter highly specific patterns do exist in humans remains to be elucidated. In the next section, we tackle the question of the functional dialogue between AMG nuclei and mPFC regions, as measured at rest using functional Magnetic Resonance Imaging (rs-fMRI).

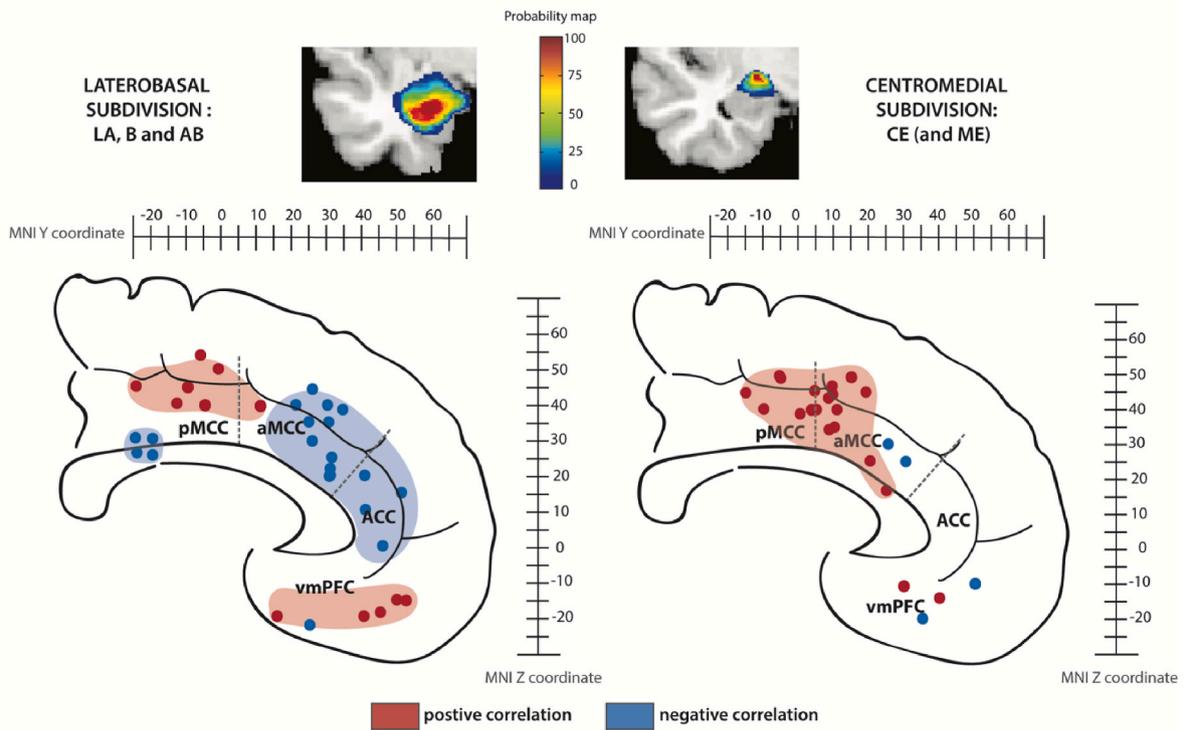## 4. Functional connectivity in the AMG-mPFC network in humans and macaques

Rs-fMRI measures the temporal correlation of spontaneous low-frequency fluctuations of the BOLD signals between different brain regions in the absence of any specific task or stimulus (Biswal et al., 1995). It has the great advantage to provide *in-vivo* information on brain network functional connectivity (FC) as well as the connectivity profile of a particular brain region. While the spatial resolution of fMRI does not permit direct comparisons with the tract-tracing anatomical studies described above, it can provide key information about the functional relationships between anatomically interconnected regions (Greicius et al., 2009).

