Neuroscience and Biobehavioral Reviews 149 (2023) 105171

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review article

The human cerebellum in reward anticipation and outcome processing: An activation likelihood estimation meta-analysis☆

Eline S. Kruithof*, Jana Klaus, Dennis J.L.G. Schutter

Department of Experimental Psychology, Helmholtz Institute, Utrecht University, Heidelberglaan 1, 3584 CS, Utrecht, the Netherlands

ARTICLE INFO

Keywords:
Anticipation
Cerebellum
Functional magnetic resonance imaging
Meta-analysis
Outcome
Predictive coding
Reward

ABSTRACT

The cerebellum generates internal prediction models and actively compares anticipated and actual outcomes in order to reach a desired end state. In this process, reward can serve as a reinforcer that shapes internal prediction models, enabling context-appropriate behavior. While the involvement of the cerebellum in reward processing has been established in animals, there is no detailed account of which cerebellar regions are involved in reward anticipation and outcome processing in humans. To this end, an activation likelihood estimation meta-analysis of functional neuroimaging studies was performed to investigate cerebellar functional activity patterns associated with reward anticipation and outcome processing in healthy adults. Results showed that reward anticipation ($k = 31$) was associated with regional activity in the bilateral anterior lobe, bilateral lobule VI, left Crus I and the posterior vermis, while reward outcome ($k = 16$) was associated with regional activity in the declive and left lobule VI. These findings demonstrate distinct involvement of the cerebellum in reward anticipation and outcome processing as part of a predictive coding routine.

1. Introduction

The cerebellum is a brain structure located in the posterior fossa and is well known for its involvement in motor function (Manto et al., 2012; Stoodley et al., 2012; Stoodley and Schmahmann, 2009) and more recently also for contributing to higher order mental functions (E et al., 2014; Schmahmann, 2019; Stoodley et al., 2012; Stoodley and Schmahmann, 2009). Within the domain of motor learning, the cerebellum generates internal forward models to predict motor sequences, which are then compared to the actual sensory feedback following action execution (Blakemore et al., 2001; Ebner and Pasalar, 2008; Ito, 2008; Wolpert et al., 1995, 1998). A mismatch between the predicted and actual outcome gives rise to a prediction error signal which is used by the cerebellum to update the internal model and improve motor performance (Shadmehr et al., 2010; Wolpert et al., 1995). The ability of the brain to generate predictions (inferences) and test those predictions against outcomes is crucial for controlling and guiding situation-appropriate behaviors. The process of minimizing the difference between expectation and outcome is part of a routine called predictive coding and serves to maintain bodily homeostasis (Friston, 2010). The central idea behind predictive coding is the formation of internal models that are used to reach a desired end state (e.g., learning a motor skill) and reduce uncertainty (Friston, 2010). Prior research has shown that the cerebellar involvement in predictive coding extends to higher order mental functions (for a review see Koziol et al., 2014). This idea fits the universal cerebellar transform hypothesis which posits that the cerebellum performs a single, generic computation on information supporting motor-, cognition- and emotion-related functions (Schmahmann et al., 2019, but see Diedrichsen et al., 2019, for an alternative account). In the active process of bridging the gap between the current and desired (future) end state, reward serves as a positive reinforcer that shapes internal models, enabling context-appropriate behavior. Reward is imperative to guiding movement, cognition and emotion, providing a common signal underlying these processes. Reward anticipation refers to the phase in which the prospect of a reward becomes evident as signaled by a cue. The absence of an anticipated reward generates a prediction error and indicates the need to adjust the internal model with the aim to minimize the prediction error, allowing for more accurate predictions about future rewards in connection to behavior.

A neurofunctional link between the cerebellar cortex and reward

---

☆ This work was supported by the Dutch Research Foundation (NWO, VI.C.181.005). The funding source was not involved in the conduct of the research and the preparation of the manuscript.

* Corresponding author.
E-mail address: e.s.kruithof@uu.nl (E.S. Kruithof).

https://doi.org/10.1016/j.neubiorev.2023.105171
Received 19 May 2022; Received in revised form 10 March 2023; Accepted 11 April 2023

processing has been demonstrated on the cellular level in the animal brain (for a review see Kostadinov and Häusser, 2022). Granule cells have been shown to be implicated in encoding anticipation, outcome and unexpected omission of reward (Wagner et al., 2017). Activation of Purkinje cells (PCs) caused by excitation of the mossy fiber-granule cell-parallel fiber pathway (Apps and Garwicz, 2005) is argued to carry learning-contingent reward error signals during visuomotor learning (Sendhilnathan et al., 2020). In addition to the mossy fibers that innervate granule cells, climbing fibers directly activate PCs upon presentation of a cue signaling a forthcoming large relative to a small reward (Larry et al., 2019) and following the delivery of unexpected rewards (Heffley and Hull, 2019). In agreement with the classic cerebellar learning theory (Albus, 1971; Ito and Kano, 1982; Marr, 1969), climbing fibers may drive learning by detecting mismatches between reward anticipation and outcome (Kostadinov et al., 2019). Furthermore, climbing fibers facilitate learning through long-term depression at parallel fiber-PC synapses (Albus, 1971; Ito and Kano, 1982; Marr, 1969). This modulates the PC inhibitory effect on the deep cerebellar nuclei (DCN), providing a communication channel between the cerebellum and reward-dedicated extracerebellar regions. Optogenetic stimulation of fibers that run from the DCN to the ventral tegmental area (VTA), for example, increases activity of VTA neurons and causes a strong preference for exploring locations that were accompanied by optogenetic stimulation in mice (Carta et al., 2019). Further evidence for the connection between the cerebellum and reward comes from results showing that silencing the dentate nucleus in mice through optogenetic stimulation of PCs lowers firing rates in neocortical motor neurons and reduces running speed and licking in anticipation of reward (Chabrol et al., 2019).

In line with these basic neuroscience studies, results from whole-brain functional neuroimaging meta-analyses of human studies point towards a role of the cerebellum in reward processing as well (Wilson et al., 2018; Jauhar et al., 2021). In one meta-analysis, neural activation patterns during the monetary incentive delay task were examined across fifteen studies in healthy volunteers (Wilson et al., 2018). Results showed activity of the striatum, insula, thalamus, amygdala, anterior cingulate gyrus and the supplementary motor area (SMA) during reward anticipation, regions that are part of the brain's salience network (Seeley et al., 2019). In addition, right-sided cerebellar activation in lobules I-V was observed. While the anterior cerebellum is not considered part of the salience network, this result does suggest a role for the cerebellum in motivational salience and reward-based learning (Wilson et al., 2018). Involvement of the anterior cerebellum in reward processes and associated motor preparation is further illustrated by its connections to the basal ganglia (Pierce and Péron, 2022) and results from other meta-analyses on emotion and motivation (Habas, 2022a). In another more recent meta-analytic study, neural activity associated with monetary reward anticipation and outcome to predictive rewards was contrasted to a no-win condition and a less than anticipated reward condition in healthy adult volunteers (Jauhar et al., 2021). Results from pooled data of forty-five eligible studies showed activation in the ventral striatum, cingulate cortex, SMA, insula and several clusters in the anterior (lobules IV-V) and posterior cerebellum (lobule VI and Crus I). While the relevance and meaning of the cerebellar activation during reward anticipation were not discussed in detail, the activated cerebellar regions are in agreement with the earlier discussed optogenetic stimulation findings in mice (Carta et al., 2019) and what is currently known about their functional connections to the extracerebellar regions of the salience and cortico-striatal network (Habas, 2022b). In contrast, analyses of the pooled data of twenty-eight studies on reward outcome yielded significant activation in the ventral striatum and the cingulate cortex, but not in the cerebellum (Jauhar et al., 2021). The lack of cerebellar activation appears at odds with animal research showing reward outcome-related activation of the cerebellum on the cellular level (Wagner et al., 2017; Sendhilnathan et al., 2020).

Furthermore, distinct cerebellar regions involved during monetary reward anticipation and outcome processing have been found in individuals with psychiatric disorders. For example, individuals with major depressive disorder (MDD) display decreased regional activity in the right lobules IV-VI in comparison to healthy controls (Yang et al., 2022), while individuals with schizophrenia show reduced activation of the anterior vermis during monetary reward anticipation (Leroy et al., 2020). Upon reward delivery, individuals with MDD show hypo-activation of left lobule VI and Crus I (Yang et al., 2022), while increased activity is seen in the left anterior cerebellum and left lobule VI of individuals with schizophrenia (Zeng et al., 2022). Although the effects found in the group of schizophrenia patients are likely to be influenced by medication use, involvement of the cerebellum during the different reward processing phases is nonetheless notable and concurs with documented alterations in reward sensitivity in MDD and schizophrenia (Halahakoon et al., 2020; Whitton et al., 2015).

Despite the growing body of neuroscientific research on the cerebellum in reward processing, its specific contribution to reward anticipation and outcome remains understudied. To this end, an activation likelihood estimation (ALE) meta-analysis of functional neuroimaging studies was performed to investigate cerebellar functional activity patterns of reward anticipation and outcome processing in healthy adults. Distinct patterns of activity were expected for the reward anticipation and outcome condition, as reward anticipation likely relies on prediction and preparatory feedforward processes, whereas reward outcome depends on evaluative feedback processes.

2. Methods

2.1. Literature search and study selection

To identify studies eligible for inclusion, the databases PubMed and Web of Science were searched on February 21, 2022, using the terms ('reward*') AND ('fMRI' OR 'functional MRI' OR 'functional magnetic resonance imaging') AND ('task*' OR 'paradigm*' OR 'game*') AND ('money' OR 'monetary') in the query. The terms 'task* ' and 'money* ' were used to restrict the search to studies that employed a reward-related task with money as reward, without limiting the search to one particular monetary reward task, such as the monetary incentive delay task. The monetary incentive delay task (Knutson et al., 2000) establishes for each trial whether a reward will be given, followed by participants' speeded response to a learned visual cue and feedback on whether performance was sufficient. This task design allows for the segregation of reward anticipation and outcome, the two stages that are at the center of the present meta-analysis (Wilson et al., 2018).

