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# Is there a *prediction network*? Meta-analytic evidence for a cortical-subcortical network likely subserving prediction

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ABSTRACT

Predictive coding is an increasingly influential and ambitious concept in neuroscience viewing the brain as a ‘hypothesis testing machine’ that constantly strives to minimize prediction error, the gap between its predictions and the actual sensory input. Despite the invaluable contribution of this framework to the formulation of brain function, its neuroanatomical foundations have not been fully defined. To address this gap, we conducted activation likelihood estimation (ALE) meta-analysis of 39 neuroimaging studies of three functional domains (action perception, language and music) inherently involving prediction. The ALE analysis revealed a widely distributed brain network encompassing regions within the inferior and middle frontal gyri, anterior insula, premotor cortex, pre-supplementary motor area, temporoparietal junction, striatum, thalamus/subthalamus and the cerebellum. This network is proposed to subserve domain-general prediction and its relevance to motor control, attention, implicit learning and social cognition is discussed in light of the predictive coding scheme. Better understanding of the presented network may help advance treatments of neuropsychiatric conditions related to aberrant prediction processing and promote cognitive enhancement in healthy individuals.

## 1. Introduction

Over the last decade the notion of prediction is gaining increasing recognition in neuroscience as a fundamental principle of brain function underlying perception, cognition and action (Clark, 2013). Contrary to the traditional dogma that the brain passively waits for sensory input which it then processes and ultimately transforms into action, it has become accepted that organisms actively predict future events, through the formation of internal models of the world based on past causal regularities (Hohwy, 2013). Optimized predictions allow organisms to better cope with environmental challenges (Klemmer, 1956; Schmidt, 1968), thus conferring a biological advantage (Kveraga et al., 2007). Although commonly considered revolutionary, predictive accounts of perception exist for centuries. The 19th century physiologist Hermann von Helmholtz first formalized the idea that perception entails unconscious inference of the causes of sensations (Hohwy, 2013). However, Helmholtz's views strongly correspond with 18th century Kantian "Copernican revolution" stating that "objects (of external perception) must conform to our cognition" (Swanson, 2016), and its early roots can be even traced back to Ibn al Haytham's writings, from the beginning of the first millennium, suggesting that "many visible properties are perceived by judgment and inference" (Hohwy, 2013).

A particularly comprehensive and influential thesis emphasizing the role of prediction in brain function is the theory of *predictive coding*, seeded in the 1950's *information theory* (Elias, 1955) and markedly elaborated over the last two decades by Karl Friston (2002, 2005, 2010). *Predictive coding* basically assumes that brain computation involves accumulating evidence for competing expectations about the causes of sensations in a bottom up or forward fashion and testing those expectations by generating predictions in a top-down or backward

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fashion. Belief updating is fundamental to this process and rests upon the transfer of prediction errors (the mismatch between ascending sensory information and descending predictions) up the hierarchy to revise expectations and provide better predictions that are transferred down the hierarchy. A Bayesian reading of this sort of belief updating means that hypothesis generation at every neural level relies on calculating its posterior probability (the probability of the hypothesis given the evidence) as the product of its likelihood (how well the hypothesis predicts the evidence) and the prior probability (the probability of the hypothesis considered independently of the evidence). In an iterative process, (empirical)[2] prior probabilities at each level are updated according to prediction errors, in order to minimize the ensuing prediction error. Along the cortical hierarchy, predictions and prediction errors are presumed to be transferred by the same route in reciprocal directions (Friston, 2005; Friston and Kiebel, 2009; Friston et al., 2017; Hohwy, 2013).

A critical step in the evolution of *predictive coding* has been its extension to account not only for perception but also for action (Friston, 2012). It was argued that to better cohere with sensory input the brain can either: (a) change its predictions, or (b) change the sampling of the environment such that sensory samples conform to predictions, or even execute an action to modify the sensory input itself. While the former process is referred to as perceptual inference, the second reflects action, and consequently, the combined process has been designated *active inference* (Friston, 2009). *Active inference* implies that perceptions and actions are intertwined for the sake of reducing prediction error (Friston, 2009). Additional aspect of *active inference* is the predictions of the precision (inverse variance) of prediction errors, which are often considered the computational homologues of attention (Feldman and Friston, 2010; Brown et al., 2011). The higher is the expected precision of a prediction error (the more it is expected to reduce uncertainty), the more attention it will draw (Koelsch et al., 2018). Shortly, *predictive coding* argues that all neural activity is orchestrated around the minimization of prediction error, striving to attain a fully predicted representation of the world (Clark, 2013).

Since first introduced to explain low-level perceptual processing in the visual system (Rao and Ballard, 1999), *predictive coding* has been applied to various cortical and subcortical areas (Huang and Rao, 2011) and has been claimed to underlie even the highest-level cognitive processes (Apps and Tsakiris, 2014; Pickering and Garrod, 2013; Van de Cruys and Wagemans, 2011), hence it is considered a general neural computational strategy (Bubic et al., 2010). Nonetheless, a functional topographic organization based on spatiotemporal scales has been advocated, such that predictions related to fast fluctuations in sensory input and smaller receptive fields may be processed at lower levels of the cortical hierarchy, i.e., primary sensory and motor cortices, whereas predictions related to slow changes and larger receptive fields may be processed at higher levels, i.e., cortical association regions of the frontal lobe (Hohwy, 2013; Kiebel et al., 2008). Accordingly, the level of integration and abstraction of predictions is expected to increase with ascent through the cortical hierarchy (Fitch and Martins, 2014; Hohwy, 2013). Friston and his colleagues have sketched a general profile of brain regions possibly involved in predictive processing, including the primary sensory and motor cortices, motor association cortices, dorsal and ventral prefrontal cortices, parietal cortex, anterior cingulate cortex, insula, hippocampus, amygdala, basal ganglia, thalamus, hypothalamus, cerebellum and the superior colliculus (Friston et al., 2016, 2017; Owens et al., 2018). However, we are not aware of a full evidence-based functional neuroanatomy account of *predictive coding*.

In line with Helmholtz's view emphasizing perceptual inference as an unconscious process (Hohwy, 2013), we were intrigued to explore the neuroantomical basis of the implicit mechanisms underlying generation and updating of perceptual predictions. The term 'prediction' is used in this review to denote the implicit process incepted by Helmholtz and later developed within the *predictive coding* scheme. Music, a complex, multidimensional sequential stimulus, is an ideal system to explore prediction, since it inevitably evokes implicit formation of both "what" (pitch/timbre)- and "when" (rhythm)-related expectations as it unfolds (Huron, 2006). Additionally, the complex hierarchical structure of music (Lerdahl and Jackendoff, 1983) imposes expectancy at both local (between elements that directly follow each other) and non-local (between remote events) levels (Bigand and Pineau, 1997). Importantly, musical expectancy relies to a large extent on unconscious knowledge of culture-specific structural musical regularities which are acquired through repeated exposure irrespective of formal musical education (Bharucha and Todd, 1989). The core role of expectancy in music has long been appreciated (Huron, 2006; Meyer, 1956) while the promising contribution of music to the study of prediction is increasingly recognized in recent literature (Koelsch et al., 2018).

