



Large-scale neural systems linking bodily self-awareness and valuation in decision-making

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ARTICLE INFO

Keywords:

Bodily self-awareness
Interoception
Sense of agency
Cocaine use disorder
Decision-making
Meta-analyses

ABSTRACT

Adaptive decision-making depends on the integration of reward valuation with internal bodily and action-related signals; yet, this broader neural architecture is not fully captured by reward-centric models. Emerging evidence suggests that bodily self-awareness - including interoception and sense of agency - may shape reward-driven behaviour, but its large-scale neural organization and clinical relevance remain unclear.

Here, we integrated existing evidence to examine the systems-level relationship between neural circuits supporting bodily self-awareness and those involved in reward valuation. We combined three coordinate-based meta-analyses of functional neuroimaging studies investigating interoception, sense of agency, and cognitive impulsivity with a targeted re-analysis of previously published and publicly available resting-state datasets in healthy individuals and in participants with cocaine use disorder.

Across meta-analytical and resting-state connectivity analyses, interoception and agency converged within insular and salience-network regions, whereas cognitive impulsivity engaged distinct fronto-striatal and default mode network regions. These systems exhibited opposing functional connectivity profiles, consistent with a relative functional differentiation between bodily self-awareness and valuation-related processes. Critically, this organization was altered in cocaine use disorder: the caudate nucleus showed reduced integration with interoceptive and agency-related networks and increased coupling with cognitive impulsivity-related circuits.

These findings identify a large-scale neural architecture linking bodily self-awareness and valuation systems and suggest that cocaine use disorder is associated with altered integration among these systems.

1. Introduction

Everyday decisions - from resisting immediate temptations to pursuing long-term goals - often feel shaped not only by external information but also by internal bodily sensations (i.e., interoception) and the sense of control over one's actions (i.e., sense of agency). Yet, how such aspects of bodily self-awareness contribute to human decision-making

remains insufficiently understood at the level of large-scale brain systems. While valuation-based models (Rangel et al., 2008) have provided influential accounts of how options are represented and compared, they devote less attention to how bodily and action-related signals contribute to maladaptive choices in individuals without overt cognitive impairment. The Somatic Marker Hypothesis (SMH; Damasio, 1996) provides a complementary embodied account, proposing that bodily states

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associated with past outcomes bias future decisions by influencing behaviour. Originally derived from neuropsychological observations of patients with frontal lobe damage, the SMH proposes that bodily signals - somatic markers - assign emotional value to potential outcomes, thereby guiding behaviour away from unfavourable consequences (Damasio, 1996). Thus, from an adaptive perspective, somatic markers were hypothesized to provide a shortcut for decision-making by signalling whether similar past outcomes were beneficial or harmful. Empirical support for this account was provided by the Iowa Gambling Task (IGT; Bechara et al., 1994), which captures decisions under uncertainty. Healthy individuals progressively learn to avoid disadvantageous options, whereas patients with ventromedial prefrontal cortex (VMPFC) damage persist in making maladaptive choices - a phenomenon termed “myopia for the future” - and show no anticipatory bodily signals (i.e., skin conductance response) before risky choices.

At the neural level, the SMH implicates interactions among the VMPFC/OFC, insula, somatosensory cortices, amygdala, cingulate cortex, basal ganglia, and brainstem nuclei (Poppa and Bechara, 2018). Within this framework, these regions link external events with actual or internally simulated bodily states, allowing the affective consequences of previous outcomes to influence future choices. Although the amygdala is considered important for establishing associations between stimuli and bodily responses, the VMPFC/OFC is proposed to support the reactivation of these representations during subsequent decision-making (Bechara and Damasio, 2005).

Despite its influence, the SMH has faced persistent empirical and theoretical challenges. Behavioural and psychophysiological findings often diverge from its predictions: some healthy individuals perform well on the IGT without anticipatory physiological responses (Crone et al., 2004), whereas others exhibit intact physiological signals yet fail to adopt advantageous strategies (Bechara and Damasio, 2005). These inconsistencies have encouraged the use of more precisely specified paradigms for isolating components of maladaptive choice. One such paradigm is the delay discounting task (DDT), which assesses preferences between smaller immediate rewards and larger delayed rewards, providing a widely used index of cognitive impulsivity (Giorgetta et al., 2014; Grecucci et al., 2014). Importantly, impulsivity is a multicomponent construct which can be assessed by different behavioural tasks and psychometric scales (Evenden, 1999). The DDT captures a specific dimension of cognitive impulsivity, whereas other paradigms are used for the assessment of dissociable facets of impulsive behaviour, such as motor impulsivity (the failure to inhibit a prepotent or already-initiated response, measured by go/no-go or stop-signal paradigms), attentional impulsivity or lack of premeditation. Throughout this manuscript, we therefore use the term ‘cognitive impulsivity’ specifically to denote this discounting-based, value-related dimension of impulsive choice, rather than impulsivity as a unitary construct. Notably, DDT performance is altered across a wide range of psychiatric and neurological conditions (Amlung et al., 2019; Garofalo et al., 2022) and consistently engages neural systems, including the VMPFC and striatum (Lempert et al., 2017; Mattavelli et al., 2024).

Within embodied accounts of decision-making, the mere presence of bodily signals may not be sufficient to guide choice adaptively (Dunn et al., 2006). Their influence on choice may therefore depend, at least partly, on how effectively they are perceived and integrated through interoceptive processing. Interoception - the processing of internal bodily signals - has therefore gained attention as a critical factor in decision-making processes. Several accounts propose that interoceptive sensitivity may shape how bodily signals are incorporated into choice. In particular, some studies suggest that individuals with higher interoceptive ability rely more on bodily cues during decision-making, adopting more risk-averse strategies when bodily feedback is salient (Salvato et al., 2019) and improving decision-making performance following interoceptive training (Sugawara et al., 2020). Nevertheless, the contribution of interoception to decision-making remains debated, and decision-making itself is increasingly recognized as a multiprocess

cognitive competence that likely encompasses additional components of embodied cognition.

From this perspective, bodily self-awareness extends beyond interoception to include the sense that one’s actions cause changes in the external world, namely the sense of agency (Haggard, 2017). Although interoception and agency rely on distinct mechanisms, both contribute to bodily self-awareness. Interoception concerns the monitoring and representation of internal bodily states, whereas agency concerns the experience of initiating and controlling actions and their consequences. Therefore, they can be understood as complementary facets of self-awareness, emerging from different underlying mechanisms while jointly contributing to the representation and monitoring of the embodied self.

Surprisingly, agency has received relatively little attention within the decision-making literature, despite Damasio’s original acknowledgement of an ‘operative self’ in the original SMH formulation. It is increasingly recognized that a strong sense of agency is associated with greater confidence and decisiveness in decision-making, whereas diminished agency is associated with hesitation and indecision (Bhanji et al., 2016; Damen, 2019). Altered agency has been reported in conditions characterised by impulsivity and impaired self-regulation, including substance use disorders (Betz et al., 2019; García-Rodríguez et al., 2013; Struglia et al., 2011), as well as in schizophrenia, a disorder marked by passivity experiences and impaired decision-making (Betz et al., 2019; Frith, 2005; Struglia et al., 2011; Synofzik et al., 2013). Together, these findings suggest that both interoception and agency represent key, yet under-integrated, components of embodied decision-making.

Neuroimaging findings further suggest that the systems supporting interoception and agency partially overlap with regions implicated in embodied accounts of decision-making. In the case of interoception, the supporting neural systems include the insula, anterior cingulate cortex, and somatosensory cortices (Bechara and Damasio, 2005; Craig, 2009; Critchley et al., 2004; Medford and Critchley, 2010; Salvato et al., 2019; Schulz, 2016). The sense of agency, on the other hand, relies on a distributed network that includes the supplementary motor area, posterior insula, postcentral gyrus, and superior temporal region (Seghezi et al., 2019; Zito et al., 2020). Thus, the insula represents a candidate region of anatomical convergence between interoceptive and agentic processes, providing a plausible neural substrate for their integration within a broader embodied decision-making framework, although this hypothesis has not yet been directly tested.

Taken together, these findings raise the hypothesis of a partially shared neural architecture connecting interoception, agency, and the systems implicated in embodied choice, consistent with the existence of a coordinated, systems-level network supporting embodied decision-making. This view emphasises the importance of examining these components together within an integrated neurofunctional account.

Here, we propose a systems-level framework of embodied decision-making that integrates interoceptive and agentic dimensions of bodily self-awareness with delay-discounting-related cognitive impulsivity as a specific form of value-based choice. We hypothesized that interoception and agency would show partial convergence within neural systems supporting bodily and action-related monitoring, while displaying differentiated large-scale organization relative to valuation-related circuitry.

To test this framework, we combined three coordinate-based meta-analyses with seed-based resting-state functional connectivity analyses using the resulting domain-specific maps. We first characterized the network organization of these systems in healthy individuals and then examined whether their relative connectivity profiles were altered in cocaine use disorder, a condition marked by maladaptive value-based decision-making.

2. Materials and methods

Our PRISMA-compliant meta-analyses (Supplementary Figures S1–S3) involved a series of analytical steps, starting from selecting the raw data (data collection and data preparation) to the classification of the peaks associated with brain functional activation in *agency*, *delay discounting*, and *interoceptive* tasks (Page et al., 2021). We created a separate dataset of functional data for each task. Then, using the software GingerALE (<https://www.brainmap.org/ale/>, version 3.0.2; Turkeltaub et al., 2012) we conducted three separate meta-analyses, one for each task adhering to current best-practice guidelines for fMRI meta-analyses (Müller et al., 2018). Coordinates associated with distinct contrasts from the same study that fulfil the search criteria for a given meta-analysis were pooled into a single experiment to avoid dependence across maps resulting from multiple experiments with the same participants (Müller et al., 2018; Turkeltaub et al., 2012). Following the single-domain analyses, we quantitatively compared the resulting activation maps through conjunction and contrast analyses to identify shared and domain-specific neural substrates. To further explore the overlap among the networks involved in the processes of interest we then performed a series of seed-based functional connectivity analyses on resting-state fMRI data considering the clusters identified in the meta-analyses as regions of interest.