The initial search yielded 794 results in PubMed and 801 results in Web of Science. After removing duplicates, 886 unique records were identified. Eighty six records were excluded based on the title as those were obviously not related to the topic (e.g., addiction, smoking cessation treatment), leaving 800 articles for full-text screening. English-language functional magnetic resonance imaging (fMRI) studies in healthy adults were selected if they included a reward anticipation or reward outcome contrast as main effect. We did not include contrasts that compared different reward magnitudes (e.g., a high compared to low reward) or that compared reward with loss. Moreover, studies were selected if they reported significant hemodynamic cerebellar activity in the reward-specific contrast. Although our search comprised whole-brain analyses, we subsequently treated the cerebellum as a region of interest by only including coordinates from this region. This approach is similar to a previous ALE meta-analysis focusing on the cerebellum (Klaus and Schutter, 2021). Usually, meta-analyses focusing on the cerebellum already include 'cerebell* ' as a search term in the query. However, cerebellar activity is not always mentioned in the title or abstract but can be reported in the supplementary materials. By not including 'cerebell* ' as a search term in the query, we were able to identify eligible studies that would otherwise not have been discovered.

If a study assessed the effect of a drug or stress manipulation on reward anticipation and/or outcome, the main effect was included in case of an absent interaction effect with the stress or drug manipulation. In case of a significant interaction effect, only the control (i.e., placebo or no-stress) group was included. If a study sample consisted of both adults and underage participants, only the adult sample (> 18 years) was included in the analysis if cerebellar coordinates were reported for the adult group separately. Likewise, if a study sample consisted of both non-healthy and healthy participants, only the healthy participant group was included in the analysis if cerebellar coordinates were reported for the healthy participant group separately. One study (Kirk et al., 2015) reported two reward anticipation contrasts for two separate healthy samples. If cerebellar activity was mentioned in the paper and/or was evident in figures but the coordinates were not reported, we reached out to the corresponding author to request the cerebellar coordinates. Of the thirteen requests, coordinates for three studies were received and were included in the meta-analysis. Ten studies (Benningfield et al., 2014; Boecker-Schlier et al., 2017; Graf et al., 2018; Jung et al., 2011; Kollmann et al., 2017; Kumar et al., 2014; Murao et al., 2017; Schott et al., 2007; Schouw et al., 2013; Scult et al., 2017) could not be included because we were unable to retrieve the cerebellar coordinates.

Fig. 1 depicts the PRISMA flowchart of the study selection procedure. Forty-four studies were included in the final analysis, including 31 studies for the reward anticipation condition and 16 studies for the reward outcome condition. Three included studies reported significant cerebellar activation in both the reward anticipation and outcome contrast. The absence of a reward-specific contrast or significant cerebellar activation in these contrasts were the main reasons for exclusion. Table 1 summarizes all studies included in the meta-analysis.

2.2. *ALE meta-analysis*

An ALE meta-analysis estimates convergence of activity across fMRI studies (Eickhoff et al., 2009). Foci reported in individual studies are treated as spatial probability distributions centered at a coordinate, accounting for spatial uncertainty resulting from differences in sample sizes and between-template variability (Eickhoff et al., 2009). True convergence is then differentiated from random clustering by testing the ALE results against a spatial null distribution. Significant clusters were identified by applying a cluster-level family-wise error threshold of $p < .01$ and a cluster-forming threshold of $p < .001$, using 5000 permutations. Analyses were performed in Montreal Neurological Institute (MNI) reference space using NiMARE (version 0.0.10, https://github.com/neurostuff/NiMARE). Coordinates originally reported in Talairach space were converted into MNI space using the Lancaster transform *icbm2tal* (Lancaster et al., 2007). Since analyses were restricted to cerebellar coordinates, we used a mask corresponding to the cerebellum as defined in the MNI structural atlas (Collins et al., 1995; Mazziotta et al., 2001) in FSL (Smith et al., 2004). This mask was the null space in all analyses, allowing for a region of interest-specific analysis of reported activation peaks (see Klaus and Schutter, 2021).

To estimate publication bias, we computed the fail-safe N per study, defined as 5 × number of included studies + 10 (Rosenthal, 1979) for the reward anticipation ($N = 170$) and reward outcome condition ($N = 90$). Using the *create_coordinate_set* function in NiMARE, we then created 170 and 90 random foci, added them to the respective datasets, and repeated the analyses. If the clusters are still present, then this is indicative for a sufficiently robust ALE finding (Chen et al., 2022).

Results were visualized in Mango (version 4.1, http://rii.uthscsa.edu/mango/mango.html) by overlaying the ALE results onto a standard MNI template (colin27_T1_seg_MNI.nii; http://www.brainmap.org/ale/Colin27_T1_seg_MNI.nii.gz). Additionally, results were plotted on cerebellar flatmaps using the SUIT toolbox (Diedrichsen and Zotow, 2015) in MATLAB (version R2020b).

3. Results

Table 2 reports the ALE results for the reward anticipation and reward outcome condition.

3.1. *Reward anticipation*

Thirty-one studies investigating reward anticipation reported 58 foci in 918 participants. The ALE analysis for reward anticipation yielded two cerebellar clusters (top panel of Fig. 2). The peak coordinate of the largest cluster was located in right lobules I-IV. This cluster extended to bilateral lobule V, right lobule VI, and the posterior vermis (i.e., declive, tuber, pyramid and uvula). The peak coordinate of the second cluster was located in left lobule VI and this cluster extended to left Crus I. Both clusters were still observed after adding 170 random foci.

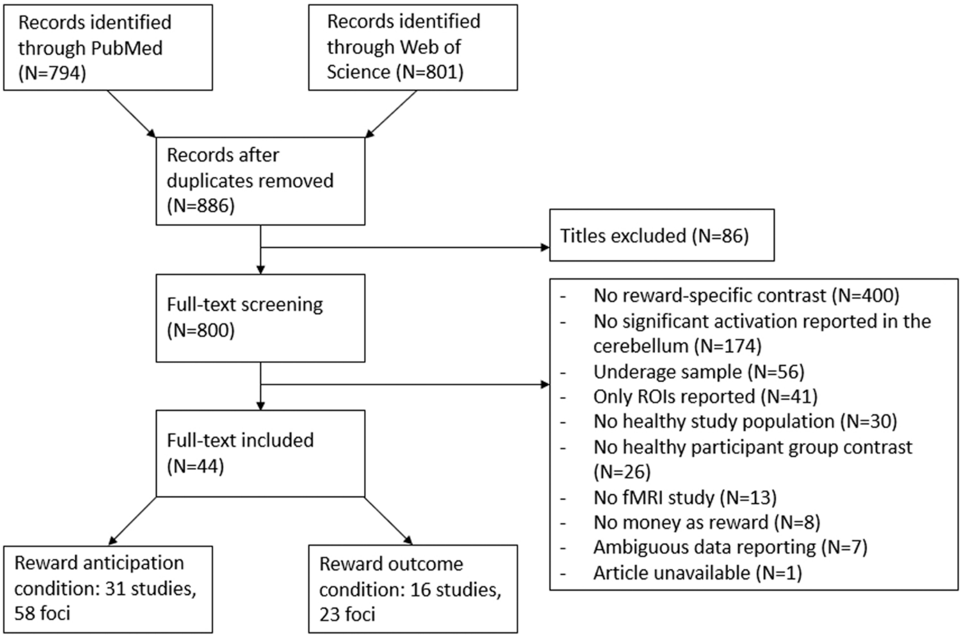

Fig. 1. PRISMA flowchart of the study selection procedure.

Table 1
Overview of studies included in the meta-analysis.

Study	N (female)	Age (M ± *SD*)[a]	Task	Performance-dependent reward (success rate)[b]	Number of coordinates included
Reward anticipation					
Abler et al. (2007)[c]	8 (4)	31.3 ± 8.8	MIDT	Yes (60%)	1
Adcock et al. (2006)	12 (3)	NA (18–35 *)	MIDT	Yes (66%)	1
Apaydın et al. (2018)	18 (11)	25.8 ± 5.8	Temporal attention task	Yes	1
Bayard et al. (2020)	29 (15)	28.94 ± 6.47	MIDT	Yes (50%)	8
Behan et al. (2015)	20 (11)	23.05 (18–35 *)	Monetary incentive delay-Go/NoGoTask	Yes	2
Bjork et al. (2008)	23 (11)	32 ± 8	MIDT	Yes (66%)	1
Bjork et al. (2010)	24 (12)	29.3 ± 5.7	MIDT	Yes (66%)	1
Dhingra et al. (2021)[c]	63 (27)	37 ± 11	MIDT	Yes (67%)	2
Dillon et al. (2010)[c]	32 in reward anticipation contrast (16). 31 in reward outcome contrast.	21.68 ± 3.35	MIDT	No	1
Fauth-Bühler et al. (2014)	89 (0)	36.2 ± 9.4	Effort-dependent instrumental motivation task	Yes	3
Grimm et al. (2021)	45 (23)	22.81 ± 2.71	MIDT	Yes	1
Herbort et al. (2016)	23 (23)	25.78 ± 5.75	MIDT	Yes (66%)	3
Ikeda et al. (2019)	15 (8)	31.7 ± 4.2	MIDT	Yes (66%)	2
Juckel et al. (2012)	13 (2)	25.69 ± 4.84	MIDT	Yes	1
Kaufmann et al. (2013)	19 (11)	34.9 ± 11.8	MIDT	Yes (66%)	1
Kirk et al. (2015)	78 (35)	40.2 ± 10.3 (meditators), 36.5 ± 9.7 (controls)	MIDT	Yes	Controls (2), meditators (2)
Knutson et al. (2001)	9 (7)	26.45 ± 5.85	MIDT	Yes (66%)	1
Knutson et al. (2003)	12 (6)	31 (NA)	MIDT	Yes (66%)	1
Libedinsky et al. (2011)	22 (0)	22.7 ± 3.2	MIDT	Yes (60%)	1
Montoya et al. (2014)	20 (0)	23 ± 3.4	MIDT	Yes	1
Murphy et al. (2017)	33 (6)	42 ± 8.6	MIDT	Yes (66%)	1
Ossewaarde et al. (2011)	28 (28)	22.8 (18–38 *)	MIDT	Yes (33%)	2
Pfabigan et al. (2014)	25 (13)	23.8 ± 3.6	MIDT	Yes (50%)	3
Saji et al. (2013)	18 (10)	29.6 ± 6.94	MIDT	Yes (66%)	2
Schlagenhauf et al. (2008)	10 (1)	31.8 ± 8.7	MIDT	Yes (67%)	2
Schneider et al. (2018)	46 (25)	28.08 ± 4.17	MIDT	Yes (50%)	4
Schreiter et al. (2016)	20 (12)	41.45 ± 7.33	MIDT	Yes	1
Spaniol et al. (2015)	31 (18)	25.44 ± 3.79 (younger adults), 68.47 ± 5.38 (older adults)	MIDT	Yes (66%)	2
Treadway et al. (2013)	38 (18)	22 (18–34 *)	MIDT	Yes (66%)	2
Van Leeuwen et al. (2019)	73 (0)	33.1 ± 2 (control-no stress), 35.4 ± 2 (control-stress), 33.4 ± 2.6 (siblings of schizophrenia patients-no stress), 32.6 ± 1.7 (siblings of schizophrenia patients-stress)	MIDT	Yes (55%)	1