So far, research of the neural correlates of musical expectations has largely focused on the violation of "what"-related expectancies. Several neuroimaging studies using chord-sequence paradigms pointed out the activation of the inferior frontal gyrus (IFG), mainly Brodmann area (BA) 44, to violation of musical expectations (e.g., unexpected cadence, according to the Western tonal system) (Bianco et al., 2016; Koelsch et al., 2002, 2005; Maess et al., 2001; Seger et al., 2013; Tillmann et al., 2003, 2006). Supported by earlier evoked response potential studies (Koelsch et al., 2000; Patel et al., 1998) this IFG response was compared to Broca's area activation to syntactic and semantic incongruities in language (Friederici et al., 2000; Friederici, 2002; Lau et al., 2008) and accordingly ascribed to violation of implicitly learned musical syntactic rules (Patel, 2003; Tillmann et al., 2006). However, a scrutinized reading of these studies revealed that violation of musical expectancies consistently activated additional brain areas, such as the anterior insula (AI), middle frontal gyrus (MFG), premotor cortex (PMC), supplementary motor area (SMA), pre-SMA, anterior cingulate cortex (ACC), inferior parietal lobule (IPL), intraparietal sulcus (IPS), lateral temporal regions, striatum, thalamus and the cerebellum (Bianco et al., 2016; Koelsch et al., 2002, 2005; Maess et al., 2001; Seger et al., 2013; Tillmann et al., 2003, 2006) (Fig. 1A). In general, at least for some regions, activations were more pronounced in the right hemisphere.

Musical "when"-related expectations have been much less explored. A few neuroimaging studies of beat perception reported the involvement of the basal ganglia, cerebellum, PMC, pre-SMA and SMA, and less frequently the IFG, IPL and other regions, in the formation of rhythmic expectations (Grahn and Rowe, 2009, 2013; Bengtsson et al., 2009). Interestingly, rhythmic entrainment, the capacity to synchronize to external musical beat, a robust and intuitive behavior central to music perception and production, is known to involve anticipation (Levitin et al., 2018) and has been associated with a similar set of brain regions (Levitin et al., 2018; Merchant et al., 2015). Furthermore, *timing* in general (which essentially corresponds with temporal prediction) has been linked to a network encompassing the IFG, insula, dorsolateral prefrontal cortex (DLPFC), dorsal and ventral PMCs, SMA, pre-SMA, IPL, basal ganglia and the cerebellum (Coull et al., 2011, 2016; Coull and Nobre, 2008; Lewis and Miall, 2003; Macar et al., 2002; Wiener et al., 2010). A comparable network has been associated with violation of temporal predictions (Carvalho et al., 2016; Coull et al., 2000; Pecenka et al., 2013; Chen et al., 2008).

Noticing the remarkable resemblance between brain regions implicated in the processing of "what"- and "when"- related musical expectations, as well as the overlap between regions subserving prediction formation and violation, a question was raised whether these brain structures constitute a network devoted to prediction, or even underlie higher hierarchical levels of predictive processing, as musical expectancy inevitably involves implicit rule abstraction (achieved through repeated exposure to musical regularities) and lower temporal timescale processing (of long-distance dependencies) (Koelsch, 2013).

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[2] Empirical priors are expectations at intermediate levels of a hierarchical generative model. In other words, they are prior beliefs that are contextualized by ascending empirical evidence and descending priors from higher levels (Friston et al., 2017).

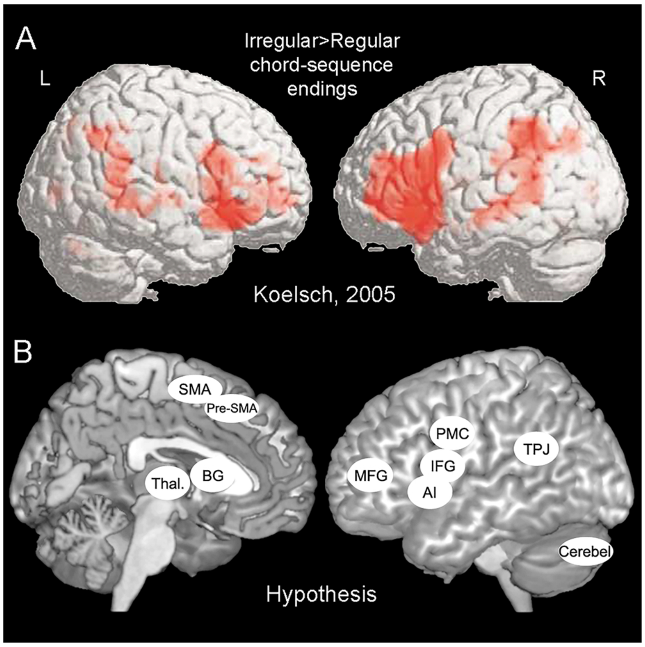

**Fig. 1.** A. fMRI data obtained from 20 subjects using a chord-sequence paradigm. The statistical parametric maps show areas that are more strongly activated during the processing of irregular relative to regular chords (adapted from Koelsch, 2005, with permission of Elsevier). B. Brain regions hypothesized to be involved in higher-level predictive processing based on musical prediction literature. AI, anterior insula, BG, basal ganglia, Cerebel., cerebellum, IFG, inferior frontal gyrus, MFG, middle frontal gyrus, PMC, premotor cortex, Pre-SMA, pre-supplementary motor area, SMA, supplementary motor area, Thal., thalamus, TPJ, temporoparietal junction.

To explore this idea and extend beyond the musical domain, we employed activation likelihood estimation (ALE) meta-analysis to neuroimaging studies involving predictive processing in three functional domains: music, language and action perception. These functional domains were chosen as they all lean on hierarchically organized sequential information which entails implicit abstract rule learning and prediction at the non-local level, i.e., necessarily involve higher-level predictive processing (Christiansen and Chater, 2015; Fitch and Martins, 2014; Janacsek and Nemeth, 2012).[3] Moreover, the inclusion of action perception paradigms enabled expanding the spectrum of predictions being studied to cover “where”- in addition to "what"- and "when"-related expectations.

If the functional anatomy of the brain, at a macroscopic scale, supports a predictive coding account of brain function, one would expect to see activations in a particular set of brain regions for any neuronal processing that issued predictions, or belief updating following violations of those predictions. Given the hierarchical nature of the generative models that underwrite predictive coding, we would anticipate higher-level inference to be represented high in the cortical hierarchy (i.e., association cortices). Additionally, as the enactive generalization of *predictive coding* (i.e., *active inference*) suggests that, ultimately, predictions are in the service of motor and autonomic function (Adams et al., 2013), we would also anticipate engagement of cortical and subcortical regions related to somatic (e.g., PMC, SMA, basal ganglia and cerebellum) and visceral (e.g., AI and ACC (Taylor et al., 2016)) motor control. And finally, following the integration of attention into predictive processing schemes (Feldman and Friston, 2010), we would expect the involvement of brain regions previously associated with attention (e.g., IPS, frontal eye field (FEF), IPL and IFG (Corbetta and Schulman, 2002)), irrespective of the processing domain.