3. Data collection and preparation

3.1. Sense of agency dataset

We identified neuroimaging studies exploring the neural correlates of the *sense of agency*, using the following procedure, illustrated in Supplementary Figure S1. We first retrieved neurofunctional studies included in Seghezzi et al. (2019), then we entered the same search queries in the PubMed database to update the search from March 2019 to February 2023 (<https://pubmed.ncbi.nlm.nih.gov/>): (“fMRI”) OR (“functional neuroimaging”) OR (“PET”) OR (“neural basis”) OR (“neural correlate”) AND (“sense of agency”) [All Fields]. Then, we ran a preliminary selection based on the titles and abstracts of the papers, through which we included only the studies that matched the following criteria:

- Studies including healthy subjects.
- Studies reporting results using stereotaxic coordinates (either MNI or Talairach atlases).
- Studies reporting whole-brain peaks (no region-of-interest analyses).
- For studies assessing the effects of hormonal or drug treatments, we considered only studies that reported foci belonging to the pre-treatment condition.

This selection, initially based on titles and then on abstracts, yielded the identification of 32 candidate papers for the first meta-analysis of *agency* data. We made a further selection by inspecting the manuscripts and applying the inclusion criteria in detail. Further, we conducted an up-to-date manual scan of the references of the selected articles to ensure that all relevant papers had been included. All manuscripts were screened independently by two reviewers (LZ, FD); any discrepancy was resolved through a collaborative discussion. All the relevant data were then entered on the predefined spreadsheet by two investigators independently (LZ, FD). By applying such criteria, we included 23 papers yielding a total of 25 contrasts and 188 foci. The final dataset comprised a total of 411 participants. The mean age of the participants was 27.49 years (age range: 20.9 – 44.5). Information about the (mean) age of participants was not available for 3 (Chambon et al., 2013; Leube et al., 2003; Matsuzawa et al., 2005) out of 23 studies. Further information about the included studies is available in Table 1 and Supplementary Table S1a. Talairach coordinates were converted using the Talairach to MNI (SPM) transformation tool implemented in the GingerALE

Table 1

Studies included in the three ALE-based meta-analyses.

Meta-analysis	Studies
Sense of Agency	Abdulkarim et al. (2023); Caspar et al. (2021); Chambon et al. (2013); David et al. (2007); De Bézenac et al. (2016); Farrer et al. (2003); Farrer and Frith (2002); Fukushima et al. (2013); Hackley et al. (2020); Kontaris et al. (2009); Koreki et al. (2019); Kühn et al. (2013); Leube (2003); Leube et al. (2003); Matsuzawa et al. (2005); Ohata et al. (2020); Renes et al. (2015); Salgado-Pineda et al. (2022); Sasaki et al. (2018); Schnell et al. (2007); Spengler et al. (2009); Tsakiris et al. (2010); Zapparoli et al. (2020)
Cognitive Impulsivity	Albrecht et al. (2011); Ballard and Knutson (2009); Benoit et al. (2011); Castrellon et al. (2019); Christakou et al. (2011); Dennis et al. (2020); Eppinger et al. (2012); Eppinger et al. (2018); Grosskopf et al. (2021); Jimura et al. (2018); Kable and Glimcher (2007); Kable and Glimcher (2010); Le Bouc and Pessiglione (2022); Li et al. (2013); Luo et al. (2009); Massar et al. (2015); Mavrogiorgou et al. (2017); McClure et al. (2004); Peters and Büchel (2009); Peters and Büchel (2010); Pine et al. (2009); Pine et al. (2010); Ripke et al. (2012); Sasse et al. (2015); Seaman et al. (2018); Sripada et al. (2011); Wang et al. (2014); Xu et al. (2009); Zha et al. (2019); Zhuang et al. (2020)
Interoception	Araujo et al. (2015); Avery et al. (2015); Bauer et al. (2014); Becker et al. (2015); Binks et al. (2014); Blefari et al. (2017); Brannan et al. (2001); Caseras et al. (2013); Coen et al. (2009); Critchley et al. (2004); Denton et al. (1999a); Denton et al. (1999b); Egan et al. (2003); Ernst et al. (2013); Evans et al. (2002); Farb et al. (2013); Farrell et al. (2006); Haase et al. (2015); Haase et al. (2016); Haruki and Ogawa (2021); Haruki and Ogawa (2023); Hassanpour et al. (2018); Immordino-Yang et al. (2014); Isaev et al. (2002); Kuehn et al. (2016); Liotti et al. (2001); May et al. (2014); Oberndorfer et al. (2013); Perini et al. (2015); Pollatos et al. (2007); Simmons et al. (2013); Stern et al. (2017); Terasawa et al. (2013); Tracy et al. (2007); Wang et al. (2014); Zaki et al. (2012)

software.

3.2. Cognitive impulsivity dataset

We identified neuroimaging studies exploring the neural correlates of *delay discounting*, using the following procedure, illustrated in Supplementary Figure S2. We first retrieved studies included in Mattavelli et al. (2024), then the same search string was entered in the PubMed database (<https://pubmed.ncbi.nlm.nih.gov/>) to update the search from December 2020 to February 2023:

(“fMRI”) OR “functional MRI” OR “functional magnetic resonance imaging” OR “blood oxygenation level dependent (BOLD)” AND (“DD” OR “temporal discounting” OR “delay of gratification” OR “inter-temporal decision making” OR “intertemporal choice”) [All Fields].

After removing duplicates, the dataset of newly retrieved manuscripts comprised 48 studies. Then, we ran a preliminary selection based on the titles and abstracts of the papers, including only studies that met the same criteria as above (healthy participants, whole-brain analyses reporting peaks in MNI or Talairach space, pre-treatment data in studies with hormonal or drug treatments).

This selection, initially based on titles and abstracts, yielded the identification of 22 candidate papers for the meta-analysis of *delay discounting* data. We made a further selection by inspecting the entire manuscripts and applying the inclusion criteria in detail. Further, we conducted an up-to-date manual scan of the references of the selected articles to ensure that all relevant papers had been included. All manuscripts were screened independently by two reviewers (IG, GM); any discrepancy was resolved through a collaborative discussion (IG, GM). All the relevant data were then entered on the predefined spreadsheet by the two investigators independently. By applying such criteria, we included 30 papers (28 from the previously published meta-analyses and two studies resulting from the updated search) yielding a total of 37

contrasts and 372 foci. The final dataset comprised a total of 916 participants. The mean age of the participants was 25.29 years (age range: 21–35). Further information about the included studies is available in Table 1 and Supplementary Table S1b. Talairach coordinates were converted using the Talairach to MNI (SPM) transformation tool implemented in the GingerALE software.

3.3. Interoception dataset

We identified neuroimaging studies exploring the neural correlates of *interoception*, using the following procedure, illustrated in Supplementary Figure S3. Studies included in a previously published meta-analysis (Salvato et al., 2020) were retrieved. To update the search with studies published between January 2018 and February 2023, we entered the same queries in the PubMed database (<https://pubmed.ncbi.nlm.nih.gov>): ((“fMRI”) OR (“functional neuroimaging”) OR (“PET”) OR (“neural basis”) OR (“neural correlate”)) AND ((“interoception”) OR (“cardioception”) OR (“visceral perception”) OR (“body emotions”) OR (“bodily emotions”) OR (“heartbeat”) OR (“heartbeat detection”)) [All Fields]. After removal of duplicates, the dataset of newly retrieved manuscripts comprised a total of 139 studies. The preliminary selection based on the titles and abstracts of the papers was conducted with the same criteria as above (healthy participants, whole brain analyses reporting peaks in MNI or Talairach, pre-treatment data in case of studies with hormonal or drug treatments).

This selection, initially based on titles and then on abstracts, yielded the identification of 50 candidate papers for the third meta-analysis of *interoception* data. We made a further selection by inspecting the entire manuscripts and applying the inclusion criteria in detail. Further, we conducted an up-to-date manual scan of the references of the selected articles to ensure that all relevant papers had been included. All manuscripts were screened independently by two reviewers (IG, GR); any discrepancy was resolved through a collaborative discussion. By applying such criteria, we included 36 papers yielding a total of 80 contrasts and 740 foci. The final dataset comprised a total of 1604 participants. The mean age of the participants was 29.53 years (age range: 15–55). Further information about the included studies is available in Table 1 and Supplementary Table S1c.

Talairach coordinates were converted using the Talairach to MNI (SPM) transformation tool implemented in the GingerALE software.

4. Activation likelihood estimation meta-analyses

Coordinate-based ALE meta-analyses estimate the spatial convergence of coordinates between experiments relative to the null hypothesis that these experiment foci are uniformly and randomly distributed across the brain.