(*continued on next page*)

Table 1 (*continued*)

Study	N (female)	Age (M ± *SD*)[a]	Task	Performance-dependent reward (success rate)[b]	Number of coordinates included
Yan et al. (2016)	22 (11)	19.78 ± 0.8	MIDT	Yes (66%)	1
Reward outcome					
Abler et al. (2007)[c]	8 (4)	31.3 ± 8.8	MIDT	Yes (60%)	1
Camara et al. (2009)	17 (10)	21.6 ± 2.6	Monetary gambling task	No	2
Dhingra et al. (2021)[c]	63 (27)	37 ± 11	MIDT	Yes (67%)	1
Dhingra et al. (2020)	54 (24)	40 ± 14	MIDT	Yes (67%)	2
Dillon et al. (2010)[c]	32 in reward anticipation contrast (16). 31 in reward outcome contrast.	21.68 ± 3.35	MIDT	No	1
Ernst et al. (2005)	14 (6)	26.7 ± 5	Wheel of Fortune task	No	2
Fujiwara et al. (2009)	17 (5)	NA (20–29 *)	Free-choice task	Yes	1
Gaillard et al. (2019)	23 (14)	24.7 ± 0.9	Fribourg reward task	Yes	1
Katahira et al. (2015)	25 (12)	24.44 ± 5.28	Decision-making task	Yes (65%)	1
Koch et al. (2008)	28 (17)	24.6 ± 5.5	Trial-and-error learning task	Yes	1
Kube et al. (2018)	23 (11)	30 ± 5	Probabilistic reinforcement learning task	Yes (70%)	2
Mucci et al. (2015)	22 (12)	31.91 ± 8.49	MIDT	Yes (66%)	1
Vaidya et al. (2013)	18 (9)	27.72 ± 1.36	MIDT	Yes (66%)	2
Van de Steen et al. (2020)	368 (199)	29 (22–36 *)	Monetary Incentive Gambling task	No	3
Yao et al. (2020)	27 (0)	22 ± 1.92	MIDT	Yes (67%)	1
Zhornitsky et al. (2021)	45 (16)	41.8 ± 8.4	MIDT	Yes (67%)	1

MIDT = Monetary Incentive Delay task. NA = not available.

[a] Age range reported if age mean and/or SD were not indicated.

[b] Reported if available.

[c] Both the reward anticipation and outcome contrast were included for this study.

3.2. *Reward outcome*

Sixteen studies investigating reward outcome reported 23 foci in 783 participants. The ALE analysis yielded one cluster (bottom panel of Fig. 2). The peak coordinate of the cluster was located in the declive and this cluster extended to left lobule VI. This cluster was still observed after adding 90 random foci.

4. Discussion

Reward is an important signal for learning and behavioral adaptation. To examine the involvement of specific cerebellar regions in reward processing, we performed an ALE meta-analysis on fMRI studies to map regional cerebellar activity associated with reward anticipation and outcome processing in healthy adult volunteers. Results showed dissociable cerebellar substrates for reward anticipation and outcome. More specifically, reward anticipation was associated with regional activity in the bilateral anterior lobe, bilateral lobule VI, left Crus I and the posterior vermis, while reward outcome was associated with regional activity in the declive and left lobule VI.

4.1. *Reward anticipation*

The largest cluster had its peak coordinate in right lobules I-IV and extended to bilateral lobule V, right lobule VI and the posterior vermis (i.e., declive, tuber, pyramid and uvula). Given the involvement of the anterior lobe in sensorimotor functions (Stoodley et al., 2012; Stoodley and Schmahmann, 2009), activity in these regions is suggested to relate to preparations for an upcoming motor response. In reward tasks that involve reward anticipation, a target is presented after the anticipation phase. Participants are instructed to respond to the target by pressing a button. Doing so in time usually leads to reward in the majority of trials. According to the cerebellar somatotopic map, activity patterns overlap with regions involved in facial (e.g., eyes) as well as right arm, hand and finger movements (Boillat et al., 2020; Grodd et al., 2001). These body parts can be assumed to be involved during reward anticipation, but more readily play a role in response to target presentation (e.g., button press with the right hand). This supports the idea of preparatory motor-related activity in cerebellar lobules during reward anticipation, which is linked to the future usage of the body parts represented in these areas. Cerebellar forward models predict the sensory consequences of movement based on an efference copy of the motor command (Blakemore et al., 2001; Miall and Wolpert, 1996; Wolpert et al., 1998). Thus, the efference copy represents a motor signal that precedes the movement (Miall and Wolpert, 1996) and allows comparison of the sensory feedback (e.g., through proprioception) to sensory predictions resulting specifically from one's own movement (Pynn and DeSouza, 2013; Wolpert et al., 1995). A similar principle may apply to the identification of mismatches between reward anticipation and outcome. This information can then be used to update the internal model in order to improve motor performance (Shadmehr et al., 2010; Wolpert et al., 1995). As such, the cluster of activity in the anterior lobe is proposed to represent the efference copy necessary for reinforcement learning.

The largest cluster extended to right lobule VI. Lobule VI is part of the

Table 2
ALE results for reward anticipation and reward outcome.

				Peak MNI coordinates			
Condition	Cluster	Cluster size (mm^3)	T	X	Y	Z	Location of cluster
Reward anticipation	1	10,589	3.7	8	-50	0	Right lobules I-IV Left lobules I-IV Bilateral lobule V Right lobule VI Posterior vermis (declive, tuber, pyramid and uvula)
	2	2997	3.7	-30	-60	-18	Left lobule VI Left Crus I
Reward outcome	1	433	2.05	-4	-68	-16	Declive Left lobule VI

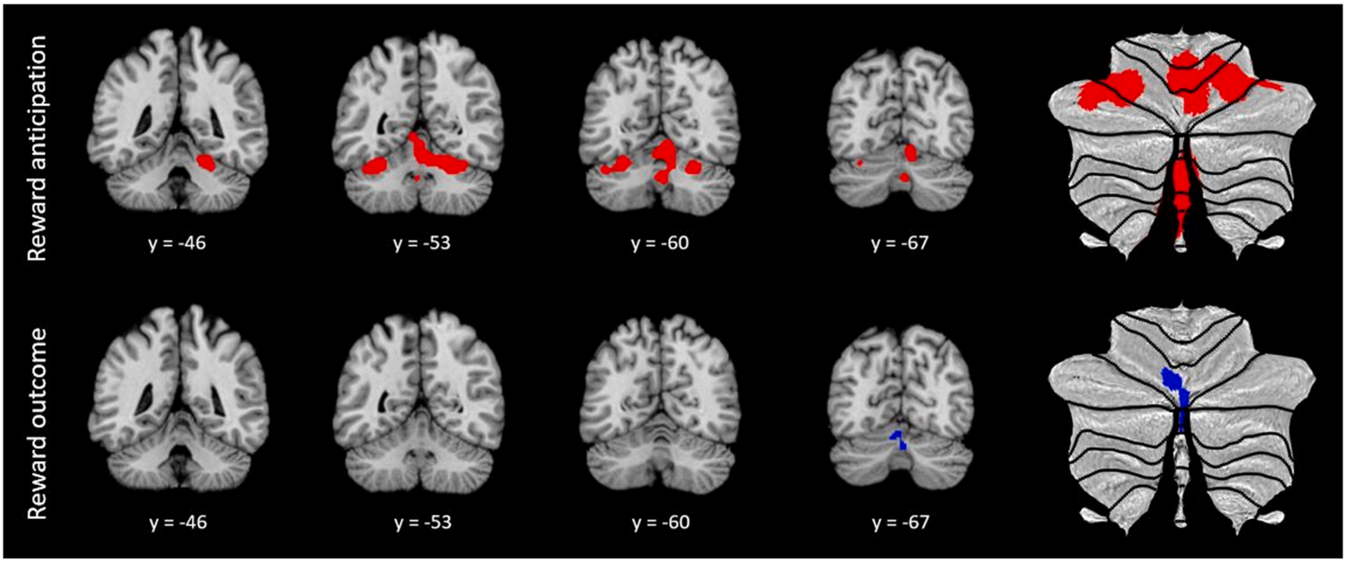

Fig. 2. ALE results for reward anticipation (top) and reward outcome (bottom) overlaid on the Colin27 template (left) and mapped onto a cerebellar flatmap (right; Diedrichsen and Zotow, 2015).

brain's salience network (Habas et al., 2009; Sang et al., 2012), implicated in detecting and responding to relevant internal and external stimuli (Seeley, 2019). Upon detection of the salient event, the salience network recruits attentional resources to facilitate task-relevant behavior (Menon and Uddin, 2010; Peters et al., 2016). It coordinates brain network dynamics by deactivating the default mode network (DMN) and activating the central executive network in response to a salient event (Goulden et al., 2014; Sridharan et al., 2008). A failure to deactivate the DMN is associated with lapses of externally focused attention (Weissman et al., 2006) and impaired inhibitory control on a stop-signal task (Bonnelle et al., 2012), demonstrating how the salience network influences behavior. In the context of reward anticipation, right lobule VI as part of the salience network may be involved in the regulation of attentional resources following the salient cue, enabling fast responses to relevant stimuli.