Numerous studies in humans have described the functional dialogue between AMG and mPFC while considering the whole extent of the AMG or focusing on AMG subdivisions (Amunts et al., 2005). These studies have shown that the fluctuations of activity in the whole AMG is positively correlated with those in more ventral mPFC regions and negatively correlated with those in more dorsal mPFC regions (Roy et al., 2009; Kim et al., 2011a). To identify the respective FC of AMG nuclei with mPFC, we focused on human rs-fMRI studies (see Table S2 and methods in supplementary materials with the associated references) that relied on the most widely used nomenclature in the field: laterobasal subdivision (LB, composed of LA, B, AB nuclei), and centromedial subdivision (CM, composed of CE and ME) (Amunts et al., 2005; Eickhoff et al., 2005). Our intent was to identify the FC organization pattern and the regulatory interactions between AMG nuclei and mPFC focusing on the sign of correlation (positive vs negative) (Gopinath et al., 2015). Note that we only targeted correlations within hemispheres and we did

A. Structural connection: macaque *rhesus* tracer studies
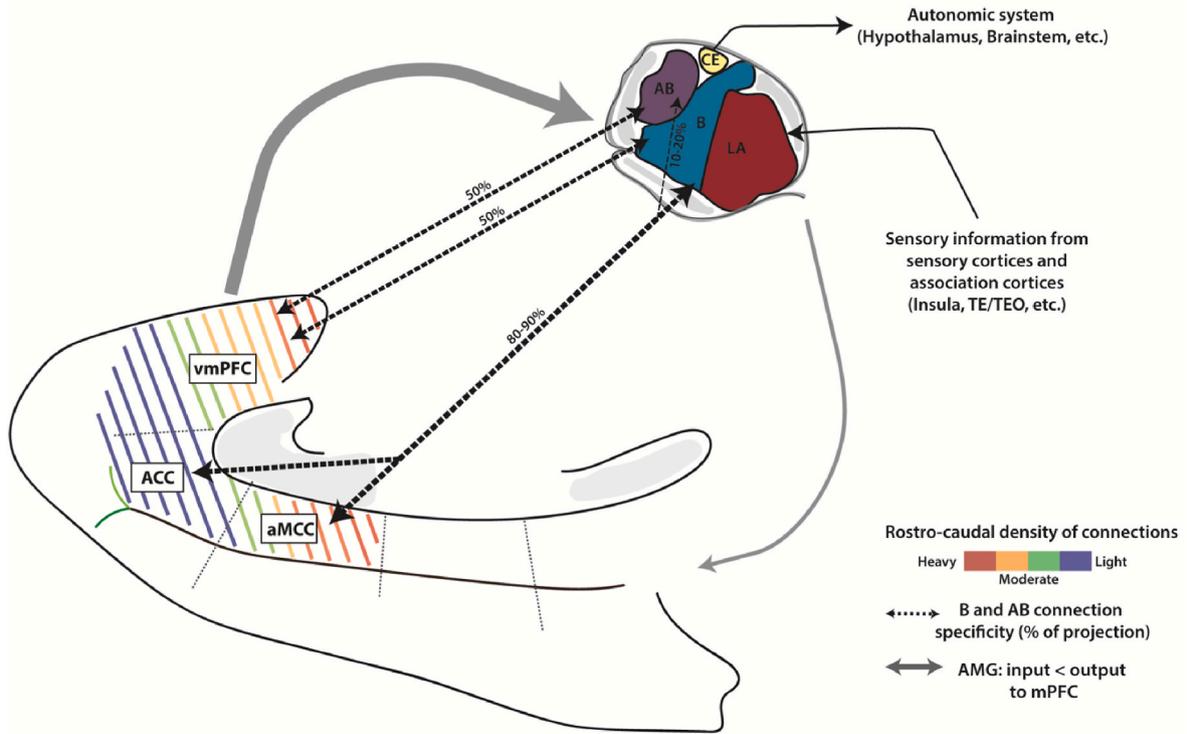
B. Functional connectivity in human resting-state fMRI study