In a “single dataset” analysis (e.g., using activation foci from one task only), the algorithm computes a map that contains, in every voxel, the probability that a given peak of activation included in the database lies within that specific voxel. This statistical index, called Activation Likelihood Estimation (ALE), represents the probability that at least one local maximum of activation lies within a specific voxel. A statistical computation is then performed across all voxels to identify foci that consistently represent a convergence of results from the studies entered into the meta-analysis. In the subsequent “contrast datasets” analysis, it is possible to quantitatively compare results from two different single-dataset analyses (e.g., the activation foci for agency and cognitive impulsivity). Through this computation, the user can identify the foci that are specifically associated with either a single dataset, more than the other, or the “conjunction” between two datasets. For each task, we performed a “single dataset” analysis by applying, as recommended, a cluster-level threshold of $p < 0.05$ family-wise error corrected, and a cluster-forming threshold of $p < 0.001$ uncorrected (Müller et al., 2018), with 1000 threshold permutations. Given that the input files for the contrast analysis were already conservatively thresholded, a less

stringent threshold was chosen for this additional examination, following the approach used in previous studies (Awana et al., 2026; Papitto et al., 2020). Thus, in the contrast-analysis we employed a threshold of $p < 0.01$ uncorrected, 10,000 permutations, and a minimum volume of 200 voxels for the following contrasts: (i) agency vs. interoception, (ii) cognitive impulsivity vs. agency, and (iii) interoception vs. cognitive impulsivity. Results were visualized on a ch2better template using the MRICroGL software (Rorden and Brett, 2000). Meta-analytic clusters resulting from the single dataset analyses of each task were then used as regions of interest (ROIs) in two functional connectivity analyses. Specifically, for each domain, the thresholded single-domain ALE map was entered as one seed in the subsequent seed-based functional connectivity analysis. Thus, the connectivity model included three distinct ALE-derived seeds, one for agency, one for delay-discounting-related impulsive choice, and one for interoception.

5. Re-analyses of previously published data and public datasets

To further explore the meta-analytical results, we performed a targeted re-analysis of previously published and publicly available resting-state datasets, selecting the meta-analytical clusters from the single-dataset analyses (i.e., agency, cognitive impulsivity, and interoception) as ROIs in seed-based functional connectivity analyses.

In the first re-analysis, seed-based resting-state functional connectivity was calculated from extracted ROIs in a sample of healthy young adults (Zapparoli et al., 2018). This approach, supported by meta-analytical results and cognitive decoding, can provide complementary insights into possible interactions among brain functional networks that sustain distinct healthy processes. In the second re-analysis, we ran a functional connectivity analysis based on resting-state data from the SUDMEX CONN dataset (Angeles-Valdez et al., 2022). Seed-based resting-state functional connectivity was calculated from the meta-analytical ROIs in a sample of healthy adults and adults with cocaine use disorder (CUD). This approach aimed to provide complementary information about possible dysfunctional interactions between brain functional networks that contribute to pathological processes. Full details on data acquisition, preprocessing, and statistical procedures are reported in the original publications and in the Supplementary Materials.

6. First dataset

6.1. Participants

Twenty-four healthy adult subjects (mean age: 27.1 ± 5.7 years; mean education level 14.9 ± 3.2 years; 8 males and 16 females) without any cognitive, neurological, or psychiatric illness participated in the resting-state fMRI study. They were all right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Each subject was asked to stay awake with their eyes closed. The study protocol was approved by the local Ethics Committee (IRCCS San Raffaele), and informed written consent was obtained from all subjects.

6.2. fMRI data acquisition, preprocessing and first-level analyses

MRI scanning was performed with a Siemens Avanto 1.5 T scanner equipped with gradient-echo echo-planar imaging. Before the acquisition of functional data, high-resolution T1-weighted structural images were acquired (flip angle 35° , TE 5 ms, TR 21 ms, FOV 256×192 mm, matrix 256×256 , TI 768, 160 slices with $1 \text{ mm} \times 1 \text{ mm} \times 1 \text{ mm}$ voxels). Echo-planar imaging gradient-echo fMRI scans [flip angle 90° , echo time (TE) = 60 ms, TR = 3000 ms, field of view = 280×210 mm, and matrix = 96×64 , slice thickness = 5 mm] were then acquired (212 volumes).

Resting-state BOLD raw data were pre-processed and analysed with

CONN, version 22a (<https://web.conn-toolbox.org>) (Whitfield-Gabrieli and Nieto-Castanon, 2012). Pre-processing was performed according to the default pipeline implemented in the CONN toolbox, including realignment with correction of susceptibility distortion interactions, slice timing correction, outlier detection, direct segmentation and MNI-space normalization, and smoothing. Functional data were realigned using the SPM realign & unwarp procedure, in which all scans were coregistered to the first scan using a least-squares approach and a 6-parameter (rigid-body) transformation, and resampled using B-spline interpolation to correct for motion and magnetic susceptibility interactions. Temporal misalignment between different slices of the functional data was corrected following SPM slice-timing correction procedure. Potential outlier scans were identified using ART (Whitfield-Gabrieli et al., 2011) as acquisitions with framewise displacement above 2 mm or global BOLD signal changes above 9 standard deviations, and a reference BOLD image was computed for each subject by averaging all scans excluding outliers. Functional and anatomical data were normalized into standard MNI space, segmented into grey matter, white matter, and CSF tissue classes, and resampled to 2 mm isotropic voxels using a direct normalization procedure with SPM's unified segmentation and normalization algorithm. Last, functional data were smoothed using spatial convolution with a Gaussian kernel of 10 mm full-width half-maximum.

After preprocessing, functional data were denoised using a standard denoising pipeline including the regression of potential confounding effects characterized by white matter timeseries (5 CompCor noise components), CSF timeseries (5 CompCor noise components), motion parameters and their first order derivatives (12 factors), outlier scans, and linear trends within each functional run, followed by bandpass frequency filtering of the BOLD timeseries between 0.008 Hz and 0.09 Hz. CompCor noise components within white matter and CSF were estimated by computing the average BOLD signal as well as the largest principal components orthogonal to the BOLD average, motion parameters, and outlier scans within each subject's eroded segmentation masks.

In the first level analysis, seed-based connectivity maps were estimated, characterizing the spatial pattern of functional connectivity with a seed area. Seed regions included the meta-analytical clusters identified from the single-dataset analyses of agency, cognitive impulsivity, and interoception. Functional connectivity strength was represented by Fisher-transformed bivariate correlation coefficients from a weighted general linear model, estimated separately for each seed area and target voxel, modeling the association between their BOLD signal timeseries.

6.3. Second-level analyses

Group-level analyses were performed using a separate General Linear Model (GLM). Voxel-level hypotheses were evaluated using multivariate parametric statistics with random-effects across subjects and sample covariance estimation across multiple measurements. Cluster-level inferences were based on parametric statistics from Gaussian Random Field theory (Worsley et al., 1996). At the group level, we first computed the positive functional connectivity of each ROI (i.e., each task). Then, we computed the following conjunction analysis to determine the brain areas whose positive functional connectivity is shared across the ROIs: agency $\cap$ cognitive impulsivity $\cap$ interoception (voxel-level $p < 0.001$ uncorrected, $p < 0.05$ FWE-corrected at cluster-level). Finally, we computed the following contrasts to determine the differences in functional connectivity patterns across the three networks: (i) agency $>$ interoception (inclusive mask with positive connectivity of agency) and interoception $>$ agency (inclusive mask with positive connectivity of interoception); (ii) cognitive impulsivity $>$ agency (inclusive mask with positive connectivity of cognitive impulsivity) and agency $>$ cognitive impulsivity (inclusive mask with

positive connectivity of agency); (iii) interoception $>$ cognitive impulsivity (inclusive mask with positive connectivity of interoception) and cognitive impulsivity $>$ interoception (inclusive mask with positive connectivity of cognitive impulsivity). Inclusive masks were thresholded at voxel-level, uncorrected $p < 0.001$. All the results were thresholded using a voxel-level threshold of $p < 0.001$ uncorrected, FWE-corrected at the cluster level with a threshold of $p < 0.05$ (Flandin and Friston, 2019).

6.4. Cognitive decoding

The Neurosynth decoder (<https://neurosynth.org>) was used to obtain a set of terms for each ROI's brain network in the functional connectivity analyses. The masks representing the positive connectivity of the agency, cognitive impulsivity, and interoception meta-analytical networks were used as input to the decoder to obtain 100 terms associated with the functional map. These terms were then screened to exclude words associated with discrete anatomical areas (e.g., cingulum, planum temporale, nucleus accumbens), and the remaining were used for interpretation.

7. Second dataset

7.1. Participants

Sixty healthy adult volunteers (healthy controls (HC) mean age: 30.6 ± 8.3 years, 2 missing data; mean education years 12.6 ± 3.3 years, 4 missing data; 47 males and 11 females, 2 missing data) and sixty-five individuals with CUD (mean age: 31.2 ± 7.4 years; mean education years 11.1 ± 3.2 years, 6 missing data; 58 males and 7 females) were selected for the resting-state functional connectivity analyses. Groups did not differ with respect to age ($U=1766$, $p=.55$) and gender distribution ($\chi^2(1)=1.7$, $p=.2$), while HC had more years of education compared to CUD ($U=1307$, $p=.01$). The majority of participants were right-handed (89.4%), followed by mixed handers (5.7%) and left-handers (4.9%). Groups did not differ in terms of laterality distribution ($\chi^2(2)=.07$, $p=.97$). Please refer to the original publication for further details on participants (Angeles-Valdez et al., 2022).

7.2. fMRI data acquisition, preprocessing and first-level analyses

MRI scanning was performed with a Philips Ingenia 3 T MR system (Philips Healthcare, Best, The Netherlands, and Boston, MA, USA), equipped with a 32-channel dS Head coil. For each participant, the following sequences were acquired: 1) resting-state, 2) T1-weighted and 3) High Angular Resolution Diffusion Imaging (DWI-HARDI), for a total scan time of approximately 50 min. During the resting-state, participants were asked to keep their eyes open, to relax and, as far as possible, not to think about anything. For the complete details on the structural and functional MRI sequences, please refer to the original publication (Angeles-Valdez et al., 2022). Preprocessing and first-level analyses were performed using the same analytical pipeline described for Study 1.