In summary, we hypothesized that a particular set of cortical and subcortical brain regions would be engaged in higher-level prediction across functional domains, stimulus dimensions and processing modalities. To address this, we characterized functional anatomy using meta-analysis of activation studies involving prediction formation or violation in three functional domains: music, language and action perception. To ensure a general conclusion, we included predictions about “what”, “when” and “where” in auditory and visual paradigms. The theoretical predictions, detailed above, supplemented by empirical findings from the musical literature lead us to formulate three main hypotheses: (i) the array of discrete brain regions constituting a network dedicated to domain-general predictive processing principally encompasses the IFG and adjacent AI, MFG, PMC, SMA/pre-SMA region, TPJ region (including IPL (supramarginal gyrus (SMG)/angular gyrus) and posterior superior temporal sulcus (PSTS)/gyrus), basal ganglia, thalamus and the cerebellum (Fig. 1B); (ii) prediction formation and violation are handled by the same network; and (iii) predictions concerning different stimulus attributes (i.e., content, timing, location) are mediated by a similar network. The presented meta-analysis supports these three hypotheses and primarily delineates the neuroanatomical infrastructure of higher-level prediction. Interpreting the results through the lens of *predictive coding* allows linking the proposed network for higher-level prediction to additional central cognitive processes such as attention, associative learning and social cognition, thus providing an integrated perspective on an elemental brain system likely pivotal in health and disease.

## 2. Materials and methods

### 2.1. Literature search and eligibility criteria

A systematic search of the literature was conducted using PubMed database (http://www.ncbi.nlm.nih.gov/pubmed) to identify peer-reviewed studies of potential relevance to the current hypotheses. The initial search selected research publications containing the following terms in their title or abstract: ((((fMRI OR functional magnetic resonance imaging OR functional MRI OR PET OR positron emission tomography)) AND (prediction OR expectancy OR expectation OR anticipation OR unexpected OR surpris* OR entropy OR prediction error OR irregular OR unrelated OR incongruent)) AND (sequen* OR order* OR scramble* OR revers* OR context OR structure OR progression* OR cadence OR sport*)) AND (music* OR harmonic OR melodic OR rhythmic OR language OR linguistic OR semantic OR syntactic OR phonological OR action OR motor OR movement OR kinematic*). The terms reflect our specific interest in neuroimaging studies involving higher-level predictive processing across the three functional domains. Search results were limited to English-language, human-only studies with available full-text. This search strategy yielded 342 articles.

Next, titles, abstracts and (if needed) full-texts were screened for eligibility based on the following inclusion and exclusion criteria (Table 1). Articles were included if they reported the analysis of original task-based functional MRI or PET neuroimaging studies applying paradigms related to prediction formation or violation within the fields of action perception, language or music. Consistent with the functional domains, either auditory or visual paradigms were included. Predictions concerned various aspects of the presented experience (“what”, “when” and/or “where”). Studies were excluded if they did not report: (a) results of healthy adult human population; (b) the analysis of a relevant task; (c) the analysis of a relevant contrast; (d) whole-brain results; or (e) peak activation coordinates in standard stereotactic space (Talairach (Talairach and Tournoux, 1988) or Montreal Neurologic

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[3] The understanding that hierarchical structures that underlies music (Lerdahl and Jackendoff, 1983) and language (Bolhuis et al., 2014; Hauser et al., 2002) relies on core features of motor activity has been highlighted by Karl Lashley in the early 1950’s (Fitch and Martins, 2014). In his prescient article “The problem of serial order in behavior”, Lashley underscored the criticality of hierarchically organized plans to complex sequential behaviors (Lashley, 1951), which in our context links these behaviors to higher-level prediction.

**Table 1**
Summary of inclusion and exclusion criteria for meta-analysis.

| | Inclusion | Exclusion |
|---|---|---|
| Publication type | Peer-reviewed, full text, English-language publication | Not original research paper |
| Neuroimaging technology | fMRI/PET | All others |
| Population | Adult healthy | Unhealthy |
| Paradigm | Involves prediction (formation/violation) of *what*, *when* or *where* aspects of structural/sequential motoric, linguistic or musical stimuli | Involves action execution, reward-/punishment- prediction, within-paradigm learning or oddball stimuli |
| Reported results | | - No relevant contrast<br>- No significant results<br>- No whole-brain results<br>- No coordinates reported |

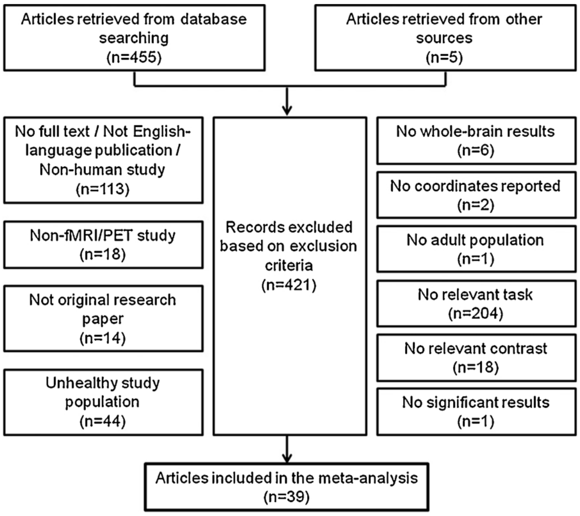

**Fig. 2.** Flow chart of literature search.

Institute (MNI)) (Fig. 2). As for exclusion criteria (b), several points should be emphasized: (1) tasks which involved action execution were excluded to avoid interference by motor-related activations; (2) studies of reward/punishment prediction were excluded to avoid direct activation of the limbic/paralimbic system; (3) studies based on within-paradigm learning were discarded to minimize the contribution of online learning (see Discussion); and (4) as we were particularly interested in higher levels of perceptual prediction, those implemented in the perception of hierarchical complex structures, we excluded oddball paradigms which are expected to mostly induce local, rather than non-local, predictions (Koelsch, 2012), and to activate a partially distinct brain network possibly involving primary sensory cortices (Bubic et al., 2009; Kim, 2014; Koelsch et al., 2002).

A total of 34 studies met these eligibility criteria. Five additional relevant studies were identified by searching the reference lists of publications that passed the screening process. Consequently, a final set of 39 papers was included in the meta-analysis (Fig. 2, Table 2).

### 2.2. *Activation likelihood estimation meta-analysis*

Activation likelihood estimation, a widely accepted technique for coordinate-based meta-analysis (Eickhoff et al., 2009), was used to assess the co-localization of activations related to prediction formation and/or violation across the selected studies. The analysis was conducted using BrainMap GingerALE software (GingerALE v.2.3.6, www.brainmap.org) (Eickhoff et al., 2009, 2012; Turkeltaub et al., 2012). Briefly, this popular random-effect meta-analytic method assesses the overlap between foci by applying four main steps: (1) modeling each focus as three-dimensional probability distribution using a Gaussian blur adjusted to reflect the uncertainty of the reported spatial location due to between-template and between subject variance; (2) combining probability distributions of all activation foci within a given experiment to produce a modeled activation (MA) map; (3) compiling MA maps of all experiments included in the meta-analysis to form an ALE map which depicts activation probability of each grey matter voxel across studies; and (4) assessing the resulting ALE map against a null-distribution of random spatial association between experiments, thus estimating above-chance convergence of activation foci across studies (Eickhoff et al., 2012).

Peak activation coordinates of all relevant contrasts reported in the selected studies were collected. Foci that were reported in Talairach space were converted to MNI space using the Lancaster et al. (2007) transform implemented in GingereALE v.2.3.6. Statistical threshold method was set to false discovery rate (FDR), $q = 0.05$, with minimum cluster size of 200 mm$^3$. Final clusters of activation were overlaid on the standard MNI template in MRIcron (www.mricro.com) (Rorden et al., 2007). The identification of brain regions was aided by the automatic anatomical labeling (AAL) (Tzourio-Mazoyer et al., 2002) and Brodmann atlases implemented in MRIcron and the Talairach Daemon (Talairach.org) implemented in GingereALE v.2.3.6.