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Fig. 3. AMG-mPFC dialogue: two different levels of analysis between macaque structural connectivity and human functional connectivity. A. Diagram representing the structural connectivity based on tract-tracing studies in macaques between the AMG nuclei, *i.e.*, LA, B/BL, AB/BM, CE, and the various mPFC regions. AMG and mPFC share strictly ipsilateral and bidirectional connections. The mPFC sends more projections to the AMG than it received (*i.e.*, "senders", wide gray arrows). The colored dotted lines in the mPFC represent the rostro-caudal gradient of density of structural connections between AMG and mPFC, *i.e.*, high density (red-orange) with vmPFC and aMCC to low density with ACC (green-blue). The dotted arrows in black represent the preference of connectivity between B/BL and MCC/ACC on one hand, and between AB/BM with vmPFC on the other hand. **B**. Correlation peaks for each selected study between mPFC and the laterobasal (LB, which includes LA, B/BL, and AB/BM nuclei) and centromedial (CM, which includes CE and ME nuclei) AMG subdivisions as defined by Amunts et al. (2005) in humans. We selected studies identifying significant peaks of activation with MNI coordinates and we focused on ipsilateral connectivity. Note that some studies did not directly use Amunts et al. (2005) parcellation, they instead used it as a reference for their own clustering of the AMG. Location (Y, and Z MNI stereotaxic coordinates values) of significant correlation peak values are displayed on a medial sagittal section of the human brain. Negative correlations are represented in blue and positive correlations in red. Results show a differential functional connectivity pattern between the 2 AMG subdivisions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

not take into consideration any lateralization effect as this was outside the scope of the present review (see Table S2). The corresponding correlation peaks for each selected study is displayed on sagittal brain diagrams between Y MNI coordinates from −26 to 52 and Z coordinates from −22 to 50 for LB and CM nuclei (blue and red correspond to negative and positive correlations, respectively; Fig. 3B). Not surprisingly, as LB subdivision occupies the major portion of AMG, we confirm that it displays a similar FC pattern with mPFC subregions than when considering the whole AMG (Roy et al., 2009; Kim et al., 2011a): positive correlations with vmPFC, negative correlations with ACC and aMCC, and positive correlations with pMCC. A recent study that used a finer data-driven parcellation of AMG and high-resolution data further suggested that the strongest FC was observed between AB/B nuclei -as compared to LA nucleus-with mPFC regions, with a trend toward a preferential functional coupling between the AB nucleus and vmPFC (area 25) on one hand and between the B nucleus and aMCC on the other hand (Klein-Flügge et al., 2022). By contrast, the activity of CM subdivision appeared to display a very distinct functional connectivity pattern with mPFC: positive correlations with mPFC regions, more specifically with the MCC regions (both aMCC and pMCC). These patterns of connectivity between the various AMG nuclei and mPFC regions point toward the existence of complex relationships that might be dynamically and differentially adjusted depending on the environmental context.

How are the functional relationships organized between AMG and mPFC in macaques at rest? To the best of our knowledge, only a handful of studies have examined this interplay in macaques (Neubert et al., 2015; Grayson et al., 2016; Folloni et al., 2019b; Morin et al., 2020; Reding et al., 2020). Two points need to be raised. Firstly, these studies have been carried out under anaesthesia (*e.g.*, isoflurane). Yet, several studies have demonstrated that anaesthesia strongly affects brain activity, and in particular the functional dialogue within the frontal cortex (Hutchison et al., 2014; Barttfelda et al., 2015; Uhrig et al., 2018; Giacometti et al., 2022). Anaesthesia notably causes a global decrease of negative correlations in the brain (Hutchison et al., 2014; Barttfelda et al., 2015; Uhrig et al., 2018; Hori et al., 2020; Giacometti et al., 2022), thus calling for some caution when directly comparing studies conducted in anaesthetized macaques *versus* in awake humans using similar parameters. Furthermore, to the best of our knowledge, so far macaques rs-fMRI studies have only examined the FC of the whole extent of AMG. These studies showed 1) positive correlations between the AMG, and the vmPFC, the ACC, and the ACC/aMCC limit, and 2) negative correlation between the AMG and aMCC (Neubert et al., 2015; Folloni et al., 2019b; Reding et al., 2020).