7.3. Second-level analyses

Similarly to Study 1, group-level analyses were performed using a separate General Linear Model. Voxel-level hypotheses were evaluated using multivariate parametric statistics with random-effects across subjects and sample covariance estimation across multiple measurements. Cluster-level inferences were based on parametric statistics from Gaussian Random Field theory (Worsley et al., 1996). At the group level, resting-state functional connectivity patterns were analysed with a mixed ANOVA with *group* (HC vs. CUD) as a between-subjects factor and

network (agency vs. cognitive impulsivity vs. interoception) as a within-subjects factor. We computed the group-by-network interaction to identify brain regions whose connectivity profiles differ across the three networks in CUD compared to HC. All the results were thresholded using a voxel-level threshold of $p < 0.001$ uncorrected, FWE-corrected at the cluster level with a threshold of $p < 0.05$ (Flandin and Friston, 2019). The connectivity values for the clusters showing a significant group-by-network interaction were extracted and analysed using a mixed ANOVA in Jamovi (version 2.6) to assess the interaction effect. Post-hoc comparisons were Holm-corrected for multiple comparisons. Because the two groups differed significantly in years of education, the analysis was repeated with education included as a covariate. Clusters remaining significant in this covariate-adjusted analysis are identified in the Results.

8. Results

8.1. ALE meta-analyses of single datasets

8.1.1. Agency

The meta-analysis of neuroimaging studies on agency revealed significant convergence across studies in the insular cortex, bilaterally, and in the left putamen (Supplementary Table S2 and Fig. 1, blue).

8.1.2. Cognitive impulsivity

The results of the meta-analysis of studies on cognitive impulsivity (operationalized through parameters reflecting impulsive behaviour in the DDT) showed significant convergence across studies in a fronto-striatal network, including the ventral (nucleus accumbens) and dorsal striatum (caudate head and putamen), bilaterally, the pallidum, the VMPFC, the superior medial PFC, and the ACC. In addition, the left supramarginal and angular gyri, and the middle and posterior cingulate cortex showed significant convergence across studies (Supplementary Table S2 and Fig. 1, red).

8.1.3. Interoception

The meta-analysis of studies on interoception showed significant convergence in a bilateral cortical network including the insular cortex, the precentral and postcentral gyri, the inferior frontal cortex (pars opercularis), and the Rolandic operculum. In addition, the SMA, middle cingulum, left inferior parietal cortex and the left supramarginal gyrus showed a significant convergence across studies (Supplementary Table S2 and Fig. 1, green). Of note, the bilateral clusters in the insular cortex showed an anatomical overlap with the results of the meta-analysis on agency (Supplementary Table S2 and Fig. 1, cyan).

8.2. Contrast dataset

8.2.1. Agency vs. interoception

Agency $\cap$ interoception. The conjunction analysis showed statistically significant anatomical overlap in the insular cortex, bilaterally.

Agency $>$ interoception. The contrast meta-analysis showed greater convergence for studies on agency compared to interoception in the left putamen.

Interoception $>$ agency. On the other hand, greater convergence for interoception compared to agency was found in the right Rolandic operculum, middle cingulum, and left supramarginal gyrus (Supplementary Table S3 and Fig. 2A).

8.2.2. Cognitive impulsivity vs. agency

Agency $\cap$ cognitive impulsivity. The conjunction analysis showed no anatomical overlap between the meta-analysis of studies on agency and cognitive impulsivity.

Cognitive impulsivity $>$ agency. Greater convergence for studies on cognitive impulsivity compared to agency was found in a fronto-striatal network including the ventral (left nucleus accumbens) and dorsal striatum (left caudate nucleus), the VMPFC, the superior medial PFC, and the ACC. In addition, the left supramarginal and angular gyri, and the middle and posterior cingulate cortex showed greater convergence across studies on cognitive impulsivity.

Agency $>$ cognitive impulsivity. Compared to studies on cognitive impulsivity, the meta-analysis of studies on agency showed greater convergence in the left insular cortex, extending to the putamen (Supplementary Table S3 and Fig. 2B).

8.2.3. Interoception vs. cognitive impulsivity

Cognitive impulsivity $\cap$ interoception. The conjunction analysis showed no anatomical overlap between the meta-analysis of studies on interoception and cognitive impulsivity.

Interoception $>$ cognitive impulsivity. Compared to studies on cognitive impulsivity, the meta-analysis of studies on interoception showed greater convergence in a largely bilateral cortical network including the insular cortex, the right precentral and postcentral gyri, and inferior frontal cortex (pars opercularis), and the Rolandic operculum. In addition, the SMA, middle cingulum, left inferior parietal cortex and the left supramarginal gyrus showed greater convergence for studies on interoception compared to cognitive impulsivity.

Cognitive impulsivity $>$ interoception. Greater convergence for studies on cognitive impulsivity compared to interoception was found in a fronto-striatal network including the ventral (nucleus accumbens) and dorsal striatum (caudate head and putamen), bilaterally, the pallidum,

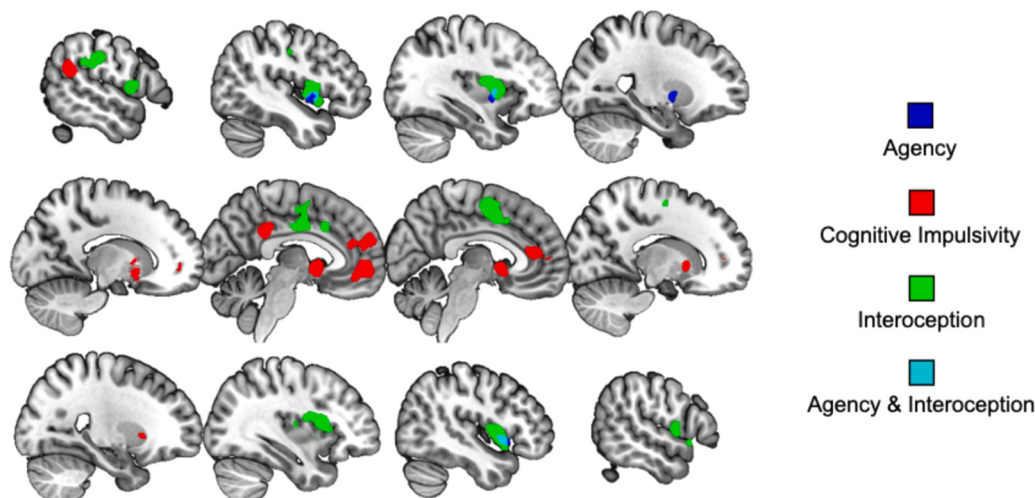


Fig. 1. Results of the single dataset ALE meta-analyses.

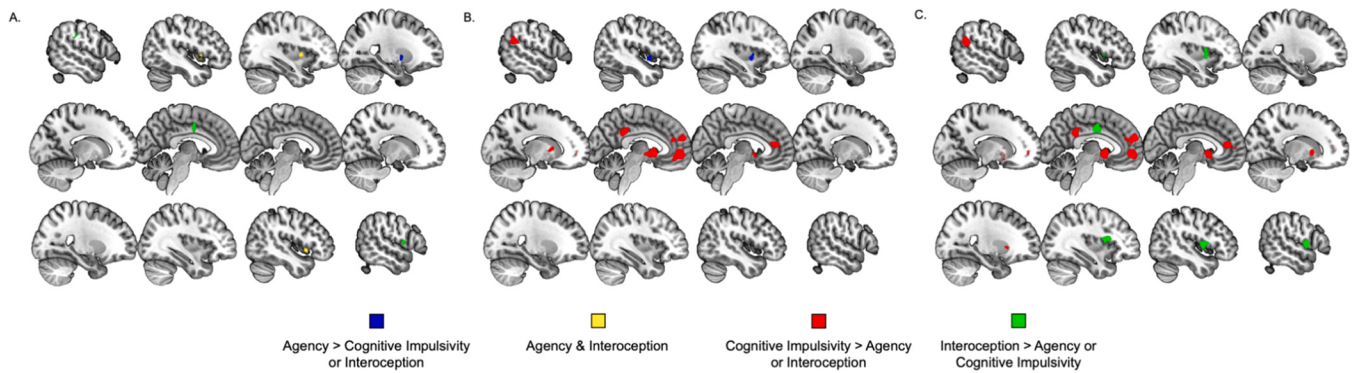


Fig. 2. Results of the contrast dataset ALE meta-analyses.

the VMPFC, the superior medial PFC, and the ACC. In addition, the left supramarginal and angular gyri, and the middle and posterior cingulate cortex showed significant convergence across studies (Supplementary Table S3 and Fig. 2C).

8.2.4. Summary of meta-analytical results

The results of the ALE meta-analyses revealed that agency and interoception recruit partly distinct but overlapping brain regions. Both converge in the bilateral insula, highlighting a shared reliance on areas supporting bodily awareness and integration of internal and external signals. Beyond this common core, agency showed greater convergence in the left putamen, linked to action–outcome processing, whereas interoception involved the right Rolandic operculum, middle cingulum, and left supramarginal gyrus, associated with sensory integration and bodily signal monitoring. In contrast, cognitive impulsivity engaged a fronto-parietal and striatal network with no overlap with agency or interoception, suggesting spatially distinct patterns of convergence; whether this reflects functionally independent mechanisms was further examined through the connectivity analyses reported below.