To evaluate differences in brain activation related to prediction formation versus prediction violation, the contrast analysis implemented in GingereALE v.2.3.6 was applied. Peak coordinates of activations derived from experimental contrasts evaluating prediction formation and prediction violation were separated and ALE maps were computed for each set of studies. The voxel-wise difference between the two ALE maps was calculated using an FDR correction, $q = 0.05$.

## 3. Results

### 3.1. *Eligible studies*

The final set of 39 articles which met all inclusion and exclusion criteria provided a total of 764 participants and 537 activation foci. Included studies were associated with at least one of the three functional domains: action perception (10), language (17) or music (13). Paradigms involved prediction formation (21) and/or violation (22), concerning the content (30), timing (6) or location (6) of stimuli. Predictive processing was either task-irrelevant (20) or relevant (19) (Table 2).

### 3.2. *General meta-analysis*

The ALE meta-analysis of the pooled 39 experiments revealed significant convergence in several cortical and subcortical clusters: bilateral AI, IFG and ventral PMC, right Pre-SMA, MFG, SMG and subthalamus, and left PSTS, caudate and cerebellar lobule VII (Crus I/II) (Table 3, Figs. 3 and 4). Lowering the cluster size threshold to 100 mm$^3$ revealed additional activations within the FEF (volume = 176 mm$^3$,

**Table 2**
Details of studies included in the meta-analysis.

| Authors and Year | N | Imaging Modality | Experimental Paradigm | Experimental Contrast | P/PE |
|---|---|---|---|---|---|
| **Music** | | | | | |
| Bengtsson et al. (2009) | 17 | fMRI | Listening to rhythmic sequences | Nonmetric > Metric sequences | PE |
| Bianco et al. (2016) | 29 | fMRI | Listening to harmonically congruent or incongruent chord progressions | Incongruent > Congruent progressions, in expert pianists | PE |
| Danielsen et al. (2014) | 19 | fMRI | Listening to a previously unheard naturalistic groove with drum breaks at uneven intervals | Transitions > Continuous | PE |
| Grahn & Rowe (2009) | 36 | fMRI | Pitch change detection task while listening to rhythmic sequences | Beat (volume + duration) > No beat (volume + duration),<br>No beat (volume) > Beat (volume) | P<br>PE |
| Grahn & Rowe (2013) | 24 | fMRI | Beat saliency judgments while listening to rhythmic sequences | Beat > No beat,<br>No beat > Beat | P<br>PE |
| Koelsch et al. (2002) | 10 | fMRI | Cluster and deviant instrument detection while listening to chord progressions with infrequent unexpected events | Clusters > In-key chords | PE |
| Koelsch et al. (2005) | 20 | fMRI | Regularity judgments of chord progression endings | Neapolitan > Tonic chords, in adults | PE |
| Leaver et al. (2009) | 20 | fMRI | Anticipatory imagery during silence periods between (familiar or unfamiliar) CD tracks | Anticipatory silence (familiar music) > Nonanticipatory silence (unfamiliar music) | P |
| Osnes et al. (2012)[1] | 19 | fMRI | Listening to spectral mixes | Music > Neutral instructions, Vowel > Neutral instructions | P |
| Seger et al. (2013) | 11 | fMRI | Listening to short pieces of Western classical music with cadence manipulated to produce various levels of unpredictability | Parametric modulation, expectancy violation | PE |
| Sridharan et al. (2007) | 18 | fMRI | Listening to short symphonies by William Boyce | Movement transition > Auditory oddball task | P |
| Tillmann et al. (2003) | 15 | fMRI | Intonation judgments on related and unrelated musical targets presented at the end of musical sequences | Unrelated > Related consonant targets | PE |
| Tillmann et al. (2006) | 20 | fMRI | Phoneme and timbre judgments on related and less-related musical targets presented at the end of instrumental and sung sequences | Less-related > Related targets | PE |
| **Language** | | | | | |
| Abutalebi et al. (2007) | 12 | fMRI | Listening to narratives containing switches to second language | Irregular > Regular switches, in bilinguals | PE |
| Bonhage et al. (2015) | 18 | fMRI | Syntactic and semantic word prediction during reading | Conjunction of Regular sentences > Non-word lists and Jabberwocky sentences > Non-word lists | P |
| Caplan et al. (1998) | 8 | PET | Plausibility judgment of visually presented sentences of various syntactic complexity levels | Center-embedded > Right branching sentences | P |
| Diaz & Hogstrom (2011) | 16 | fMRI | Relatedness judgments of pairs of English sentences varying in their figurativeness and congruence | Incongruent > Congruent | PE |
| Dien & O'Hare (2008) | 13 | fMRI | Reading semantically and syntactically congruent and incongruent sentences | Incongruent > Congruent | PE |
| Guediche et al. (2016) | 20 | fMRI | Listening to sentence pairs, acoustically clear prime followed by a degraded target sentence | Related > Unrelated sentences | P |
| Henderson et al. (2016) | 40 | fMRI | Paragraph reading | High > Low syntactic surprisal | PE |
| Hoenig & Scheef (2009) | 22 | fMRI | Semantic judgments of visually presented target words following contexts of varying ambiguity | Incongruent > Congruent words | PE |
| Kiehl et al. (2002) | 28 | fMRI | Semantic judgments of visually presented sentences | Incongruent > Congruent terminal words | PE |
| Lesage et al. (2017) | 17 | fMRI | Plausibility judgments of visually presented sentences | Parametric modulation, predictability of the upcoming sentence ending | P |
| Lyu et al. (2016) | 30 | fMRI | Speaker gender judgments while processing auditory presented sentences | Unexpected > Expected phrases | PE |
| Matchin et al. (2017) | 16 | fMRI | Probe word task during reading | Natural sentence > Natural list, Jabberwocky sentence > Jabberwocky list | P |
| Moberget et al. (2014) | 32 | fMRI | Semantic judgments of visually presented sentences | Congruent > Scrambled sentences,<br>Incongruent > Congruent sentences | P<br>PE |
| Obleser & Kotz (2010) | 16 | fMRI | Listening to sentences of varying levels of acoustic degradation and cloze probability | Low cloze > High cloze sentences and Highly > Moderately degraded | PE |
| Rothermich & Kotz (2013) | 16 | fMRI | Metric and semantic congruency judgments of auditory presented sentences | Metric task: Semantically incongruent > Congruent trials, Metrically incongruent > Congruent trials.<br>Semantic task: Semantically incongruent > Congruent trials | PE |
| Willems et al. (2016) | 24 | fMRI | Listening to stories and their reverse speech version | Parametric modulation, Entropy, Real speech > Reversed speech,<br>Surprisal, Real speech > Reversed speech | P<br>PE |
| **Action perception** | | | | | |
| Abreu et al. (2012) | 16 | fMRI | Predicting the fate of free throws while watching video clips of basketball players | Forward > Reverse clips, in experts | P |

(continued on next page)