Overall, the current available evidences from anaesthetized macaques suggests that the FC between vmPFC with AMG share similarities with awake humans while the FC between ACC and AMG displays some differences between the two species. Whether these difference are driven by the state (anaesthesia vs awake) or represent mere interspecies differences is further discussed in the last section of the review.

5. Multiple routes of communication within the amygdala-mPFC network in macaques and humans: functional significance and future directions

The goal of the review was to scrutinize anatomical and functional relationships within AMG-mPFC circuitries and identify potential homologies and differences between macaques and humans. We highlighted in particular: 1) differences between AB and B nuclei structural connectivity with mPFC regions from tract tracing studies in macaques (Fig. 3A), and 2) differential pattern of functional connectivity between the mPFC regions and the laterobasal (LA, B and AB) or centromedial AMG subdivisions (CE and ME) from rs-fMRI studies in humans (Fig. 3B). These evidences suggest multiple routes of communications between AMG nuclei -or subdivisions- and mPFC. Below we discuss how these different AMG-mPFC routes might enable the integration of information from the internal and external environments to support flexible behavior (Saez et al., 2015). Specifically, we propose that two routes within the AMG-mPFC network support distinct temporal dynamics of integration necessary for behavioral adaptation, the former dealing with long-term contextual adaptation (vmPFC-LB) and the latter dealing with online monitoring of actions (LB-aMCC and CM-aMCC). In addition, we highlight an expansion of the LA nucleus in humans compared to macaques and discuss potential commonalities and differences between both species in AMG-mPFC circuits.

5.1. Two routes with distinct behavioral adaptation temporalities within AMG-mPFC

Among the LB subdivision, B and AB nuclei share strong bidirectional structural connections with mPFC regions, especially with vmPFC and aMCC (Fig. 3A). Of note, the projections from mPFC towards AMG nuclei are denser that their counterparts (Ghashghaei et al., 2007), suggesting a moderating role of mPFC onto the AMG, that is gradually setup from the end of infancy to adolescence (Gee et al. 2013, 2022; Tottenham, 2015). While evidence of the functional relationships between AMG nuclei and mPFC using rs-fMRI remain elusive to date in macaque, evidence from human studies show a differential functional relationship with two particular regions of mPFC in humans: 1) a positive *versus* negative functional coupling at rest between the LB subdivision and the vmPFC versus the aMCC, respectively, and 2) a positive functional coupling between the CM subdivision and the aMCC (Fig. 3B). Interestingly, vmPFC and MCC sustain different and complementary aspects of flexible decision-making necessary for behavioral adaptation (Quilodran et al., 2008; Grabenhorst and Rolls, 2011; Amiez et al., 2012; Boorman et al., 2013; Scholl et al., 2015; Procyk et al., 2016; Wittmann et al., 2016; Juechems et al., 2019), that might in part be reflected in their differential dialogue with the LB and CM subdivisions.

On one hand, vmPFC is thought to integrate contextual and value information with previous knowledge to update decisions accordingly (Grabenhorst and Rolls, 2011; Boorman et al., 2013; Vassena et al., 2014; Scholl et al., 2015; Wittmann et al., 2016; Schneider and Koenigs, 2017; Juechems et al., 2019; Dal Monte et al. 2020, 2022; Gangopadhyay et al., 2021). This integration depends, at least in part, on