In addition, involvement of the posterior vermis (i.e., declive, tuber, pyramid and uvula) was observed during reward anticipation. The vermis is involved in emotion processing and has therefore also been termed the 'limbic cerebellum' (Baumann and Mattingley, 2012; Schmahmann et al., 2007). Moreover, owing to its connections to the hypothalamus and reticular formation (Sprague and Chambers, 1954; Wen et al., 2004; Zhu et al., 2006), the vermis is implicated in the regulation of autonomic arousal (Demirtas-Tatlidede et al., 2011; Maschke et al., 2000). According to the somatic marker hypothesis, autonomic signals (i.e., somatic markers such as heart rate) to different outcome scenarios can be used to (implicitly) guide decision-making (Damasio, 1994). Anticipatory autonomic responses to maladaptive behavioral strategies function as a teaching signal which shape advantageous behavioral choices over time (Bechara et al., 1996, 1997). The somatic marker hypothesis can be linked to predictive coding in the context of interoception (i.e., awareness of bodily signals; Seth et al., 2012). Within the framework of interoceptive predictive coding, emotional states are proposed to arise from predictions about interoceptive signals (Seth et al., 2012). The role of the vermis in emotion processing and the regulation of autonomic arousal suggests that the posterior medial part of the cerebellum is implicated in interoceptive predictive coding. The cerebellum is proposed to receive reward signals from the basal ganglia, thereby associating particular actions with a reward value to drive learning (Kostadinov and Häusser, 2022). Speculatively, the posterior vermis may hold a representation of somatic markers, which may be used by the cerebellum in the generation of forward models to select the motor response that will most likely lead to reward.

The second cluster had its peak coordinate in left lobule VI and extended to left Crus I. Left lobule VI as well as adjacent Crus I are, like right lobule VI and right Crus I, part of the salience network (Habas et al., 2009; Sang et al., 2012). Similar to the right-sided cluster in right lobule VI, this left-lateralized cluster is arguably involved in the detection of salient cues and the allocation of attentional resources.

Next to the involvement of right lobules I-VI, left lobules IV-VI and left Crus I that was also found for reward anticipation in previous meta-analyses (Jauhar et al., 2021; Wilson et al., 2018), our meta-analysis identified additional involvement of the posterior vermis. The meta-analyses are similar with respect to the healthy adult sample and the focus on monetary reward. However, in contrast to previous whole-brain meta-analyses, the current study used the cerebellum as the null space, thereby likely increasing the statistical sensitivity to detect clusters in the vermis.

As mentioned earlier, there is evidence that individuals with schizophrenia and MDD show abnormal cerebellar activity associated with reward anticipation as compared to healthy controls (Leroy et al., 2020; Yang et al., 2022). Individuals with MDD showed reduced activity in the anterior lobe and right lobule VI during reward anticipation (Yang et al., 2022). While a possible confounding role of medication cannot be excluded, the affected regions concur with the results of our meta-analysis. Moreover, a recent coordinate-based meta-analysis of functional neuroimaging studies reported decreased activity in the anterior vermis (culmen) during reward anticipation in individuals with schizophrenia as compared to healthy controls (Leroy et al., 2020). Since schizophrenia is associated with difficulties in using reward signals to select and perform goal-directed actions (Barch and Dowd, 2010; Gold et al., 2008; Strauss et al., 2014), the decreased anticipatory activity in the culmen may suggest deficiencies in reward learning. The blunted vermal activity may be a consequence of reduced input from the dopaminergic neurons in the basal ganglia (Kostadinov and Häusser, 2022). Support for this possibility comes from studies showing striatal under-activation during reward anticipation in both individuals with schizophrenia as well as in individuals with MDD (Arrondo et al., 2015; Leroy et al., 2020; Yang et al., 2022; Zeng et al., 2022).

4.1.1. *Functional connectivity*

To explore possible functional connections between the clusters observed in the current studies and other extracerebellar regions, we used Neurosynth (https://neurosynth.org/locations/) to generate resting-state maps based on peak coordinates obtained in the ALE analyses as voxel-based seeds. The peak coordinate in right lobules I-IV showed functional connections to the rostral anterior cingulate cortex (ACC; Fig. 3A). A recent study in mice showed that the rostral ACC predicts future states given a particular chosen action and monitors whether outcomes match these predictions (Akam et al., 2021). Moreover, the rostral ACC is suggested to use learned values of actions (Kennerley et al., 2006) and action-state transitions (Akam et al., 2021) to guide subsequent choices, thus controlling action selection. Similarly, the cerebellar anterior lobe predicts consequences of actions using the efference copy to compare outcomes against expectations. In case of a prediction violation, the resulting error signal is then arguably used to update the internal model to improve the anticipated outcome of subsequent actions.

To provide a more representative picture of the functional connections of this large cluster, we selected two additional coordinates in right lateral lobule VI ($x = 24$, $y = -62$, $z = -20$) and the posterior vermis (i.e., pyramid; $x = 0$, $y = -68$, $z = -34$). Right lateral lobule VI showed positive functional connections to the thalamus, anterior insula, dorsal ACC, amygdala and dorsal striatum (Fig. 3B), regions which are part of the brain's salience network (Habas et al., 2009; Seeley et al., 2007). This observation supports the idea that this region is part of the network involved in the detection of potentially relevant information during reward anticipation. The peak coordinate in the pyramid showed positive functional connections to the anterior insular cortex (Fig. 3C), which contains a meta-representation of interoceptive (bodily) states that contributes to subjective feelings (Craig, 2003, 2009). Activity in the anterior insula was positively associated with interoceptive awareness in a heartbeat detection task (Critchley et al., 2004; Pollatos et al., 2007; Zaki et al., 2012), also preceding disadvantageous behavioral choices (Werner et al., 2013). To minimize interoceptive prediction errors with the goal of reaching bodily homeostasis, the anterior insula, together with the ACC, engages subcortical regions (such as the brainstem) as targets for visceromotor control (Seth, 2013). As such, the anterior insula is able to detect as well as regulate physiological changes. The connections of the pyramid with the anterior insular region provide a neural basis for interoceptive predictive coding during reward anticipation through the processing of somatic markers.

The peak coordinate of the second cluster in left lobule VI showed positive functional connections to the thalamus, anterior insula and SMA (Fig. 3D). Similar to right lobule VI from the first cluster, this implies involvement in the brain's salience network (Habas et al., 2009; Seeley et al., 2007). In addition, the peak coordinate of the second cluster in left lobule VI showed negative functional connections to the prefrontal cortex (PFC), PCC and precuneus. This could suggest salience network-mediated deactivation of the DMN (which includes the medial PFC, PCC and precuneus; Raichle et al., 2001; Yeo et al., 2011) to facilitate attention towards external salient events (Goulden et al., 2014; Menon and Uddin, 2010; Peters et al., 2016; Sridharan et al., 2008).