**Table 2** (*continued*)

| Authors and Year | N | Imaging Modality | Experimental Paradigm | Experimental Contrast | P/PE |
|---|---|---|---|---|---|
| Ahlheim et al. (2016) | 19 | fMRI | Viewing video clips of action sequences structured by first- and second-order conditional probabilities (answering irrelevant questions at times) | Interaction contrast of information provided by the second- and first-order structure | P |
| Balser et al. (2014) | 32 | fMRI | Motor and spatial anticipation of strokes while watching video clips of tennis players | Anticipation > Observation only (ball-bouncing control task) | P |
| Hagura et al. (2009) | 16 | fMRI | Visuokinesthetic perception of hand movements | [Congruent > Control] > [Incongruent > Control], [Congruent + Incongruet] > Control | P |
| Lamm et al. (2007) | 17 | fMRI | Predicting the reaching range of a model's hand or foot from static photographs | Reaching range prediction > Gender matching | P |
| Schiffer & Schubotz (2011) | 14 | fMRI | Correctness judgments of pre-learned motor sequences performed by dancers | Prediction-violating > Prediction-conform movements | PE |
| Thioux & Keysers (2015) | 17 | fMRI | Goal anticipation during observation of hand grasp movements | Occlusion > Full-view | P |
| Wimshurst et al. (2016) | 15 | fMRI | Predicting the direction of an oncoming shot in either a hockey or a badminton scenario | Action prediction, Hockey experts > Novices | P |
| Wright et al. (2010) | 8 | fMRI | Direction anticipation during observation of video clips of badminton players | Shots > No-shot motion control in recreational badminton players | P |
| Wright et al. (2011) | 24 | fMRI | Direction anticipation during observation of video clips of badminton players | Shots > No-shot motion control in badminton players of varying skill levels | P |

Note. N = sample size, fMRI = functional magnetic resonance imaging, P = prediction formation, PE = prediction violation (error), PET = positron emission tomography. [1]Relevant to both music and language.

**Table 3**
Results of the general ALE meta-analysis.

| Cluster No. | Anatomical region | Volume ($mm^3$) | ALE value | MNI Coordinates | | |
|---|---|---|---|---|---|---|
| | | | | X | Y | Z |
| 1 | R IFG (BA 44) | 2032 | 0.0284 | 46 | 20 | 14 |
| | R PMC | | 0.0282 | 52 | 10 | 22 |
| 2 | R AI | 1656 | 0.0520 | 34 | 22 | −4 |
| 3 | L AI | 912 | 0.0374 | −32 | 20 | 2 |
| 4 | L Crus I | 888 | 0.0332 | −10 | −78 | −26 |
| | L Crus II | | 0.0226 | −16 | −74 | −36 |
| 5 | L PMC | 704 | 0.0276 | −48 | 6 | 22 |
| 6 | L PSTS | 688 | 0.0271 | −64 | −36 | 10 |
| | L PSTS | | 0.0253 | −54 | −38 | 10 |
| 7 | L Caudate | 536 | 0.0316 | −10 | 12 | 2 |
| 8 | R Pre-SMA | 472 | 0.0329 | 8 | 10 | 62 |
| 9 | R IFG/Frontal Operculum | 344 | 0.0249 | 48 | 16 | −2 |
| 10 | L IFG (BA 45) | 344 | 0.0260 | −50 | 34 | 0 |
| 11 | R Subthalamus | 312 | 0.0256 | 10 | −14 | −6 |
| 12 | R MFG | 288 | 0.0236 | 44 | 46 | 12 |
| 13 | R SMG | 216 | 0.0226 | 64 | −26 | 36 |
| | R SMG | | 0.0208 | 58 | −24 | 44 |

Note. Statistical threshold method: FDR, q = 0.05, cluster size = 200 $mm^3$. AI, anterior insula, Crus I/II, cerebellar lobule VII, Crus I/II, IFG, inferior frontal gyrus, MFG, middle frontal gyrus, PMC, premotor cortex, Pre-SMA, pre-supplementary motor area, PSTS, posterior superior temporal sulcus, SMG, supramarginal gyrus. L, left, R, right.

MNI coordinates −26, −8, 58), right putaman (120 $mm^3$, 30, −4, −10), right dorsal ACC (112 $mm^3$, 6, 26, 40), left thalamus, ventrolateral nucleus (104 $mm^3$, −14, −12, 2) and right thalamus, mediodorsal nucleus (104 $mm^3$, 4, −12, 6). The emerging cortical-subcortical network appeared essentially bilateral, with some right predominance in cortical cerebral clusters and obvious left predominance in cerebellar clusters.

### 3.3. *Contrast analysis*

Contrast analysis assessing the difference between activations related to prediction violation (22 studies, 464 participants, 268 foci) versus prediction formation (21 studies, 416 participants, 269 foci) revealed significant clusters within the left (volume = 1448 $mm^3$, MNI coordinates −57, −36, 10) and right (volume = 312 $mm^3$, MNI coordinates 52, −32, 0) PSTS. The opposite contrast did not reveal any significant cluster. The emergence of the PSTS in the contrast analysis could reflect enhanced recruitment of the PSTS in prediction violation relative to prediction formation; however, a higher representation of linguistic and musical paradigms among prediction violation contrasts precludes this conclusion. In general, the contrast analysis results do not support a major difference between brain regions mediating prediction formation and violation.

## 4. Discussion

Our ALE meta-analysis supports three main conclusions: (i) a widely distributed brain network comprising both cortical (IFG, AI, MFG, PMC, Pre-SMA, TPJ) and subcortical (striatum, thalamus/subthalamus, cerebellum) brain regions is engaged during prediction; (ii) this network mediates both prediction formation and violation; (iii) this network is activated irrespective of the aspect of stimulus being predicted (i.e., "what", "when" or "where"). The proposed network emerged from meta-analytic study of three distinct functional domains all relying on sequential hierarchical structures, therefore, it is proposed to subserve domain-general higher-level predictive processing. The fact that the same network appears to mediate both prediction generation and violation is consistent with the *predictive coding* theory (Friston, 2005; Friston et al., 2009). The third conclusion is mentioned with caution, due