information processed within the LB subdivision associated with choices, value and rewards evaluation in both social and non-social contexts coded in abstract conceptual format (Gupta et al., 2011; Wellman et al., 2016; O'Neill et al., 2018; Grabenhorst et al., 2019; Dal Monte et al., 2020; Elorette et al., 2020; Jezzini and Padoa-Schioppa, 2020; Grabenhorst and Schultz, 2021; Dal Monte et al., 2022). For instance, the level of complexity in the social network enhances the strength of connectivity between vmPFC and LB (Bickart et al., 2012). Beyond its interactions with the LB subdivision (B and AB nuclei), vmPFC also received inputs from the entorhinal cortex (EC), a gateway to the hippocampus, mediating long-term contextual and episodic memory functions (Joyce and Barbas, 2018; Calderazzo et al., 2021). Through these connections, the LB-vmPFC circuit might thus be in an ideal position to update decisions based on stored information and support longer term (as opposed to short-term) behavioral adaptation. Previous studies have suggested strong interactions between another region of the PFC (the orbitofrontal cortex) and the LB subdivision in shaping behavioral responses depending on the environment (Saez et al., 2017; Zikopoulos et al., 2017). Here, we further suggest that the circuit formed by the vmPFC and the LB subdivision also participate in these processes and it would be interesting in future studies to disentangle the contribution of these pathways in behavioral adaptation.

On the other hand, MCC (often referred as dACC) strongly interacts with the premotor cortex and the dorso-lateral PFC (Morecraft et al., 2012; Calderazzo et al., 2021) involved in action planning, cognitive control, and feedback-based decision, critical to rapidly adapt behaviors when required by the environment (Amiez et al., 2012; Boorman et al., 2013; Vassena et al., 2014; Procyk et al., 2016; Wittmann et al., 2016; Juechems et al., 2019). The evidences based on rs-fMRI in humans that we presented above suggest two distinct ways by which AMG and MCC might interact: 1) a negative functional coupling between the activity of MCC and the LB subdivision and 2) a positive functional coupling between the activity of MCC and the CM subdivision.

While the LB-MCC route is sustained by massive direct anatomical projections, characterized in particular by dense projections between the B nucleus and the MCC (Sharma et al., 2020), the CM-MCC route presumably reflects indirect interactions. Yet, both are likely to participate in functions that require fast stimulus-response adaptations to face immediate changes in the environment (Bickart et al., 2012; Klavir et al., 2013; Aryeh Hai Taub et al., 2018; Aryeh H. Taub et al., 2018; Terburg et al., 2018; Leitão et al., 2022). For example, during aversive learning, electrophysiological recordings in monkeys have shown that stimulus processing rapidly occurs within LB before reaching the MCC and propagates back to the LB (Klavir et al., 2013; Aryeh Hai Taub et al., 2018; Aryeh H. Taub et al., 2018). In the CM subdivision, the CE nucleus is mainly connected with autonomic centers such as the hypothalamus and brainstem regions (Aggleton, 2000; Cardinal et al., 2002). Lesion study in non-human primates has demonstrated its implication in defensive and physiological responses in anxiety-related and stress-related situations (Kalin, 2004). In humans, studies showed strong coupling between CE and MCC at rest (Bickart et al., 2012; Tillman et al., 2018). The MCC also participates in sympathetic and parasympathetic responses (Amiez and Procyk, 2019). One might thus hypothesize that the MCC, through its functional interactions with the CM, including CE, and more largely the central extended AMG, may shape avoidance-approach responses based on previous negative and/or positive feedback-based experiences that might have been previously integrated by LB-vmPFC circuit. Such regulation likely depends on dynamic and flexible interactions between AMG nuclei involving inhibitory neurons such as the intercalated interneurons masses and top-down regulation from the mPFC (Mcdonald and Augustine, 1993; Zikopoulos et al., 2017).