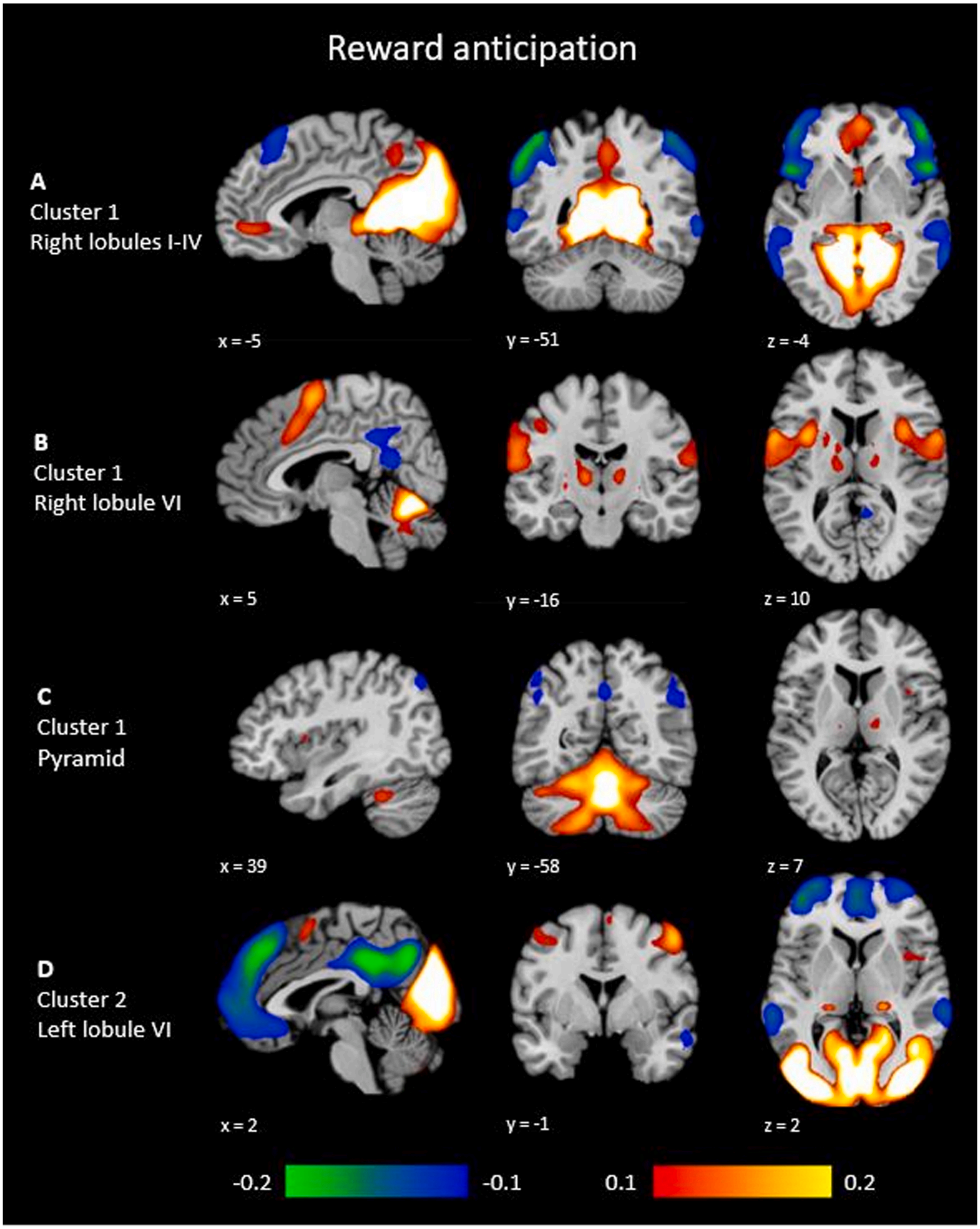

Fig. 3. Resting-state functional connectivity maps of the ALE results for reward anticipation generated via Neurosynth. Warm colors indicate a positive correlation of the seed with the associated brain region and cool colors indicate a negative correlation of the seed with the associated brain region. Color bars represent the strength of the correlation. Pearson correlation coefficients were thresholded at 0.1 for positive correlations and −0.1 for negative correlations. A) Resting-state functional connectivity map using the peak coordinate of cluster 1 ($x = 8, y = -50, z = 0$) in right lobules I-IV as seed. This coordinate has positive functional connections to the cuneus, precuneus, thalamus and rostral and subgenual ACC and negative functional connections to the angular gyrus, middle temporal gyrus, anterior insula, superior frontal gyrus and dorsolateral PFC. B) Resting-state functional connectivity map using a coordinate in right lobule VI of cluster 1 ($x = 24, y = -62, z = -20$) as seed. This coordinate has positive functional connections to the thalamus, dorsal striatum, amygdala, anterior and posterior insula, SMA and dorsal ACC and negative functional connections to the angular gyrus, posterior cingulate cortex (PCC), and fusiform gyrus. C) Resting-state functional connectivity map using a coordinate in the pyramid of cluster 1 ($x = 0, y = -68, z = -34$) as seed. This coordinate has positive functional connections to the thalamus, anterior insula and SMA and negative functional connections to the angular gyrus, precuneus and PCC. D) Resting-state functional connectivity map using the peak coordinate of cluster 2 ($x = -30, y = -60, z = -18$) in left lobule VI as seed. This coordinate has positive functional connections to the occipital cortex, cuneus, thalamus, supramarginal gyrus, anterior insula, primary motor cortex and SMA and negative functional connections to the precuneus, middle temporal gyrus, PCC, caudate, rostral ACC, subgenual ACC and PFC.

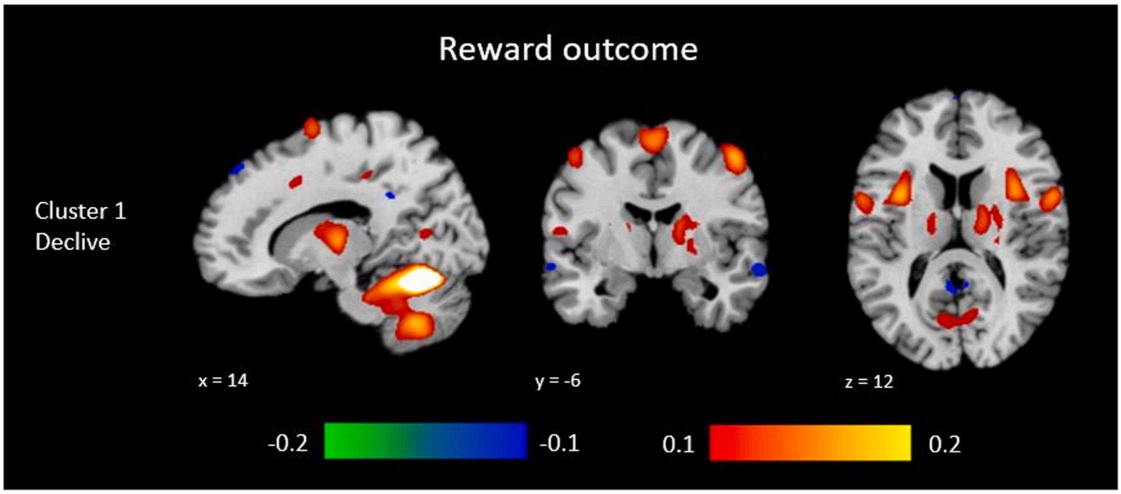

Fig. 4. Resting-state functional connectivity map based on the peak coordinate of the cluster in the ALE analysis for reward outcome ($x = -4$, $y = -68$, $z = -16$) generated via Neurosynth. Warm colors indicate a positive correlation of the seed with the associated brain region and cool colors indicate a negative correlation of the seed with the associated brain region. Color bars represent the strength of the correlation. Pearson correlation coefficients were thresholded at 0.1 for positive correlations and −0.1 for negative correlations. The peak coordinate has positive functional connections to the brainstem, cuneus, thalamus, supramarginal gyrus, putamen, globus pallidus, anterior insula, dorsal ACC and SMA and negative functional connections to the angular gyrus, precuneus, PCC and medial PFC.

4.2. Reward outcome

Our results revealed one cluster in the declive and left lobule VI for reward outcome. Left lobule VI is involved in processing sensorimotor errors (Fautrelle et al., 2011) which are used to update the forward model (Tseng et al., 2007). When processing reward prediction errors, activity in the declive was specific for learning from one's own actions as compared to observing the actions of others, suggesting that this region is involved in the integration of self-generated actions with reward outcome information (Kobza and Bellebaum, 2015). These findings suggest that the cluster of activity in the declive and left lobule VI reflects action-perception coupling, which arguably contributes to the updating and fine-tuning of the internal model as stimulus-action-reward associations are learned (Kostadinov and Häusser, 2022).

Individuals with MDD typically show lower left-sided activity in lobule VI and Crus I during reward outcome as compared to healthy controls (Yang et al., 2022). As these regions are part of the brain's salience network, this may indicate a reduction in feedback-related reward signals, which has a negative effect on learning stimulus-action-reward associations. This may suggest a role of the cerebellum in the relations between depression, reduced reward sensitivity and anhedonia. The finding that individuals with MDD show difficulties in using reward feedback signals to adjust their behavior accordingly (Pizzagalli et al., 2008; Vrieze et al., 2013) may hint at a possible cerebellar dysfunction in mood disorders (Schutter, 2022). By contrast, increased left-sided activity in the anterior cerebellum and lobule VI during reward outcome have been observed in individuals with schizophrenia in comparison to neurotypical controls (Zeng et al., 2022). The increased activity in the cerebellum may comprise an extension to the limbic-striatal over-responsiveness to reward outcome, arguably reflecting the presumed motivational significance of hedonic experience associated with reward-seeking behavior in individuals with schizophrenia (Zeng et al., 2022). Interestingly, our meta-analysis revealed reward outcome-related activation of a cluster encompassing the declive and left lobule VI, whereas, in contrast to individuals with schizophrenia, no activation was observed in the anterior lobe of healthy volunteers. The fact that left anterior lobe activation was seen in healthy volunteers during reward anticipation may hint at possible impairments in using external feedback (reward) signals to form outcome-based associations and construct internal models (i.e., model-based learning).

4.2.1. Functional connectivity

The peak coordinate of the reward outcome cluster showed positive resting-state functional connections to the basal ganglia (i.e., putamen), anterior insula and dorsal ACC (Fig. 4). Like the declive, these regions have been shown to be involved in integrating action with reward outcome specifically when reward feedback depended on one's own actions as compared to the actions of someone else (Kobza and Bellebaum, 2015). The putamen as part of the dorsal striatum maintains information about action-reward associations, allowing reinforcement of future actions that will lead to reward (Balleine et al., 2007; O'Doherty et al., 2004). In the process of learning sensorimotor-reward contingencies, cerebellar internal models are proposed to convey predictive action signals to the basal ganglia to aid in the reinforcement of these actions (Kostadinov and Häusser, 2022). These findings support the idea that the declive and left lobule VI integrate perception of reward with action to refine the internal model. This allows the cerebellum to interact with the basal ganglia to reinforce actions that will yield reward.

4.3. Limitations

The relatively low number of studies included in the reward outcome analysis increases the likelihood of both type I and type II errors (Button et al., 2013; Christley, 2010). Therefore, the reward outcome results should be interpreted with caution. Interestingly, the whole-brain approach used in the meta-analysis by Jauhar et al. (2021) did not find a cerebellar cluster for reward outcome (as opposed to reward anticipation). This may suggest that cerebellar involvement in reward outcome is more difficult to demonstrate compared to reward anticipation. Future studies will need to address this discrepancy to uncover the exact contribution of the cerebellum in this process.

Secondly, the fact that in the individual studies the focus was not the cerebellum and as a result may suffer bias by not being part of the field of view during image acquisition and/or not being rigidly preprocessed is a limitation of our study. Given the rapidly growing empirical evidence of cerebellar involvement in a multitude of social and affective functions, including in psychiatric disorders, we implore researchers to pay more attention to this often overlooked brain structure.

4.4. Future directions

Several future directions arise that could help to further understand the functional significance and meaning of the cerebellum in reward processing. A meta-analysis of fMRI studies on loss anticipation and outcome in healthy volunteers found activity in left lobule VI during loss anticipation in the monetary incentive delay task (Dugré et al., 2018). Activation of left lobule VI during both reward and loss anticipation may suggest that this region subserves a more general role in processes underlying motivational relevance, attention and executive functions. Bilateral activation of lobule VI and Crus I along with prefrontal and parietal cortical areas have been found during cognitively demanding tasks (Stoodley et al., 2012). Furthermore, left lobular VI activity has been linked to spatial tasks (Stoodley et al., 2012) which in the current context could be interpreted as heightened attention to the location of the anticipated outcome. The question how reward-specific the clusters found in the cerebellum are needs further research, as well as which particular mental process(es) these activations actually represent.