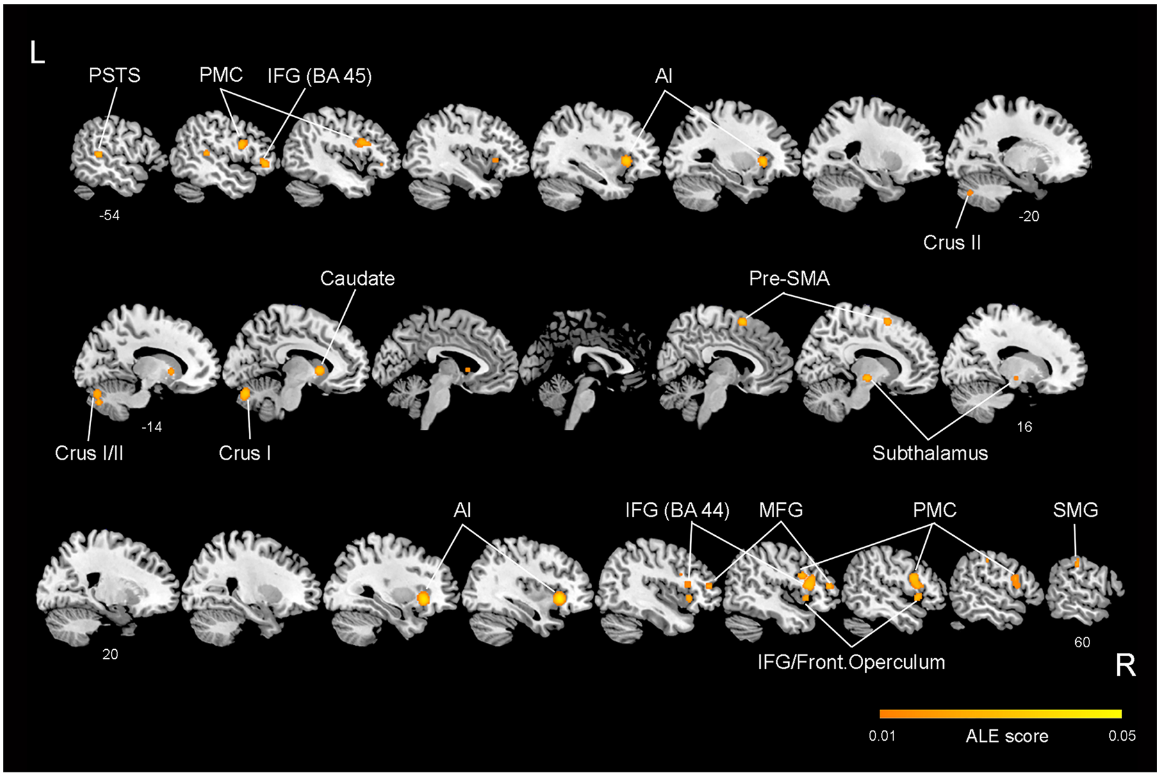

**Fig. 3.** ALE meta-analysis results of 39 neuroimaging studies involving prediction formation and/or violation in three functional domains: action perception, language and music, presented on sagittal sections (FDR, q = 0.05, cluster size = 200 $mm^3$). AI, anterior insula, Crus I/II, cerebellar lobule VII, Crus I/II, Front. Operculum, frontal operculum, IFG, inferior frontal gyrus, MFG, middle frontal gyrus, PMC, premotor cortex, Pre-SMA, pre-supplementary motor area, PSTS, posterior superior temporal sulcus, SMG, supramarginal gyrus.

to the relative paucity of studies involving "when"- and "where"-related expectations. Yet, a unified neural account of expectations regarding the content, timing or location of interrelated stimuli is in agreement with earlier literature of the dorsal pathway (Borst et al., 2011; Ungerleider and Mishkin, 1982) and accords with the crucial role spatiotemporal features play in object perception, as acknowledged by *predictive coding* and much earlier by Kant (Hohwy, 2013; Swanson, 2016).

It should be mentioned that several past studies of prediction and error-based learning support the existence of a similar network (Bubic et al., 2009; Fouragnan et al., 2018; Schultz and Dickinson, 2000; Seidler et al., 2013); however, their viewpoints were limited to either specific cognitive domains or one/several brain region/s. The significance of the current review is in its integrative and comprehensive outlook, highlighting (1) the anatomical distribution of the proposed network with special emphasis on subcortical components (discussed further in *4.1*), and (2) the network's potential functional relevance which nicely resonates with the fundamentals of *predictive coding* (discussed further in 4.2).

### *4.1. Anatomical aspects of the described network conforms with earlier prediction-related literature*

The majority of brain structures making up the currently advocated network for higher-level predictive processing have already been associated with the broad notion of *prediction*, as summarized in Table 4. Some of the emerging subcortical nodes deserve special consideration:

1 Although thalamic foci (ventrolateral and mediodorsal nuclei) did not reach statistical significance, they are strongly suspected as components of the proposed network, since the thalamus has long been mentioned in the context of error-based learning (Doya, 2000; Seidler et al., 2013) and lately implicated in the generation of forward predictive models (Rikhye et al., 2018). Further, a recent functional connectivity parcellation of the thalamus (Zhang and Li, 2017) associated the ventrolateral nucleus with a network resembling the currently reported network. The mediodorsal nucleus activation might be linked to the salience network (SN) (Menon, 2015), a well-documented large-scale brain network thought to guide optimal behavior by detecting the most relevant among concurrent internal and external stimuli (Menon and Uddin, 2010). As the SN's key hubs, AI and, to lesser extent, dorsal ACC, appear central to the proposed network, the two networks are suggested to partially overlap.

2 The unhypothesized subthalamic node requires further confirmation. In case a subthalamic localization is replicated, it might represent activation of either the subthalamic nucleus (STN) or the zona incerta (ZI). The STN undoubtedly suits the motor flavor of many components of the here described network (Purves et al., 2008). Moreover, by means of functional connectivity it has been shown to take part in a network partially overlapping with the presented network (Mathys et al., 2016). The ZI is a scarcely studied region which has been linked to visceral activity, arousal, attention and maintaining posture and locomotion (Mitrofanis, 2005). Intriguingly, it has lately been implicated in the integration of diverse sensory and motor information (Diamond and Ahissar, 2007), cerebello-cerebral convergence (Schafer and Hoebeek, 2018) and fear conditioning (Zhou et al., 2018), all relevant to the currently proposed network as discussed below.

3 The cerebellum, albeit long linked to sensorimotor prediction (Nixon, 2003), has not been integrated within the *predictive coding* framework. Over the last decades it is increasingly recognized that cerebellar function is not restricted to the sensorimotor domain but rather extends to higher-order cognition and emotion (Schmahmann, 2010). The unique and uniform microstructure of the cerebellum across regions implies a uniform computational principle across functional domains, which might be related to prediction (Imamizu and Kawato, 2009; Leggio and Molinari, 2015; Ramnani, 2006). Importantly, we here first underscore the involvement of a medial region of cerebellar