8.3. Resting-state functional connectivity data - First dataset

8.3.1. Single networks

8.3.1.1. Agency. The agency ROI was functionally connected with a largely bilateral network including the right superior PFC, the medial PFC including the ACC, the middle cingulum and the SMA, the parietal cortex including the supramarginal gyrus, and the superior temporal cortex. In addition, the amygdalae, the dorsal striatum, including the caudate and putamen, the pallidum, the thalamus, and the left cerebellum showed positive functional connectivity with the agency ROI (Supplementary Table S4 and Fig. 3A).

8.3.1.2. Cognitive impulsivity. The cognitive impulsivity ROI was functionally connected with a large fronto-parietal network including the superior and medial PFC, the VMPFC, the rectus, the ACC, and the OFC, the middle and posterior cingulum, the precuneus, and the superior and inferior parietal cortex. The analysis showed positive connectivity with regions of the temporal (temporal poles, inferior, middle, and superior temporal gyri, fusiform gyri) and occipital areas (cuneus, middle

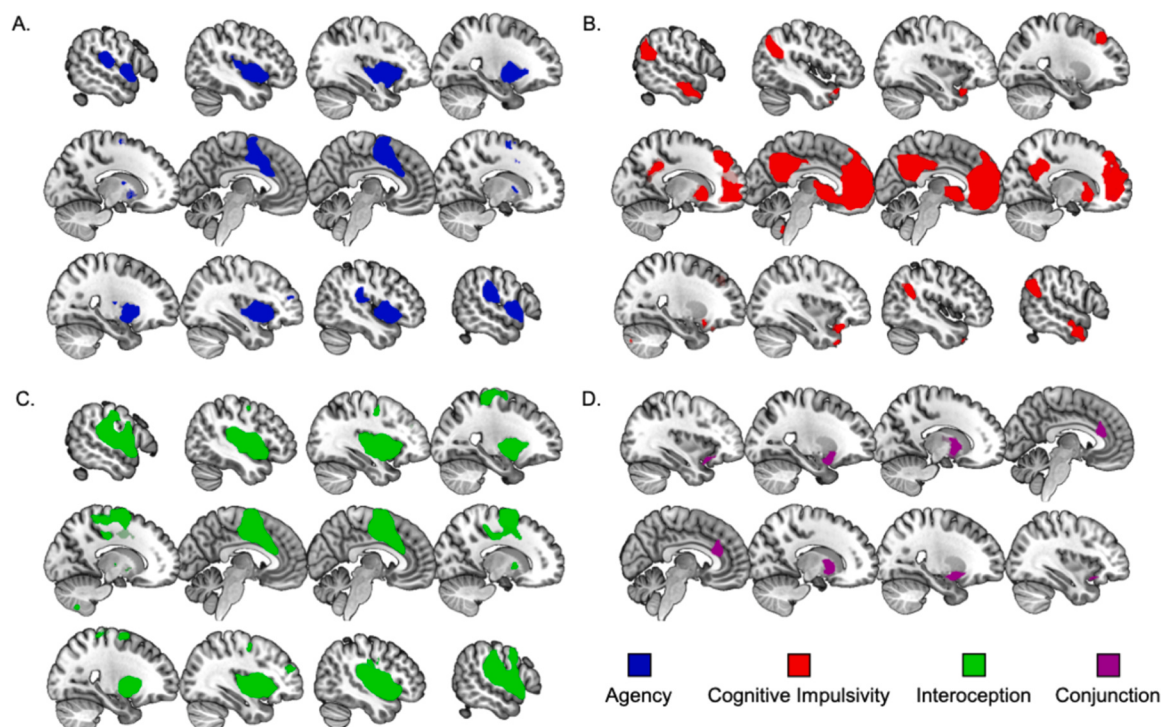


Fig. 3. Results of resting-state functional connectivity analysis mapping the positive connectivity of the three meta-analytic networks.

occipital gyrus, calcarine fissure, lingual gyri). In addition, the cognitive impulsivity ROI was functionally connected with several subcortical areas including the ventral (nucleus accumbens) and dorsal (caudate, putamen) striatum, the pallidum, the thalamus, and the cerebellum (Supplementary Table S4 and Fig. 3B).

8.3.1.3. Interoception. The interoception ROI was functionally connected with a wide bilateral fronto-temporo-parietal network, including the superior and inferior PFC, the OFC, the anterior and middle ACC, the SMA, the precentral and postcentral gyri, the insular cortex, the superior temporal cortex, and the parietal cortex including the supramarginal gyrus. The interoception network was functionally connected with several subcortical areas including the dorsal striatum (caudate, putamen) and the pallidum (Supplementary Table S4 and Fig. 3C).

8.3.1.4. Agency $\cap$ cognitive impulsivity $\cap$ interoception. The conjunction analysis showed that positive functional connectivity of the agency, cognitive impulsivity, and interoception meta-analytic networks converge in the dorsal ACC, and the bilateral dorsal striatum (putamen and caudate), extending bilaterally to the pallidum, amygdala, the bilateral ventral anterior insula and posterior orbitofrontal cortices. Further, the left thalamus, particularly the ventrolateral nucleus, and the left superior temporal pole showed significant overlap across the three meta-analytic networks (Supplementary Table S4 and Fig. 3D).

8.4. Cognitive decoding

Agency. The agency network was associated with terms related to pain and auditory perception (e.g., “pain”, “nociceptive”, “auditory”, “sound”) and to motor preparation and production (e.g., “movement”, “generation”, “motor imagery”, “preparation”) (Supplementary Figure S4A).

Cognitive impulsivity. The cognitive impulsivity network was associated with terms largely related to the default mode network including self-referential thinking and autobiographical memory (e.g., “default”, “episodic”, “self-referential”, “memory retrieval”), and with terms related to reward processing and value-based decision-making (e.g., “incentive”, “monetary”, “value”, “rewards”) and social cognition (e.g., “theory of mind”, “mentalizing”, “beliefs”, “social cognition”) (Supplementary Figure S4B).

Interoception. The interoception network was associated with terms related to motor control and execution (e.g., “production”, “movements”, “motor”), to pain perception and sensory integration (e.g., “pain”, “somatosensory”, “sensorimotor”, “tactile”, “auditory”), and to the human body (e.g., “finger”, “hand”, “foot”) (Supplementary Figure S4C).

Conjunction. The areas of convergence across the three meta-analytic networks were largely associated with terms related to reward processing and motivation (e.g., “monetary”, “reward”, “gain”, “loss”, “reinforcement”), and to impulsivity, avoidance, and dopamine (e.g., “impulsivity”, “avoidance”, “risky”, “dopamine”, “dopaminergic”) (Supplementary Figure S4D).

8.5. Contrast analyses

8.5.1. Agency vs. interoception

Agency > interoception. Compared to the interoception ROI, the agency ROI showed greater connectivity only with the ROI itself, comprising the left putamen and insula. These differences were driven by greater positive functional connectivity of the regions with the agency ROI compared to the interoception ROI. **Interoception > Agency.** Compared to the agency ROI, the interoception ROI showed greater positive connectivity with a large cortical circuit comprising the superior, inferior and medial PFC, the anterior and middle cingulate cortex, the SMA, the precentral and postcentral gyri, the paracentral lobule, the insular cortex, the superior temporal cortex, the temporal poles, and the

parietal cortex, including the supramarginal gyri. In addition, the putamen showed greater positive connectivity with interoception than with the agency ROI. These differences were driven by greater positive functional connectivity of the regions with the interoception ROI compared to the agency ROI (see Supplementary Table S5 and Fig. 4A).

8.5.2. Agency vs. cognitive impulsivity

Agency > cognitive impulsivity. Compared to the cognitive impulsivity ROI, the agency ROI showed greater positive connectivity with the lateral inferior and superior PFC, the SMA, the postcentral gyrus, the inferior and superior temporal cortex, and the superior parietal cortex. In addition, the agency network showed greater positive connectivity with the putamen and pallidum, and with the cerebellum. These differences were driven by positive functional connectivity with the agency ROI and negative connectivity with the cognitive impulsivity ROI. **Cognitive impulsivity > agency.** The cognitive impulsivity compared to the agency network showed greater positive connectivity with a large fronto-parietal network, including the superior and medial PFC, the VMPFC, the rectus, the ACC, and the OFC, the SMA, the middle and posterior cingulum, the precuneus, and the superior and inferior parietal cortex. Greater positive connectivity was also observed with regions of the temporal cortex (temporal poles, inferior, middle, and superior temporal gyri, fusiform gyri). In addition, the cognitive impulsivity network was functionally connected with several subcortical areas including the ventral (nucleus accumbens) and dorsal (caudate, putamen) striatum, the pallidum, and the cerebellum. These differences were driven by positive functional connectivity with the cognitive impulsivity ROI and negative functional connectivity with the agency ROI (see Supplementary Table S5 and Fig. 4B).

8.5.3. Interoception vs. cognitive impulsivity

Interoception > cognitive impulsivity. Compared to the cognitive impulsivity network, the interoception network showed greater positive connectivity with a large cortical circuit comprising the inferior and superior PFC, the anterior and middle cingulate cortex, the SMA, the precentral and postcentral gyri, the paracentral lobule, the insular cortex, the inferior, middle and superior temporal cortex, the temporal poles, and the parietal cortex including the supramarginal gyri and the inferior parietal cortex. In addition, the putamen and the cerebellum showed greater positive connectivity with the interoception compared to the cognitive impulsivity ROI. These differences were driven by greater positive connectivity with the interoception network and negative connectivity with the cognitive impulsivity network.