It is therefore possible that these two routes within the AMG-mPFC network support distinct temporal dynamics of integration, the former dealing with long-term contextual adaptation (vmPFC-LB) and the latter dealing with online monitoring of actions (LB-MCCa anc CM-MCCa). A

balance between these different circuits within the AMG-mPFC network would be essential to support decision-making flexibility in various environmental contexts in light to our internal state to promote behavioral adaptation. The AMG, formed by a collection of nuclei, is often viewed as a hub sustaining a high degree of information integration coordinating multiple brain circuits during behavior adaptation (Morrow et al., 2019; Putnam and Gothard, 2019). Accordingly, in humans, a disruption within these AMG-mPFC circuits leads to various mental illnesses characterized by maladaptive behavioral responses, i.e. exaggerated, reduced, or even an absence, and/or an atypical behavior (Blair, 2008; Kim et al., 2011a; Murray et al., 2011; Swartz et al., 2013; Likhtik and Paz, 2015; Nicholson et al., 2015; Mukherjee et al., 2016; Dong et al., 2019; Li et al., 2021; Cao et al., 2022; Gao et al., 2022). In particular, the LA nucleus in humans is a very sensible target to a large number of neuropsychiatric diseases. Several postmortem studies comparing patients with healthy subjects have reported morphological alterations of the LB with a special focus on the LA nucleus (*e.g.* volume and neurons numbers) in autism spectrum disorder, William syndrome, major depression disorder, panic disorder, schizophrenia, and bipolar disorders (Schumann and Amaral, 2006; Berretta et al., 2007; Bezchlibnyk et al., 2007; Kreczmanski et al., 2007; Schumann et al., 2011; Wegiel et al., 2014; Rubinow et al., 2016; Asami et al., 2018; Avino et al., 2018; Lew et al., 2018). The studies highlighted above deciphering the AMG-mPFC circuitries at the nuclei subdivisions level will undoubtedly help us to better understand these maladaptive behaviors and hopefully help to refine therapeutic strategies to help these patients.

5.2. Towards a comparison of AMG-mPFC networks in macaques and humans

Our objective was to identify potential homologies and differences in AMG-mPFC circuitries between macaques and humans. First, the CE nucleus, part of the CM and central extended AMG together with the bed nucleus of the stria terminalis (BST), is thought to have been conserved throughout the course of evolution, with limited differences between rodents and primates, hence between macaques and humans (Chareyron et al., 2011), as confirmed with the volumetric analysis presented above.

Comparatively, we highlighted in humans a selective expansion of the LA nucleus, part of the LB subdivision, and tightly connected with sensory and higher order association cortices (Stefanacci and Amaral, 2000). This volume expansion has also been associated with an increase of neuron numbers in humans (Barger et al., 2012). It is possible that this expansion allows the integration of a higher amount of multi-sensorial information that humans are facing in their daily life including their highly complex social interactions compared to macaques (see also Barger et al., 2012). Several neuroimaging studies reported an increase in AMG volume related to complex social networks (Dziura and Thompson, 2014) and the size of the social group (Sallet et al., 2011; Kanai et al., 2012). Although these studies refer to the whole AMG, and confirmation needs to be brought by, it is possible that this increase concerns in particular the LA nucleus. A recent study using electrical stimulation in epileptic patients showed that stimulation of the LA nucleus evoked an earlier response in ACC/aMCC compared to that of the B or AB nucleus (Sawada et al., 2022). While in macaques, LA only shares few direct projections with mPFC compared to AB and B, it remains to be determined whether the LA expansion might have led to differences in the organization of anatomical projections between AMG and mPFC in humans.