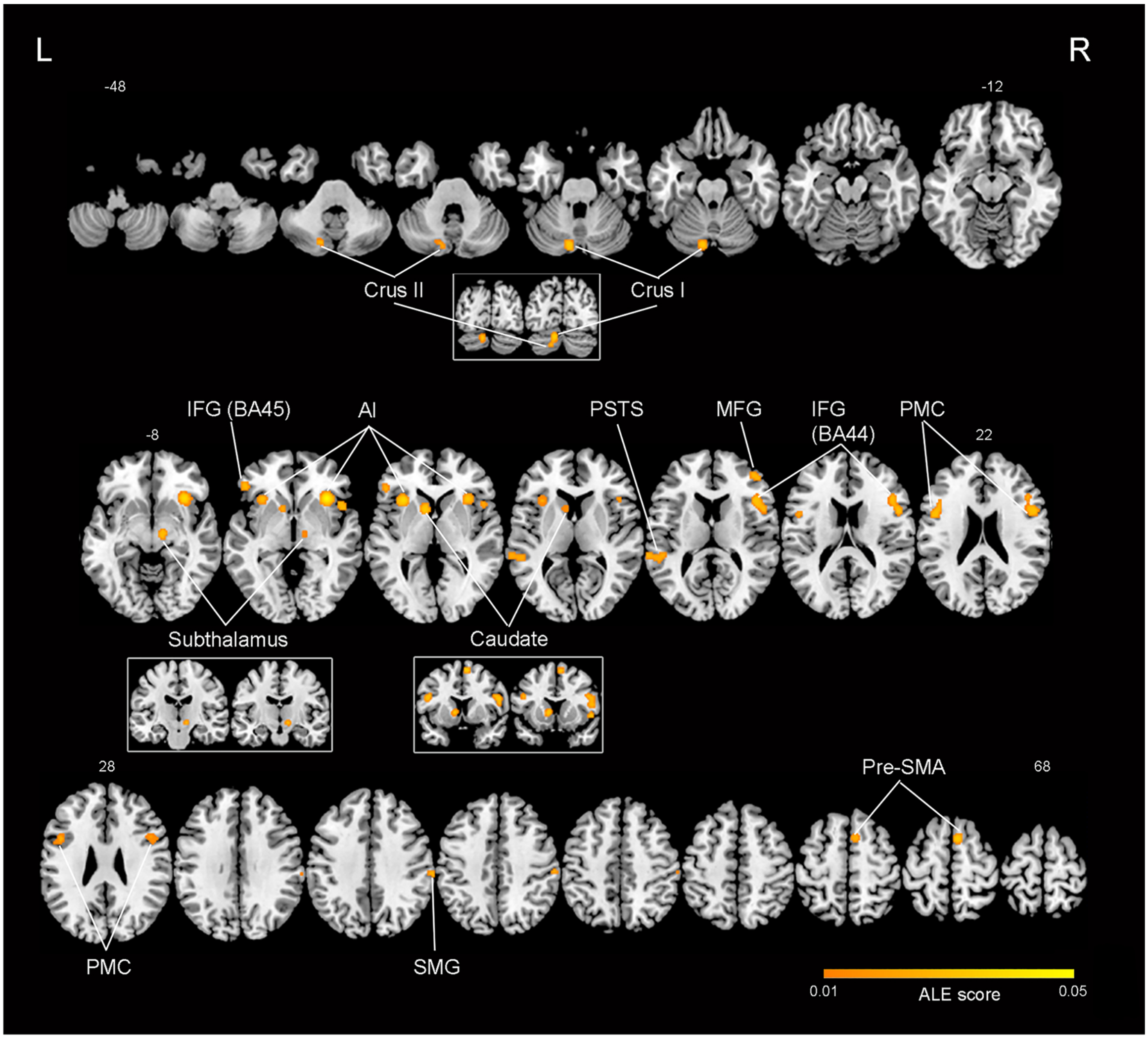

**Fig. 4.** ALE meta-analysis results of 39 neuroimaging studies involving prediction formation and/or violation in three functional domains: action perception, language and music, presented on axial sections (FDR, q = 0.05, cluster size = 200 mm$^3$). AI, anterior insula, Crus I/II, cerebellar lobule VII, Crus I/II, IFG, inferior frontal gyrus, MFG, middle frontal gyrus, PMC, premotor cortex, Pre-SMA, pre-supplementary motor area, PSTS, posterior superior temporal sulcus, SMG, supramarginal gyrus.

**Table 4**
Previous support for contribution of the proposed network nodes to prediction-related processing.

| Network node | Contribution to prediction-related processing | References |
|---|---|---|
| IFG (particularly BA 44) | Involvement in prediction violation (discussed in Section 1), recognition of structural regularities, analysis of structural relationships among events occurring within sequences and the hierarchical organization of actions during multi-component goal-directed behavior | (Fiebach and Schubotz, 2006; Koechlin and Jubault, 2006, Fitch and Martins, 2014) |
| AI | Domain-general error-related activity | (Chang et al., 2013; Dosenbach et al., 2006) |
| MFG | Sequence and error-based learning | (Heun et al., 2004; Turner et al., 2004) |
| PMC | Processing of sequentially structured events across different modalities | (Nastase et al., 2014; Opitz and Kotz, 2012; Schubotz and von Cramon, 2004) |
| Pre-SMA | Sequence processing, including response to sequential deviants, restructuring internal models while applying prediction error | (Bubic et al., 2009) |
| TPJ | Sequence learning, reorienting to unexpected stimuli and updating internal models to optimize behavioral responses | (Bo et al., 2011; Corbetta and Shulman, 2002; Geng and Vossel, 2013; Kluger and Schubotz, 2017; Seghier, 2013) |
| Striatum | Motor and non-motor sequence learning, reaction to unexpected stimuli, encoding prediction errors not necessarily related to reward | (Badgaiyan et al., 2007, den Ouden et al., 2009d, Horvitz, 2000; Penhune and Steele, 2012, Schiffer and Schubutz, 2011, Schultz and Dickinson, 2000) |
| Cerebellum | Sequence and error-based learning | (Albus, 1971; Ito, 2006; Marr, 1969) |

Note. AI, anterior insula, IFG, inferior frontal gyrus, MFG, middle frontal gyrus, PMC, premotor cortex, Pre-SMA, pre-supplementary motor area, TPJ, temporoparietal junction.

lobule VII, Crus I/II, in prediction formation and violation. A few previous studies reported activation of this region in prediction violation (Jenmalm et al., 2006; Lesage et al., 2017; Moberget et al., 2014). Furthermore, a functional connectivity study of the cerebellar lobules linked Crus I, Crus II and adjacent lobule VI to a cerebrocerebellar network highly corresponding with the presently reported network (Bernard et al., 2012).

The accurate contribution of each node to predictive processing, domain-specific anatomical variations and precise localizations within the broad anatomical regions indicated are yet to be defined. Moreover, the involvement of additional brain regions cannot be ruled out, particularly regions of the posterior lateral temporal lobe and the brainstem. It should be mentioned that medial temporal lobe structures, principally the hippocampus, have also been implicated by some studies in implicit sequence learning and prediction (Kumaran and Maguire, 2007; Schendan et al., 2003), yet findings were inconsistent and might stemmed from inclusion of episodic memory components.

### *4.2. Putative functional aspects of the described network conforms to principles of predictive coding*

The specific ensemble of brain regions derived from the current meta-analysis is reminiscent of the neuroanatomical foundations of several neural functions, extending beyond the meta-analysis focus, i.e., perceptual prediction. We suggest that motor control, implicit learning and certain aspects of attention and social cognition are all mediated by a similar network. This assertion is highly supported by the *predictive coding* framework as discussed below.

#### *4.2.1. The proposed network subserves both perception and action*

Despite the exclusion of motor execution paradigms from our meta-analysis the resulting network greatly parallels with an alleged network for motor planning (Hoshi and Tanji, 2007; Purves et al., 2008; Svoboda and Li, 2018). Moreover, studies which were excluded from the meta-analysis due to action execution reported equivalent activations (Chen et al., 2008; Grahn and Brett, 2007; Jakobs et al., 2009; Jenmalm et al., 2006; Jungblut et al., 2012; Lutz et al., 2000; Nitschke et al., 2003; Safstrom and Domellof, 2018). These observations accord with the *active inference* scheme (Friston et al., 2009) which introduces perception and action as a unified operation aimed at prediction error minimization (Friston, 2012), and treats motor commands as no more than the proprioceptive and exteroceptive predictions of the consequences of planned actions (Adams et al., 2013). Hence, embracing *predictive coding*, it is not surprising that perceptual prediction and motor control are served by the same network.

#### *4.2.2. The proposed network probably has a role in attention*

The currently advocated network is highly concordant with the previously reported ventral attention network (VAN) (Corbetta and Schulman, 2002), a cortico-cortical network principally composed of the ventral frontal cortex and the TPJ, which has been implicated in the detection of "salient and behaviorally relevant stimuli in the environment, especially when unattended" (Corbetta et al., 2008). It has already been noticed that some of the conditions that activate the VAN involve violating expectations, for instance, targets that follow invalid cues in classical attention paradigms (Corbetta et al., 2008; Vossel et al., 2014). However, to the best of our knowledge, the VAN has not been implicated in prediction formation. Consistent with the current results, the VAN has been typically reported as right-lateralized (Corbetta et al., 2008). As mentioned earlier, *attention* is considered an integral part of *active inference* being understood as the inference about the precision of prediction errors (Feldman and Friston, 2010; Brown et al., 2011). In line with *predictive coding*, it is here argued that brain areas constituting the VAN, together with subcortical regions, form a unified network subserving prediction.