Cognitive impulsivity > interoception. Compared to the interoception ROI, the cognitive impulsivity ROI showed greater positive connectivity with a large fronto-parietal network including the superior and medial PFC, the VMPFC, the rectus, the ACC, and the OFC, the SMA, the middle and posterior cingulum, the precuneus, and the superior and inferior parietal cortex. The analysis showed greater positive connectivity with regions of the temporal (temporal poles, inferior, middle, and superior temporal gyri, fusiform gyri) and occipital areas (cuneus, middle occipital gyrus, calcarine fissure, lingual gyri). In addition, the cognitive impulsivity network exhibited greater positive connectivity with several subcortical areas, including the ventral (nucleus accumbens) and dorsal (caudate, putamen) striatum, the pallidum, and the thalamus. These differences were driven by positive connectivity with the cognitive impulsivity ROI and negative connectivity with the interoception ROI (see Supplementary Table S5 and Fig. 4C).

8.6. Summary of the functional connectivity results

The functional connectivity profile of the three meta-analytic networks suggests that the agency, interoception, and cognitive impulsivity networks share a common hub but maintain distinct connectivity profiles. All three networks were functionally linked to the dorsal ACC and bilateral putamen, indicating partially overlapping integration sites.

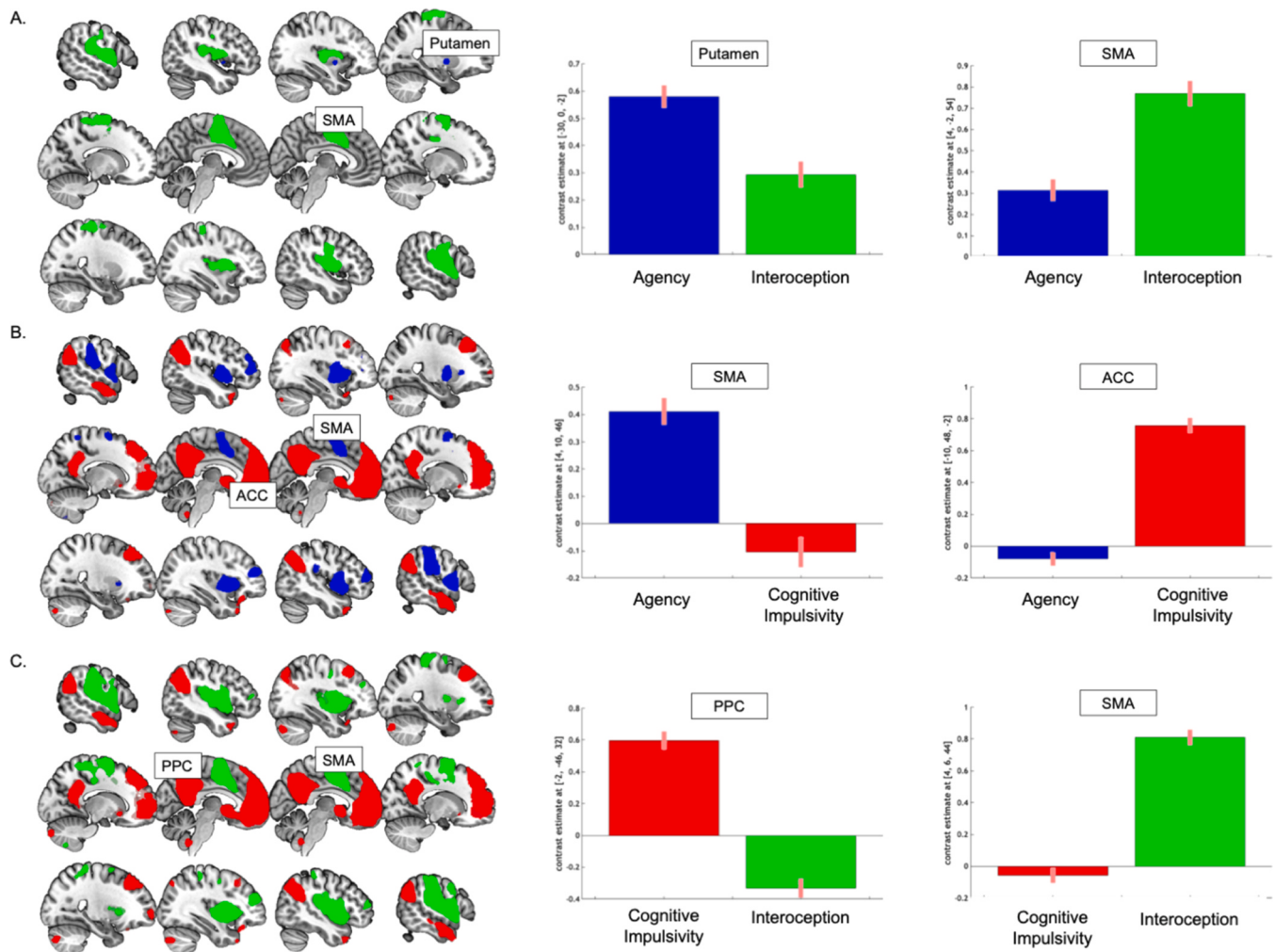


Fig. 4. Results of the resting-state functional connectivity contrast analyses between the agency, cognitive impulsivity, and interoception networks. Blue = agency, red = cognitive impulsivity, green = interoception. (A) Agency vs. interoception. (B) Agency vs. cognitive impulsivity. (C) Cognitive impulsivity vs. interoception. SMA = supplementary motor area; ACC = anterior cingulate cortex; PPC = posterior parietal cortex.

Agency and interoception showed substantial overlap, with the latter displaying stronger connectivity with the SMA, insula, and sensorimotor cortices. In contrast, the cognitive impulsivity network showed an opposing connectivity profile relative to the agency and interoception network, particularly involving the VMPFC, striatum, precuneus, and parietal cortices, indicating opposing, anti-correlated connectivity profiles between reward-based valuation systems and networks supporting bodily self-awareness and sensorimotor integration.

8.7. Resting-state functional connectivity data - Second dataset

8.7.1. Group-by-network interaction

The results of the 2×3 rmANOVA revealed four clusters showing a significant group-by-network interaction, indicating that the functional coupling of the agency, interoception, and cognitive impulsivity networks differs systematically between healthy controls (HC) and individuals with CUD; post-hoc comparisons within each cluster are detailed below.

A central finding emerged in the caudate nucleus. Compared to HC, participants with CUD displayed hypo-connectivity of the agency and interoception networks with the caudate nucleus, and hyper-connectivity of the cognitive impulsivity network (Fig. 5A).

Compared to HC, patients with CUD showed hypo-connectivity of the agency network with the paracentral lobule/SMA (Fig. 5B) and with the precentral gyrus (Fig. 5C), while no difference between groups was

observed for the cognitive impulsivity and interoception networks.

Finally, compared to HC, CUD individuals showed hyper-connectivity of the cognitive impulsivity network and hypo-connectivity of the agency network ($p = .06$) with the superior frontal gyrus (Fig. 5D), while no difference between groups was observed for the interoception network (see also [Supplementary Table S6](#)). The caudate nucleus (Fig. 5A) and precentral gyrus (Fig. 5C) clusters remained significant after controlling for education, whereas the paracentral lobule/SMA (Fig. 5B) and superior frontal gyrus (Fig. 5D) clusters did not survive, indicating that the caudate and precentral gyrus effects were not attributable to the between-group difference in educational attainment.

Collectively, this pattern suggests that, in CUD, prefrontal regions associated with valuation and self-referential processing become more tightly coupled with impulsivity-related circuits and less integrated with networks supporting volitional control. The results of the rmANOVA for each cluster and the ensuing post-hoc comparisons are reported in [supplementary materials](#) ([Supplementary Tables S7–S10](#)).

9. Discussion

The present study combined coordinate-based meta-analyses and resting-state functional connectivity analyses to characterize the large-scale neural organization linking bodily self-awareness and valuation-related processes. Three principal findings emerged. First,