Related to the previous point, to further clarify the cerebellar involvement in reward anticipation and outcome, it may be interesting to examine the impact of uncertainty, reward type and size, such as the subjective experience of reward defined as (i.e., the absence of an anticipated punishment) or the subjective experience of punishment when the size of the reward outcome is smaller than anticipated. A task-related factor that may contribute to uncertainty-related activity in the cerebellum in the context of reward processing is whether reward outcome is performance-dependent or not. When reward outcome is not coupled to performance, cerebellar prediction mechanisms (e.g., the efference copy) that promote reward learning will be relied upon less during the reward anticipation phase. In the absence of a performance-dependent reward, patterns of activity during reward outcome are expected to be present less in regions that are implicated in action-outcome coupling. Alternatively, clusters might be more prominent particularly in areas that are involved in liking (i.e., the hedonic pleasure associated with rewards). Dissociating the effects of performance-dependent and non-performance-dependent rewards was not feasible in this meta-analysis due to the low number of studies where rewards did not depend on performance ($k = 1$ for reward anticipation and $k = 4$ for reward outcome). Future research is needed to clarify the influence of performance-dependent and non-performance-dependent rewards to cerebellar activity associated with reward anticipation and outcome. With regard to reward type, an important issue is the extent to which the present results can be extrapolated to reward types other than money, including primary reinforcers such as food and sex, as well as secondary social rewards such as a receiving a compliment, interpersonal bonding and humor. A meta-analysis showed common activation of the amygdala, striatum, insula and ventromedial PFC across monetary, food, and erotic reward studies (Sescousse et al., 2013). Moreover, another more recent meta-analysis demonstrated prediction error signals in the midbrain during cognitive and reward learning tasks, and in the insular cortex for perceptual, social, cognitive, and reward prediction errors (Corlett et al., 2022). These findings suggest overlapping brain regions associated with different reward modalities. However, distinct brain regions for reward type have also been observed, which for monetary rewards include the ventral striatum and anterior orbitofrontal cortex, for erotic rewards the hypothalamus and extrastriate body area, and for food rewards the somatosensory cortex (Sescousse et al., 2013). Furthermore, a functional organization along a posterior-anterior axis has been demonstrated in the orbitofrontal cortex, with the anterior portion responding to secondary (monetary) rewards and the posterior portion responding to primary rewards (Kringelbach and Rolls, 2004; Sescousse et al., 2010, 2013). Taken together, evidence on whether monetary and non-monetary rewards recruit distinct or shared brain regions remains inconclusive. Therefore, findings from the present study should be interpreted primarily in the context of monetary reward only. Also, the effect of liking and wanting (i.e., the motivational drive to obtain rewards) may be of interest to further specify the functional significance of cerebellar activity. In addition, examining the differential involvement of the cerebellum in model-based and model-free learning may shed further light on how the cerebellum and its regions are involved in reward processing across different contexts (Pierce and Péron, 2022).

Finally, future studies in clinical populations may provide insights into reward-related symptoms in psychiatric disorders and how the symptoms relate to distinct patterns of cerebellar activity associated with reward anticipation and outcome. For example, positive symptoms of schizophrenia can go accompanied by an altered sense of agency (e.g., delusions of control), which could result from an impairment in predicting the reward outcome of self-generated actions (Synofzik et al., 2010; Voss et al., 2010; Welniarz et al., 2021). A disrupted sense of agency as observed in individuals with schizophrenia is argued to be rooted in faulty efference copy mechanisms in the cerebellum (Pinheiro et al., 2020; Thakkar et al., 2021), which could potentially hamper reward learning based on self-generated actions (Xiao et al., 2023). Lastly, a translational approach may help to integrate the analyses and results on the cellular (animal) and system's (human) level and provide a unified account of cerebellar workings on the micro- and macroscopic level.

5. Conclusion

The present meta-analysis revealed distinct patterns of activity associated with reward anticipation and outcome in the cerebellum. The findings can be conceptualized within a cerebellum-oriented framework of predictive coding, where the cerebellum is involved in prediction and associated feedforward processes during reward anticipation and evaluative feedback processed during reward outcome.

Declarations of interest

None.

Data availability

The data used for this article is available at https://surfdrive.surf.nl/files/index.php/s/s7N3IR29wg7cNym.

Data ALE reward cerebellum (Original data) (SURFdrive)

References

Abler, B., Erk, S., Walter, H., 2007. Human reward system activation is modulated by a single dose of olanzapine in healthy subjects in an event-related, double-blind, placebo-controlled fMRI study. Psychopharmacology 191, 823–833. https://doi.org/10.1007/s00213-006-0690-y.

Adcock, R.A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., Gabrieli, J.D., 2006. Reward-motivated learning: mesolimbic activation precedes memory formation. Neuron 50, 507–517. https://doi.org/10.1016/j.neuron.2006.03.036.

Akam, T., Rodrigues-Vaz, I., Marcelo, I., Zhang, X., Pereira, M., Oliveira, R.F., Costa, R.M., 2021. The anterior cingulate cortex predicts future states to mediate model-based action selection. Neuron 109, 149–163. https://doi.org/10.1016/j.neuron.2020.10.013.

Albus, J.S., 1971. A theory of cerebellar function. Math. Biosci. 10, 25–61.

Apaydın, N., Üstün, S., Kale, E.H., Çelikağ, İ., Özgüven, H.D., Baskak, B., Çiçek, M., 2018. Neural mechanisms underlying time perception and reward anticipation. Front. Hum. Neurosci. 12, 115. https://doi.org/10.3389/fnhum.2018.00115.

Apps, R., Garwicz, M., 2005. Anatomical and physiological foundations of cerebellar information processing. Nat. Rev. Neurosci. 6, 297–311. https://doi.org/10.1038/nrn1646.

Arrondo, G., Segarra, N., Metastasio, A., Ziauddeen, H., Spencer, J., Reinders, N.R., Murray, G.K., 2015. Reduction in ventral striatal activity when anticipating a reward in depression and schizophrenia: a replicated cross-diagnostic finding. Front. Psychol. 6, 1280. https://doi.org/10.3389/fpsyg.2015.01280.

Balleine, B.W., Delgado, M.R., Hikosaka, O., 2007. The role of the dorsal striatum in reward and decision-making. J. Neurosci. 27 (31), 8161–8165. https://doi.org/10.1523/JNEUROSCI.1554-07.2007.

Barch, D.M., Dowd, E.C., 2010. Goal representations and motivational drive in schizophrenia: the role of prefrontal–striatal interactions. Schizophr. Bull. 36 (5), 919–934. https://doi.org/10.1093/schbul/sbq068.

Baumann, O., Mattingley, J.B., 2012. Functional topography of primary emotion processing in the human cerebellum. NeuroImage 61, 805–811. https://doi.org/10.1016/j.neuroimage.2012.03.044.

Bayard, F., Abé, C., Wrobel, N., Ingvar, M., Henje, E., Petrovic, P., 2020. Emotional instability relates to ventral striatum activity during reward anticipation in females. Front. Behav. Neurosci. 14, 76. https://doi.org/10.3389/fnbeh.2020.00076.

Bechara, A., Tranel, D., Damasio, H., Damasio, A.R., 1996. Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. Cereb. Cortex 6, 215–225. https://doi.org/10.1093/cercor/6.2.215.

Bechara, A., Damasio, H., Tranel, D., Damasio, A.R., 1997. Deciding advantageously before knowing the advantageous strategy. Science 275, 1293–1295.

Behan, B., Stone, A., Garavan, H., 2015. Right prefrontal and ventral striatum interactions underlying impulsive choice and impulsive responding. Hum. Brain Mapp. 36, 187–198. https://doi.org/10.1002/hbm.22621.

Benningfield, M.M., Blackford, J.U., Ellsworth, M.E., Samanez-Larkin, G.R., Martin, P.R., Cowan, R.L., Zald, D.H., 2014. Caudate responses to reward anticipation associated with delay discounting behavior in healthy youth. Dev. Cogn. Neurosci. 7, 43–52. https://doi.org/10.1016/j.dcn.2013.10.009.

Bjork, J.M., Smith, A.R., Hommer, D.W., 2008. Striatal sensitivity to reward deliveries and omissions in substance dependent patients. NeuroImage 42, 1609–1621. https://doi.org/10.1016/j.neuroimage.2008.06.035.

Bjork, J.M., Smith, A.R., Chen, G., Hommer, D.W., 2010. Adolescents, adults and rewards: comparing motivational neurocircuitry recruitment using fMRI. PloS One 5 (7), e11440. https://doi.org/10.1371/journal.pone.0011440.

Blakemore, S.J., Frith, C.D., Wolpert, D.M., 2001. The cerebellum is involved in predicting the sensory consequences of action. NeuroReport 12 (9), 1879–1884.

Boecker-Schlier, R., Holz, N.E., Hohm, E., Zohsel, K., Blomeyer, D., Buchmann, A.F., Laucht, M., 2017. Association between pubertal stage at first drink and neural reward processing in early adulthood. Addict. Biol. 22, 1402–1415. https://doi.org/10.1111/adb.12413.

Boillat, Y., Bazin, P.L., van der Zwaag, W., 2020. Whole-body somatotopic maps in the cerebellum revealed with 7T fMRI. NeuroImage 211, 116624. https://doi.org/10.1016/j.neuroimage.2020.116624.

Bonnelle, V., Ham, T.E., Leech, R., Kinnunen, K.M., Mehta, M.A., Greenwood, R.J., Sharp, D.J., 2012. Salience network integrity predicts default mode network function after traumatic brain injury. Proc. Natl. Acad. Sci. 109 (12), 4690–4695. https://doi.org/10.1073/pnas.1113455109.

Button, K.S., Ioannidis, J.P.A., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S.J., Munafò, M.R., 2013. Power failure: why small sample size undermines the reliability of neuroscience. Nat. Rev. Neurosci. 14, 365–376. https://doi.org/10.1038/nrn3475.

Camara, E., Rodriguez-Fornells, A., Münte, T.F., 2009. Functional connectivity of reward processing in the brain. Front. Hum. Neurosci. 2, 19. https://doi.org/10.3389/neuro.09.019.2008.

Carta, I., Chen, C.H., Schott, A.L., Dorizan, S., Khodakhah, K., 2019. Cerebellar modulation of the reward circuitry and social behavior. Science 363 (6424). https://doi.org/10.1126/science.aav0581.Cerebellar.

Chabrol, F.P., Blot, A., Mrsic-Flogel, T.D., 2019. Cerebellar contribution to preparatory activity in motor neocortex. Neuron 103, 506–519. https://doi.org/10.1016/j.neuron.2019.05.022.

Chen, Y., Chaudhary, S., Li, C.-S.R., 2022. Shared and distinct neural activity during anticipation and outcome of win and loss: A meta-analysis of the monetary incentive delay task. NeuroImage 119764. https://doi.org/10.1016/j.neuroimage.2022.119764.

Christley, R.M., 2010. Power and error: increased risk of false positive results in underpowered studies. Open Epidemiol. J. 3, 16–19. https://doi.org/10.2174/1874297101003010016.

Collins, D.L., Holmes, C.J., Peters, T.M., Evans, A.C., 1995. Automatic 3–D model- based neuroanatomical segmentation. Hum. Brain Mapp. 3 (3), 190–208. https://doi.org/10.1002/hbm.460030304.

Corlett, P.R., Mollick, J.A., Kober, H., 2022. Meta-analysis of human prediction error for incentives, perception, cognition, and action. Neuropsychopharmacology 1–11. https://doi.org/10.1038/s41386-021-01264-3.