Regarding the rs-fMRI functional connectivity of AMG nuclei and/or subdivisions with mPFC regions, the current state of the art, especially in light with very limited evidences focusing essentially on the whole AMG functional connectivity under anaesthesia in macaques, does not allow to draw firm conclusions about potential homologies or differences between humans and macaques. Nevertheless, one could relate the FC involving vmPFC and aMCC with the whole AMG in anaesthetized macaques and whole AMG and LB subdivision in awake humans and the

similarities between the two species in terms of structural connectivity of the CE nucleus. It is possible thus that the two routes described above are present in both humans and macaques to support distinct temporal dynamics of integration necessary for behavioral adaptation, yet with some differences. Indeed, the FC between the region located between the vmPFC and aMCC, namely the ACC, and the AMG displays some differences between the two species: the activity of this region is mainly negatively correlated with that of the AMG in humans while the available evidence in macaques points toward a positive correlational relationship between these two regions. While these conclusions await further evidences, we propose tentative interpretations that might be related to these functional differences across species. One possibility is that this difference is driven by the state (anaesthesia vs awake). Alternatively, this difference might reflect mere differences between species: although the macaque mPFC possesses all the sulcal precursors of the human mPFC, the region interfacing with vmPFC and MCC (which contains ACC) is the one displaying the most notable sulcal changes across primate species (the fork composed by two sulci situated at the rostral of the cingulate sulcus 1) faces downwards in humans versus forward in macaques and baboons, and 2) is located more dorsal in non-human than in human primates; Amiez et al., 2019). Whether and how these morphological changes would affect the functional relationships between mPFC and AMG nuclei is yet to be determined. With novel tools giving access to the fine-grained parcellation of the AMG in macaque (Hartig et al., 2021), it would be possible for future studies to further refine our knowledge about the AMG nuclei FC profiles with mPFC in awake macaques, therefore providing more direct comparisons with available evidences in humans.

5.3. Limitation and further perspectives

We mainly focused the scope of the review in the adult brain, not taking into account several factors that might also affect the anatomical and functional interplay within AMG-mPFC circuits such as sex, age or personality traits (see for instance Tottenham, 2015; Reber and Tranel, 2017; Kenwood and Kalin, 2021; Ferrara and Opendak, 2023). Another limitation of our hypotheses is that evidences come from different species (humans vs macaques) and from different approaches with different spatial scales: a microscopic scale providing structural connectivity of each AMG nuclei in macaques versus a macroscopic scale in humans using rs-fMRI or DWI. In comparative neurosciences, the gap between invasive -but highly precise-techniques used in non-human primates and non-invasive -but less precise-techniques used in humans is called the "macroscopic–microscopic divide" (Barron et al., 2021). Cross-species neuroimaging comparison approaches have emerged to bridge this gap as they have the advantage to be applicable in both human and non-human primates and in particular in macaques (Barron et al., 2021; Friedrich et al., 2021). With higher field strength at 7T or even 10.5 T in macaques (Thanh Vu et al., 2017; Yacoub et al., 2020), this approach can provide a finer-grained description of brain networks. As such, future works may apply this strategy to consider the respective whole-brain functional coupling of each AMG nuclei within and across species (*e.g.* Torrisi et al., 2015; Elvira et al., 2022). The implementation of effective connectivity in these studies might also provide important insights about the directionality of the interplay within these networks (Liu et al., 2016; Berboth and Morawetz, 2021). Our further understanding of the temporal and dynamic interactions between the AMG nuclei and the mPFC in primates may also benefit from interventional optogenetic and electrophysiological approaches similar to those carried out in mice (*e.g.* Kopell et al., 2014; Felix-Ortiz et al., 2016). Some electrophysiological studies, although rare, have already provided key information about similarities and differences of the efficiency and robustness of the functioning of the mPFC-AMG network in humans versus macaques (Pryluk et al., 2019). Combining these different and complementary techniques in future studies will be essential to understand how the different AMG nuclei interact with the mPFC and other

brain networks such as the fronto-amygdala-striatal circuitry (Cho et al., 2013) to subserve differential behavioral adaptation capacities in humans and monkeys and shed light on the evolution of this network (Henke-von der Malsburg et al., 2020).

CRediT authorship contribution statement

C. Giacometti: Conceptualization, Investigation, Analyzing, Writing – original draft. **C. Amiez:** Conceptualization, Writing – review & editing. **F. Hadj-Bouziane:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.crneur.2023.100103.

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