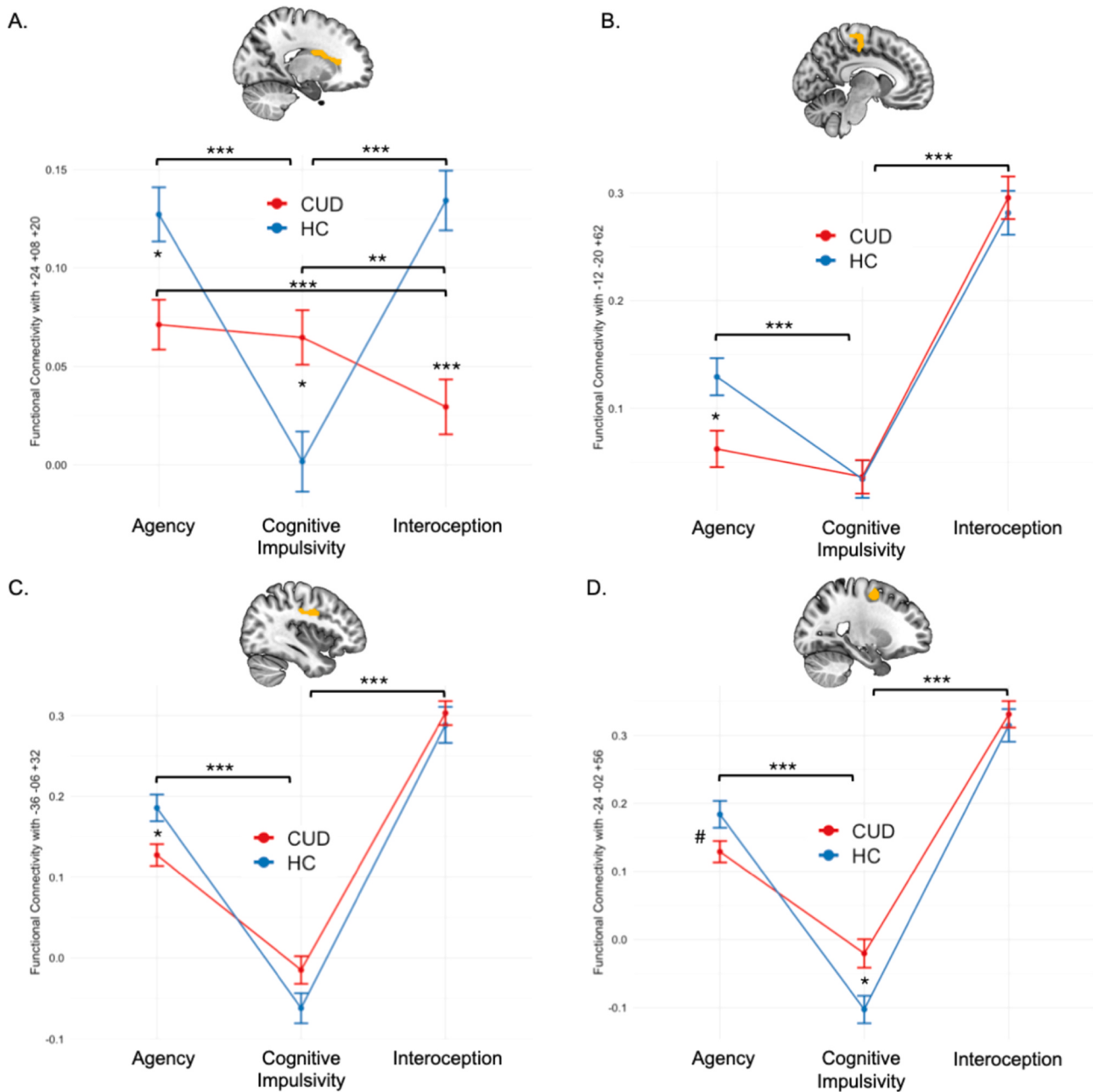


Fig. 5. Regions showing a significant Group (HC vs. CUD) $\times$ Network (agency, cognitive impulsivity, interoception) interaction in resting-state functional connectivity. (A) Caudate nucleus: relative to HC, participants with CUD showed reduced connectivity of the agency and interoception networks with the caudate, together with increased connectivity of the cognitive impulsivity network. (B) Paracentral lobule/SMA: participants with CUD showed reduced connectivity of the agency network relative to HC, with no group differences for the cognitive impulsivity or interoception networks. (C) Precentral gyrus: as in B, participants with CUD showed reduced connectivity of the agency network relative to HC, with no group differences for the other two networks. (D) Superior frontal gyrus: participants with CUD showed increased connectivity of the cognitive impulsivity network and reduced connectivity of the agency network relative to HC, with no group differences for the interoception network. #: $p = 0.06$.

interoception and agency showed partial anatomical convergence in the bilateral insula, while also recruiting domain-specific regions. Second, delay-discounting-related cognitive impulsivity showed a distinct pattern of spatial convergence involving fronto-striatal and default-mode-network regions. Third, the three meta-analytically defined systems exhibited differentiated functional connectivity profiles, and this organization was altered in cocaine use disorder, particularly in the connectivity of the caudate nucleus. The following sections discuss these findings in relation to the functional organization of bodily self-awareness, its relationship with valuation-related circuitry, and the alterations observed in cocaine use disorder.

The first meta-analytic findings delineate both shared and distinct large-scale neural architectures supporting interoception, agency, and cognitive impulsivity. The bilateral middle insula and left putamen emerged as the core neural substrate of agency, consistent with their role in action–outcome monitoring and prediction–error integration for self-generated actions (Haggard, 2017; Wen and Imamizu, 2022). Interoception was associated with the activity of a partially overlapping network involving the insula, pre- and postcentral gyri, and supplementary motor area, consistent with its established role in representing internal bodily states and transforming visceral and somatosensory signals into conscious awareness (Critchley and Garfinkel, 2017). The

convergence of interoception and agency in the bilateral middle insula identifies this region as a core hub of bodily self-awareness, linking internal bodily signals with motor and affective processes (Craig, 2009). This finding is consistent with evidence that the insula integrates viscerosensory, sensorimotor, and motivational information (Cauda et al., 2011) and supports higher-order representations of bodily selfhood and agency (Seghezzi et al., 2019; Seth, 2013). By contrast, cognitive impulsivity neural activation data converged on a distinct network encompassing the striatum, medial prefrontal cortex, anterior and posterior cingulate cortex, and supramarginal gyrus - regions centrally involved in reward valuation, self-referential processing, and future-oriented decision-making (Mattavelli et al., 2024; Raichle and Snyder, 2007). The absence of overlap between cognitive impulsivity-related regions and those supporting bodily self-awareness indicates that these processes do not consistently recruit the same loci of peak activation across studies, though this does not in itself imply functional independence; as shown by the connectivity analyses (see below), these networks are in fact functionally related, albeit through an opposing coupling pattern.

At the network level, the meta-analytical results were sharpened by intrinsic connectivity patterns. All three networks showed connectivity with the anterior insula, the dorsal anterior cingulate cortex, and the bilateral putamen, a shared core linked to reward processing and motivation (Stuber, 2023; Yarkoni et al., 2011). These regions have been proposed to integrate internal and external cues to guide adaptive responses to environmental demands (Arioli et al., 2025; Canessa et al., 2013). Beyond this shared architecture, interoception and agency networks largely overlapped within the salience network, supporting their joint role in detecting and integrating bodily and environmental signals. In contrast, cognitive impulsivity-related regions mapped more strongly onto the default mode network, including the ventromedial prefrontal cortex and posterior cingulate cortex, which are implicated in subjective value computation and internally oriented cognition (Acikalin et al., 2017). Critically, the relationship between these systems was characterized by intrinsic anti-correlations. Regions associated with cognitive impulsivity exhibited inverse functional coupling with those underpinning bodily self-awareness, suggesting a functional organization consistent with an opposing relationship between bodily self-awareness and reward-oriented decision processes. This functional organization provides a systems-level account for why impulsive choices are often associated with reduced sensitivity to bodily feedback and impaired action monitoring (Poppa and Bechara, 2018). We highlight, however, that resting-state anti-correlations reflect a static, correlational property of intrinsic connectivity and do not, by themselves, demonstrate a direct mechanistic competition between systems; task-based and effective connectivity approaches will be needed to directly test this interpretation. An anti-correlated connectivity pattern is also compatible with alternative accounts, such as functional specialization (whereby these systems process distinct classes of information without directly competing for shared resources) or complementary processing (whereby their activity is coordinated rather than opposed, alternating according to task demands). Resting-state data cannot arbitrate between these possibilities, and future task-based studies manipulating the relative demands on bodily self-awareness and valuation processes will be needed to determine whether their relationship is genuinely competitive, as we will discuss below.

From a clinical perspective, CUD provides an informative test case for examining whether the relative functional organization of bodily self-awareness and valuation-related networks is altered in a condition characterized by heightened impulsivity, altered reward sensitivity, and impaired self-awareness (Coffey et al., 2003; Fillmore and Rush, 2002; Render and Jansen, 2019). While the large-scale architecture of agency, interoception, and cognitive impulsivity networks was broadly preserved, CUD was characterized by a reconfiguration of their functional relationships. In particular, agency-related networks showed reduced coupling with sensorimotor regions, including the precentral cortex,

paracentral lobule, and supplementary motor area, indicating a weakened integration of action-related bodily feedback. The most pronounced alteration involved the caudate nucleus. In healthy individuals, the caudate preferentially couples with interoceptive and agentic networks, consistent with its role in integrating bodily signals and action monitoring into goal-directed behaviour. In CUD, this pattern was reversed: the caudate exhibited enhanced connectivity with cognitive impulsivity-related circuits and reduced integration with the bodily self-awareness system. This inversion indicates a possible pathological reallocation of striatal resources, in which reward-driven valuation gains take precedence over bodily and action-monitoring signals.

Importantly, this reorganization cannot be reduced to a simple hyper-responsivity to reward. Rather, it may reflect a systems-level imbalance characterized by reduced functional integration of valuation-related circuitry with networks associated with bodily and action-related processing. These findings extend prior evidence of fronto-striatal dysfunction in addiction (Hanlon et al., 2015; Vaquero et al., 2017) by showing that connectivity alterations in this clinical population may not be reducible to exaggerated reward sensitivity alone, but may also reflect a disruption of the intrinsic connectivity that normally anchors valuation to bodily and action-related information. As the present dataset did not include direct behavioural, interoceptive, or agency measures, whether this connectivity reorganization translates into the maladaptive decision-making typically associated with addiction remains to be directly tested.

Taken together, these findings support a reconceptualization of the SMH as a multi-component and systems-level framework. Our results are consistent with a model in which interacting components - interoceptive access to bodily states, and agentic monitoring of action-outcome relationships - jointly shape decision-making by modulating their balance with reward-driven valuation systems (Fig. 6). As illustrated in Fig. 6B, in healthy individuals interoceptive and agentic networks form a coordinated bodily self-awareness system whose functional organization is associated with greater integration of bodily and action-related signals relative to valuation-driven processes. By contrast, in CUD (Fig. 6B, right), this balance appears shifted toward cognitive impulsivity-related circuits, as reflected in the reorganization of caudate connectivity and reduced coupling between agency-related networks and sensorimotor regions. Under these conditions, bodily and action-related signals may remain present but may be less effectively integrated into decision-making, offering a candidate neural substrate potentially relevant to the disconnect between physiological responses and adaptive choice described in prior behavioural work (Crone et al., 2004; Dunn et al., 2006), which the present connectivity data cannot directly test. This interpretation should therefore be regarded as a biologically plausible hypothesis generated by the present connectivity findings rather than as a direct demonstration of altered decision-making.