#### *4.2.3. The proposed network probably underlies implicit learning*

Implicit learning, the ability to acquire unconscious knowledge about a complex, rule-governed stimulus, without intending to, is considered an elementary and ubiquitous process of human cognition (Reber, 1989). Albeit no agreement exists as to its neural infrastructure (Reber, 2013), much information has been gathered over the years. A prototypical form of implicit learning, procedural motor learning, has been associated with fronto-parietal and subcortical areas, including the SMA, pre-SMA, PMC, parietal cortex, basal ganglia and the cerebellum (Hikosaka et al., 2002). The two well-studied forms of associative learning, classical and operant conditioning, have been mostly associated with the cerebellum (Squire and Knowlton, 2000; Kim and Thompson, 1997) and the basal ganglia (Balleine et al., 2009; Garrison et al., 2013; Pessiglione et al., 2008), respectively. Furthermore, a well-known paradigm of implicit learning, artificial grammar learning (Reber, 1989), has been shown to activate the posterior IFG, prefrontal areas, premotor cortices, IPL, superior parietal lobule, striatum and the cerebellum in linguistic tasks (Bahlmann et al., 2008; Goranskaya et al., 2016) and the right IFG, MFG, dorsal PMC, pre-SMA and bilateral AI in a musical task (Cheung et al., 2018). Thus, a close resemblance is observed between regions subserving various forms of implicit learning and those constituting the currently proposed network. This finding accords with the *predictive coding* view that the iterative process of adjusting priors based on prediction errors entails *learning*, particularly associative learning (Friston, 2003, 2005).

#### *4.2.4. The proposed network might mediate mirroring and aspects of social cognition*

The coupling of action and perception discussed in 4.2.1 is nicely reflected by the unique phenomenon of *mirror neurons*, a class of neurons that discharge during both action execution and action observation (or hearing) (Gallese et al., 1996; Kohler et al., 2002). While the exact anatomical definition of the human mirror neuron system (MNS) awaits validation, there is wide agreement it encompasses the posterior IFG, ventral PMC and the IPL (Molenberghs et al., 2012; Rizzolatti and Craighero, 2004; Van Overwalle and Baetens, 2009), all major hubs of the currently presented network. Interestingly, the MNS has been predominantly linked to functional domains here presumed to rely on prediction, i.e., motor learning (Calvo-Merino et al., 2005; Iacoboni and Mazziotta, 2007), language (Pulvermuller, 2018; Rizzolatti and Arbib, 1998) and music (Molnar-Szakacs and Overy, 2006). In addition, though still controversial, it has been tied to social cognition, primarily to affective empathy, the capacity to experience the emotional state of others (Gallese, 2003). *Predictive coding* supports the association between the MNS and social cognition, while regarding mirror neurons as part of a mechanism that generates predictions about the consequences of an action, irrespective of whether it is performed by self or other. It is theorized, that during action observation, an internal model of the agent's action is formed, allowing inferring its consequences and thereby understanding the agent's goals and intentions, a faculty crucial for social interaction (Brown and Brune, 2012; Gallese, 2003; Kilner et al., 2007). Others' emotional states, being reflected by muscular activity (voluntary or involuntary) (Kret, 2015), may activate an analogous apparatus to produce empathy. Although affective empathy is challenging to study, when differentiated from related concepts, especially 'theory of mind', it has been shown to mainly engage the IFG/AI region and the SMA (Engen and Singer, 2013; Fan et al., 2011), again resonating with the here described network.

Intriguingly, rhythmic entrainment a prediction-related activity which has been associated with a neural network similar to the here proposed network (Levitin et al., 2018; Merchant et al., 2015), is definitely linked to the four discussed functions: (1) it essentially involves motor control to allow synchronization of body movements (action) to an external periodic stimulus (perception) (Levitin et al., 2018); (2) within the 'dynamic attending theory', it was suggested to involve periodic fluctuations of attention (Large and Jones, 1999); (3) it was claimed to facilitate implicit learning (Selchenkova et al., 2014; Silva and Castro, 2018); and (4) it was shown to have prosocial effects, primarily to induce social bonding, cooperative and altruistic behaviors and empathy (Rabinowitch et al., 2013; Tarr et al., 2014; Trainor and Cirelli, 2015). Neurophysiologically, rhythmic entrainment has been attributed to the synchronization of multiple timescale neural oscillators to an external/inferred beat or meter (Large et al., 2015; Nozaradan et al., 2011; Zoefel et al., 2018). Interestingly, interactions between neural oscillators have been suggested to mediate the bidirectional transfer of predictions and prediction errors, the backbone process of predictive coding, also beyond the timing domain (Arnal and Giraud, 2012; Chao et al., 2018; Engel et al., 2001; Friston et al., 2015).

### *4.3. Concluding remarks and outlook*

The current meta-analysis supports the existence of a large-scale brain network dedicated to predictive processing. Anatomically, this network consists of regions within the IFG, AI, MFG, PMC, pre-SMA, TPJ, striatum, thalamus/subthalamus and the cerebellum. Functionally, it appears to be associated with high-level perception and action, as well as with aspects of attention, implicit learning, mirroring and social cognition. The *predictive coding* model helps understand how these various brain functions, each independently being associated with analogous set of brain regions, can actually converge under one umbrella, namely implicit prediction. In light of the evidence presented, we believe that the here reported network is a fundamental and robust brain system, probably interacting with other large-scale brain networks, such as the SN (possibly through the AI and ACC), mediating interoceptive inference aspects of emotional processing (Seth and Friston, 2016) and the dorsal attention network (possibly through the FEF and IPS), mediating attention allocation aimed at prediction error minimization.

The early evolutionary roots of the proposed network (Hanus, 2016) implies that it might have originally subserved predictive processing in basic activities like sensorimotor function and social interactions, and later adopted to higher neural functions from dance and music to language and possibly mathematics (Arsalidou and Taylor, 2011; Evans and Ullman, 2016; Iacoboni, 2009; Maruyama et al., 2012). The fact that the latter mental functions are relatively unique to humans implies that the putative network has undergone changes throughout evolution, which provided it with advantages to our species. One possible advantage can be the ability to process non-adjacent dependencies, including complex hierarchical and recursive structures (Christiansen and Chater, 2015; Fitch, 2017; Fuster, 1990; Koechlin and Jubault, 2006; Martins et al., 2017). Consistent with the view that the processing of hierarchical recursive structures relies on (1) associative learning and (2) working memory (Rey et al., 2012), the currently advocated network markedly resembles previously described networks for associative learning (see *4.2.3*) and working memory (Rottschy et al., 2012). In line with the proposition that interactions between neural oscillators may underlie predictive coding, the processing of hierarchical linguistic and musical structures has been shown to rely on hierarchical neural entrainment (Ding et al., 2016; Nozaradan et al., 2011).

Lastly, the neuroanatomical definition of a network devoted to higher-level prediction may expand the understanding of prediction-based neural processing in health and disease. Various psychological, psychiatric and neurological conditions have been linked to prediction-based processing including learning disabilities (Ullman and Pierpont, 2005; Evans and Ullman, 2016), autism spectrum disorders (van Boxtel and Lu, 2013), anxiety disorders (Lissek et al., 2005), addiction (Martin-Soelch et al., 2007) and subcortical movement disorders (Purves et al., 2008). Further characterization of the proposed network and its relations with other large-scale brain networks will likely advance diagnosis and treatment of these prevalent and devastating conditions. Moreover, it may promote cognitive enhancement in healthy individuals.

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## Declaration of Competing Interest

None of the authors has a competing interest to declare.

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