Craig, A.D., 2003. Interoception: the sense of the physiological condition of the body. Curr. Opin. Neurobiol. 13, 500–505. https://doi.org/10.1016/S0959-4388(03)00090-4.

Craig, A.D., 2009. How do you feel – now? The anterior insula and human awareness. Nat. Rev. Neurosci. 10, 59–70.

Critchley, H.D., Wiens, S., Rotshtein, P., Öhman, A., Dolan, R.J., 2004. Neural systems supporting interoceptive awareness. Nat. Neurosci. 7 (2), 189–195. https://doi.org/10.1038/nn1176.

Damasio, A.R. (1994). Descartes' error: Emotion, reason, and the human brain. New York: Grosset/Putnam.

Demirtas-Tatlidede, A., Freitas, C., Pascual-Leone, A., Schmahmann, J.D., 2011. Modulatory effects of theta burst stimulation on cerebellar nonsomatic functions. Cerebellum 10, 495–503. https://doi.org/10.1007/s12311-010-0230-5.

Dhingra, I., Zhang, S., Zhornitsky, S., Le, T.M., Wang, W., Chao, H.H., Li, C.S.R., 2020. The effects of age on reward magnitude processing in the monetary incentive delay task. NeuroImage 207, 116368. https://doi.org/10.1016/j.neuroimage.2019.116368.

Dhingra, I., Zhang, S., Zhornitsky, S., Wang, W., Le, T.M., Li, C.S.R., 2021. Sex differences in neural responses to reward and the influences of individual reward and punishment sensitivity. BMC Neurosci. 22, 12. https://doi.org/10.1186/s12868-021-00618-3.

Diedrichsen, J., Zotow, E., 2015. Surface-based display of volume-averaged cerebellar imaging data. PLoS One 10, e0133402. https://doi.org/10.1371/journal.pone.0133402.

Diedrichsen, J., King, M., Hernandez-Castillo, C., Sereno, M., Ivry, R.B., 2019. Universal transform or multiple functionality? Understanding the contribution of the human cerebellum across task domains. Neuron 102, 918–928. https://doi.org/10.1016/j.neuron.2019.04.021.

Dillon, D.G., Bogdan, R., Fagerness, J., Holmes, A.J., Perlis, R.H., Pizzagalli, D.A., 2010. Variation in TREK1 gene linked to depression-resistant phenotype is associated with potentiated neural responses to rewards in humans. Hum. Brain Mapp. 31, 210–221. https://doi.org/10.1002/hbm.20858.

Dugré, J.R., Dumais, A., Bitar, N., Potvin, S., 2018. Loss anticipation and outcome during the Monetary Incentive Delay Task: a neuroimaging systematic review and meta-analysis. PeerJ 6, e4749. https://doi.org/10.7717/peerj.4749.

E, K.H., Chen, S.H.A., Ho, M.H.R., Desmond, J.E., 2014. A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies. Hum. Brain Mapp. 35, 593–615. https://doi.org/10.1002/hbm.22194.

Ebner, T.J., Pasalar, S., 2008. Cerebellum predicts the future motor state. Cerebellum 7, 583–588. https://doi.org/10.1007/s12311-008-0059-3.

Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. Hum. Brain Mapp. 30, 2907–2926. https://doi.org/10.1016/j.neuroimage.2020.117582.

Ernst, M., Nelson, E.E., Jazbec, S., McClure, E.B., Monk, C.S., Leibenluft, E., Pine, D.S., 2005. Amygdala and nucleus accumbens in responses to receipt and omission of gains in adults and adolescents. NeuroImage 25, 1279–1291. https://doi.org/10.1016/j.neuroimage.2004.12.038.

Fauth-Bühler, M., Zois, E., Vollstädt-Klein, S., Lemenager, T., Beutel, M., Mann, K., 2014. Insula and striatum activity in effort-related monetary reward processing in gambling disorder: the role of depressive symptomatology. NeuroImage: Clin. 6, 243–251. https://doi.org/10.1016/j.nicl.2014.09.008.

Fautrelle, L., Pichat, C., Ricolfi, F., Peyrin, C., Bonnetblanc, F., 2011. Catching falling objects: the role of the cerebellum in processing sensory-motor errors that may influence updating of feedforward commands. An fMRI study. Neuroscience 190, 135–144. https://doi.org/10.1016/j.neuroscience.2011.06.034.

Friston, K., 2010. The free-energy principle: a unified brain theory. Nat. Rev. Neurosci. 11 (2), 127–138. https://doi.org/10.1038/nrn2787.

Fujiwara, J., Tobler, P.N., Taira, M., Iijima, T., Tsutsui, K.I., 2009. Segregated and integrated coding of reward and punishment in the cingulate cortex. J. Neurophysiol. 101, 3284–3293. https://doi.org/10.1152/jn.90909.2008.

Gaillard, C., Guillod, M., Ernst, M., Torrisi, S., Federspiel, A., Schoebi, D., Martin Soelch, C., 2019. Striatal responsiveness to reward under threat-of-shock and working memory load: a preliminary study. Brain Behav. 9, e01397 https://doi.org/10.1002/brb3.1397.

Gold, J.M., Waltz, J.A., Prentice, K.J., Morris, S.E., Heerey, E.A., 2008. Reward processing in schizophrenia: a deficit in the representation of value. Schizophr. Bull. 34 (5), 835–847. https://doi.org/10.1093/schbul/sbn068.

Goulden, N., Khusnulina, A., Davis, N.J., Bracewell, R.M., Bokde, A.L., McNulty, J.P., Mullins, P.G., 2014. The salience network is responsible for switching between the default mode network and the central executive network: replication from DCM. NeuroImage 99, 180–190. https://doi.org/10.1016/j.neuroimage.2014.05.052.

Graf, H., Wiegers, M., Metzger, C.D., Walter, M., Abler, B., 2018. Differential noradrenergic modulation of monetary reward and visual erotic stimulus processing. Front. Psychiatry 9, 346. https://doi.org/10.3389/fpsyt.2018.00346.

Grimm, O., Nägele, M., Küpper-Tetzel, L., de Greck, M., Plichta, M., Reif, A., 2021. No effect of a dopaminergic modulation fMRI task by amisulpride and L-DOPA on reward anticipation in healthy volunteers. Psychopharmacology 238, 1333–1342. https://doi.org/10.1007/s00213-020-05693-8.

Grodd, W., Hülsmann, E., Lotze, M., Wildgruber, D., Erb, M., 2001. Sensorimotor mapping of the human cerebellum: fMRI evidence of somatotopic organization. Hum. Brain Mapp. 13, 55–73. https://doi.org/10.1002/hbm.1025.

Habas, C., 2022a. Topography of emotions in cerebellum as appraised by functional imaging. Adv. Exp. Med. Biol. 1378, 77–86.

Habas, C., 2022b. Research note: Functional connectivity between a corticostriatal network and the cerebellum. Cerebellum 21 (3), 520–524. https://doi.org/10.1007/s12311-021-01316-w.

Habas, C., Kamdar, N., Nguyen, D., Prater, K., Beckmann, C.F., Menon, V., Greicius, M. D., 2009. Distinct cerebellar contributions to intrinsic connectivity networks. J. Neurosci. 29 (26), 8586–8594. https://doi.org/10.1523/JNEUROSCI.1868-09.2009.

Halahakoon, D.C., Kieslich, K., O'Driscoll, C., Nair, A., Lewis, G., Roiser, J.P., 2020. Reward-processing behavior in depressed participants relative to healthy volunteers: A systematic review and meta-analysis. JAMA Psychiatry 77 (12), 1286–1295. https://doi.org/10.1001/jamapsychiatry.2020.2139.

Heffley, W., Hull, C., 2019. Classical conditioning drives learned reward prediction signals in climbing fibers across the lateral cerebellum. Elife 8, e46764. https://doi.org/10.7554/eLife.46764.

Herbort, M.C., Soch, J., Wüstenberg, T., Krauel, K., Pujara, M., Koenigs, M., Schott, B.H., 2016. A negative relationship between ventral striatal loss anticipation response and impulsivity in borderline personality disorder. NeuroImage: Clin. 12, 724–736. https://doi.org/10.1016/j.nicl.2016.08.011.

Ikeda, Y., Funayama, T., Tateno, A., Fukayama, H., Okubo, Y., Suzuki, H., 2019. Bupropion increases activation in nucleus accumbens during anticipation of monetary reward. Psychopharmacology 236, 3655–3665. https://doi.org/10.1007/s00213-019-05337-6.

Ito, M., 2008. Control of mental activities by internal models in the cerebellum. Nat. Rev. Neurosci. 9 (4), 304–313. https://doi.org/10.1038/nrn2332.

Ito, M., Kano, M., 1982. Long-lasting depression of parallel fiber-Purkinje cell transmission induced by conjunctive stimulation of parallel fibers and climbing fibers in the cerebellar cortex. Neurosci. Lett. 33, 253–258. https://doi.org/10.1016/0304-3940(82)90380-9.

Jauhar, S., Fortea, L., Solanes, A., Albajes-Eizagirre, A., McKenna, P.J., Radua, J., 2021. Brain activations associated with anticipation and delivery of monetary reward: a systematic review and meta-analysis of fMRI studies. PloS One 16 (8), e0255292. https://doi.org/10.1371/journal.pone.0255292.

Juckel, G., Friedel, E., Koslowski, M., Witthaus, H., Özgürdal, S., Gudlowski, Y., Schlagenhauf, F., 2012. Ventral striatal activation during reward processing in subjects with ultra-high risk for schizophrenia. Neuropsychobiology 66, 50–56. https://doi.org/10.1159/000337130.

Jung, W.H., Kang, D.H., Han, J.Y., Jang, J.H., Gu, B.M., Choi, J.S., Kwon, J.S., 2011. Aberrant ventral striatal responses during incentive processing in unmedicated patients with obsessive-compulsive disorder. Acta Psychiatr. Scand. 123, 376–386. https://doi.org/10.1111/j.1600-0447.2010.01659.x.

Katahira, K., Matsuda, Y.T., Fujimura, T., Ueno, K., Asamizuya, T., Suzuki, C., Okada, M., 2015. Neural basis of decision making guided by emotional outcomes. J. Neurophysiol. 113, 3056–3068. https://doi.org/10.1152/jn.00564.2014.