Converging evidence from other populations supports this perspective. Impairments in agency and interoception have been associated with dysregulated behaviour and impulsivity across conditions such as schizophrenia, ADHD, and substance use disorders (Brown et al., 2018; Bruton et al., 2025; Stewart et al., 2013), whereas higher interoceptive accuracy predicts lower impulsivity (Herman et al., 2019; Reader and Salvato, 2024; Salvato et al., 2018), suggesting that bodily self-awareness may function as a protective factor against maladaptive choice.

Several limitations should be considered when interpreting the present findings.

Methodologically, the use of resting-state connectivity data does not allow causal inference and may reflect intrinsic network organization rather than task-specific dynamics; relatedly, our approach captures spatial convergence and large-scale connectivity patterns but cannot resolve finer-grained temporal dynamics or the directionality of information flow between networks. The two resting-state datasets also differed in sample size, field strength (1.5 T vs. 3 T), and acquisition instructions (eyes closed vs. eyes open); however, since all clinical vs

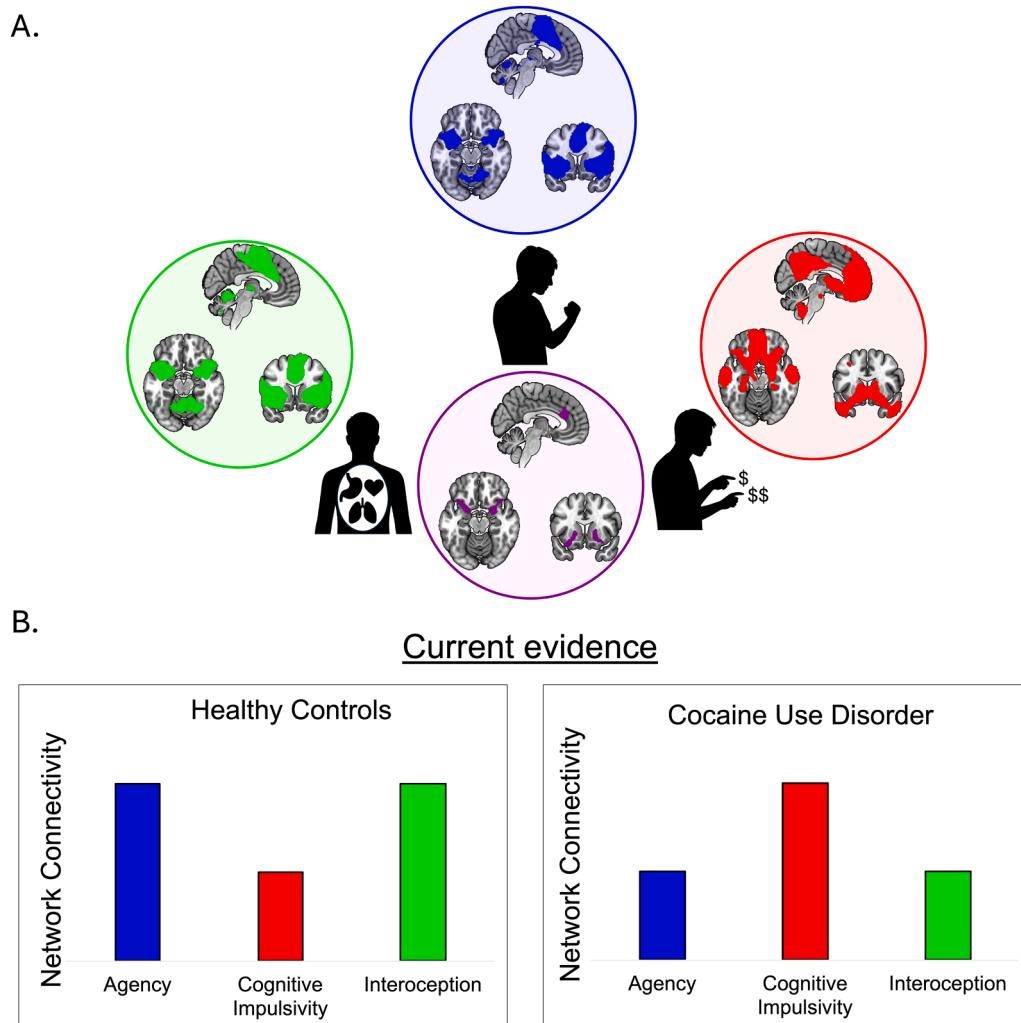


Fig. 6. (A) Interoception and sense of agency are represented as complementary components of bodily self-awareness, whereas cognitive impulsivity reflects a valuation-related dimension of choice. The central overlap illustrates the large-scale functional integration among these systems. (B) Schematic representation of the network-level balance observed in healthy controls and its alteration in cocaine use disorder. In healthy controls, agency- and interoception-related networks show relatively stronger integration than the cognitive impulsivity-related network. In cocaine use disorder, this balance is shifted toward greater integration of cognitive impulsivity-related circuitry, together with reduced agency-related sensorimotor coupling and altered caudate connectivity.

control group comparisons were conducted within the same 3 T dataset, with identical acquisition parameters for both groups, these differences cannot account for the reported group effects. Finally, because the present study was designed to test a systems-level framework rather than to provide a fully updated quantitative review of each individual domain, the literature searches for the three meta-analyses covered studies published up to February 2023 and were not further updated in order to preserve the internal consistency of the ALE-to-connectivity analytical pipeline. Accordingly, the present findings reflect the literature available up to that date. As the literatures continue to grow rapidly, future updates of the complete analytical pipeline will be needed to assess the stability of the proposed systems-level architecture as new evidence accumulates.

At the analytic level, the three meta-analytic datasets differed in size, reflecting the unequal development of the underlying neuroimaging literatures rather than differences in inclusion criteria or selective sampling. Nevertheless, all three single-domain ALE analyses exceeded the minimum number of independent experiments generally recommended for adequately powered ALE meta-analyses (Eickhoff et al., 2016). Unequal dataset sizes may still have affected statistical sensitivity across comparisons, particularly for weaker or more spatially distributed effects. Accordingly, the absence of overlap between

delay-discounting-related cognitive impulsivity and the bodily self-awareness domains should be interpreted as an absence of detectable spatial convergence under the present ALE criteria, rather than as evidence of complete functional independence. Future updates including larger agency datasets will be valuable to determine whether additional shared regions emerge as the literature continues to mature. Moreover, because the three domain-specific ALE maps differed in spatial extent, differences in seed size may have influenced the between-network connectivity comparisons, as larger seeds average the BOLD signal across a broader and potentially more heterogeneous set of voxels.

Conceptually, cognitive impulsivity was operationalized exclusively through delay discounting, which captures a specific dimension of impulsive choice; although it is strongly linked to reward valuation and addictive behaviours, the generalizability of the present findings to other forms of impulsivity, such as motor impulsivity or response inhibition, remains to be established. Accordingly, the present systems-level framework should be interpreted as specifically addressing valuation-related impulsive choice rather than impulsivity in its broader multidimensional sense.

Finally, in terms of clinical generalizability, while cocaine use disorder provided a theoretically informative clinical test case, it remains

unclear whether the observed systems-level imbalance generalizes to other conditions characterized by heightened impulsivity and disrupted self-awareness, including ADHD and schizophrenia; comparative transdiagnostic studies will be critical to determine the specificity versus generality of the proposed reweighting between bodily self-awareness and valuation-driven systems. It follows that several components of this framework remain theoretical propositions rather than findings directly established by the present data. In particular, the direction of influence between bodily self-awareness and valuation-driven systems, a causal regulatory effect of the former on the latter, and a genuinely antagonistic or competitive interaction between networks are not demonstrated by resting-state connectivity or meta-analytic convergence; these remain hypotheses to be tested through task-based, effective-connectivity, longitudinal, or perturbational approaches.

Despite these limitations, our findings position bodily self-awareness as a central dimension in contemporary models of decision-making. By reframing the SMH in terms of the balance between self-related and valuation systems, this work offers a unified conceptual framework for understanding variability in adaptive and maladaptive choice across healthy and clinical populations. More broadly, it suggests that interventions targeting interoceptive and agentic processes may represent promising avenues for modulating decision-making by acting on the neural systems that support the embodied self.

Funding

This study has been funded by a grant from the Ministero dell'Università e della Ricerca–Next Generation EU (PNRR, Missione 4 Componente 2 Investimento 1.1)–PRIN 2022–project code MUR: 2022TFFXFWR–Title: “ME in ACTION: toward a multidimensional neurocognitive model of bodily self-awareness (MECTION)” - 2022-NAZ-0180, CUP H53D23004380001 to LZ and CUP: F53D23004860001 to GS.

CRediT authorship contribution statement

Laura Zapparoli: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Giulia Mattavelli:** Conceptualization, Data curation, Formal analysis, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Irene Gorrino:** Data curation, Formal analysis, Writing – review & editing. **Franantonio Devoto:** Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Rodolfo Rizzi:** Data curation, Formal analysis, Methodology, Writing – review & editing. **Alessandro Grecucci:** Methodology, Supervision, Visualization, Writing – review & editing. **Gerardo Salvato:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Supervision, Visualization, Writing – original draft, Writing – review & editing.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.neubiorev.2026.106908](https://doi.org/10.1016/j.neubiorev.2026.106908).

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