Kaufmann, C., Beucke, J.C., Preuße, F., Endrass, T., Schlagenhauf, F., Heinz, A., Kathmann, N., 2013. Medial prefrontal brain activation to anticipated reward and loss in obsessive–compulsive disorder. NeuroImage: Clin. 2, 212–220. https://doi.org/10.1016/j.nicl.2013.01.005.

Kennerley, S.W., Walton, M.E., Behrens, T.E., Buckley, M.J., Rushworth, M.F., 2006. Optimal decision making and the anterior cingulate cortex. Nat. Neurosci. 9 (7), 940–947. https://doi.org/10.1038/nn1724.

Kirk, U., Brown, K.W., Downar, J., 2015. Adaptive neural reward processing during anticipation and receipt of monetary rewards in mindfulness meditators. Soc. Cogn. Affect. Neurosci. 10, 752–759. https://doi.org/10.1093/scan/nsu112.

Klaus, J., Schutter, D.J.L.G., 2021. Functional topography of anger and aggression in the human cerebellum. NeuroImage 226, 117582. https://doi.org/10.1016/j.neuroimage.2020.117582.

Knutson, B., Westdorp, A., Kaiser, E., Hommer, D., 2000. FMRI visualization of brain activity during a monetary incentive delay task. NeuroImage 12 (1), 20–27. https://doi.org/10.1006/nimg.2000.0593.

Knutson, B., Fong, G.W., Adams, C.M., Varner, J.L., Hommer, D., 2001. Dissociation of reward anticipation and outcome with event-related fMRI. NeuroReport 12 (17), 3683–3687. https://doi.org/10.1097/00001756-200112040-00016.

Knutson, B., Fong, G.W., Bennett, S.M., Adams, C.M., Hommer, D., 2003. A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: characterization with rapid event-related fMRI. NeuroImage 18, 263–272. https://doi.org/10.1016/S1053-8119(02)00057-5.

Kobza, S., Bellebaum, C., 2015. Processing of action- but not stimulus-related prediction errors differs between active and observational feedback learning. Neuropsychologia 66, 75–87. https://doi.org/10.1016/j.neuropsychologia.2014.10.036.

Koch, K., Schachtzabel, C., Wagner, G., Reichenbach, J.R., Sauer, H., Schlösser, R., 2008. The neural correlates of reward-related trial-and-error learning: an fMRI study with a probabilistic learning task. Learn. Mem. 15, 728–732. https://doi.org/10.1101/lm.1106408.cognitive.

Kollmann, B., Scholz, V., Linke, J., Kirsch, P., Wessa, M., 2017. Reward anticipation revisited-evidence from an fMRI study in euthymic bipolar I patients and healthy first-degree relatives. J. Affect. Disord. 219, 178–186. https://doi.org/10.1016/j.jad.2017.04.044.

Kostadinov, D., Häusser, M., 2022. Reward signals in the cerebellum: origins, targets, and functional implications. Neuron 110, 1–14. https://doi.org/10.1016/j.neuron.2022.02.015.

Kostadinov, D., Beau, M., Blanco-Pozo, M., Häusser, M., 2019. Predictive and reactive reward signals conveyed by climbing fiber inputs to cerebellar Purkinje cells. Nat. Neurosci. 22, 950–962. https://doi.org/10.1038/s41593-019-0381-8.

Koziol, L.F., Budding, D., Andreasen, N., D'Arrigo, S., Bulgheroni, S., Imamizu, H., Yamazaki, T., 2014. Consensus paper: the cerebellum's role in movement and cognition. Cerebellum 13, 151–177. https://doi.org/10.1007/s12311-013-0511-x.

Kringelbach, M.L., Rolls, E.T., 2004. The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. Prog. Neurobiol. 72, 341–372. https://doi.org/10.1016/j.pneurobio.2004.03.006.

Kube, J., Mathar, D., Horstmann, A., Kotz, S.A., Villringer, A., Neumann, J., 2018. Altered monetary loss processing and reinforcement-based learning in individuals with obesity. Brain Imaging Behav. 12, 1431–1449. https://doi.org/10.1007/s11682-017-9786-8.

Kumar, P., Berghorst, L.H., Nickerson, L.D., Dutra, S.J., Goer, F.K., Greve, D.N., Pizzagalli, D.A., 2014. Differential effects of acute stress on anticipatory and consummatory phases of reward processing. Neuroscience 266, 1–12. https://doi.org/10.1016/j.neuroscience.2014.01.058.

Lancaster, J.L., Tordesillas-Gutiérrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., Fox, P.T., 2007. Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. Hum. Brain Mapp. 28, 1194–1205. https://doi.org/10.1002/hbm.20345.

Larry, N., Yarkoni, M., Lixenberg, A., Joshua, M., 2019. Cerebellar climbing fibers encode expected reward size. Elife 8, e46870.

Leroy, A., Amad, A., D'hondt, F., Pins, D., Jaafari, N., Thomas, P., Jardri, R., 2020. Reward anticipation in schizophrenia: a coordinate-based meta-analysis. Schizophr. Res. 218, 2–6. https://doi.org/10.1016/j.schres.2019.12.041.

Libedinsky, C., Smith, D.V., Teng, C.S., Namburi, P., Chen, V.W., Huettel, S.A., Chee, M. W., 2011. Sleep deprivation alters valuation signals in the ventromedial prefrontal cortex. Front. Behav. Neurosci. 5, 70. https://doi.org/10.3389/fnbeh.2011.00070.

Manto, M., Bower, J.M., Conforto, A.B., Delgado-García, J.M., Da Guarda, S.N.F., Gerwig, M., Timmann, D., 2012. Consensus paper: roles of the cerebellum in motor control – the diversity of ideas on cerebellar involvement in movement. Cerebellum 11 (2), 457–487 https://doi.org/10.1007/s12311-011-0331-9.Consensus.

Marr, D., 1969. A theory of cerebellar cortex. J. Physiol. 202, 437–470.

Maschke, M., Drepper, J., Kindsvater, K., Kolb, F.P., Diener, H.C., Timmann, D., 2000. Fear conditioned potentiation of the acoustic blink reflex in patients with cerebellar lesions. J. Neurol., Neurosurg. Psychiatry 68, 358–364.

Mazziotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., Mazoyer, B., 2001. A probabilistic atlas and reference system for the human brain: international Consortium for Brain Mapping (ICBM). Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci. 356, 1293–1322. https://doi.org/10.1098/rstb.2001.0915.

Menon, V., Uddin, L.Q., 2010. Saliency, switching, attention and control: a network model of insula function. Brain Struct. Funct. 214, 655–667. https://doi.org/10.1007/s00429-010-0262-0.Saliency.

Miall, R.C., Wolpert, D.M., 1996. Forward models for physiological motor control. Neural Netw. 9 (8), 1265–1279.

Montoya, E.R., Bos, P.A., Terburg, D., Rosenberger, L.A., van Honk, J., 2014. Cortisol administration induces global down-regulation of the brain's reward circuitry. Psychoneuroendocrinology 47, 31–42. https://doi.org/10.1016/j.psyneuen.2014.04.022.

Mucci, A., Dima, D., Soricelli, A., Volpe, U., Bucci, P., Frangou, S., Maj, M., 2015. Is avolition in schizophrenia associated with a deficit of dorsal caudate activity? A functional magnetic resonance imaging study during reward anticipation and feedback. Psychol. Med. 45, 1765–1778. https://doi.org/10.1017/S0033291714002943.

Murao, E., Sugihara, G., Isobe, M., Noda, T., Kawabata, M., Matsukawa, N., Noma, S.I., 2017. Differences in neural responses to reward and punishment processing between anorexia nervosa subtypes: an fMRI study. Psychiatry Clin. Neurosci. 71, 647–658. https://doi.org/10.1111/pcn.12537.

Murphy, A., Nestor, L.J., McGonigle, J., Paterson, L., Boyapati, V., Ersche, K.D., Elliott, R., 2017. Acute D3 antagonist GSK598809 selectively enhances neural response during monetary reward anticipation in drug and alcohol dependence. Neuropsychopharmacology 42, 1049–1057. https://doi.org/10.1038/npp.2016.289.

O'Doherty, J., Dayan, P., Schultz, J., Deichmann, R., Friston, K., Dolan, R.J., 2004. Dissociable roles of ventral and dorsal striatum in instrumental conditioning. Science 304 (5669), 452–454.

Ossewaarde, L., Van Wingen, G.A., Kooijman, S.C., Bäckström, T., Fernández, G., Hermans, E.J., 2011. Changes in functioning of mesolimbic incentive processing circuits during the premenstrual phase. Soc. Cogn. Affect. Neurosci. 6, 612–620. https://doi.org/10.1093/scan/nsq071.

Peters, S.K., Dunlop, K., Downar, J., 2016. Cortico-striatal-thalamic loop circuits of the salience network: a central pathway in psychiatric disease and treatment. Front. Syst. Neurosci. 10, 104. https://doi.org/10.3389/fnsys.2016.00104.

Pfabigan, D.M., Seidel, E.M., Sladky, R., Hahn, A., Paul, K., Grahl, A., Lamm, C., 2014. P300 amplitude variation is related to ventral striatum BOLD response during gain and loss anticipation: an EEG and fMRI experiment. NeuroImage 96, 12–21. https://doi.org/10.1016/j.neuroimage.2014.03.077.

Pierce, J.E., Péron, J.A., 2022. Reward-based learning and emotional habit formation in the cerebellum. Adv. Exp. Med. Biol. 1378, 125–140.

Pinheiro, A.P., Schwartze, M., Kotz, S.A., 2020. Cerebellar circuitry and auditory verbal hallucinations: an integrative synthesis and perspective. Neurosci. Biobehav. Rev. 118, 485–503. https://doi.org/10.1016/j.neubiorev.2020.08.004.

Pizzagalli, D.A., Iosifescu, D., Hallett, L.A., Ratner, K.G., Fava, M., 2008. Reduced hedonic capacity in major depressive disorder: evidence from a probabilistic reward task. J. Psychiatr. Res. 43, 76–87. https://doi.org/10.1016/j.jpsychires.2008.03.001.

Pollatos, O., Schandry, R., Auer, D.P., Kaufmann, C., 2007. Brain structures mediating cardiovascular arousal and interoceptive awareness. Brain Res. 1141, 178–187. https://doi.org/10.1016/j.brainres.2007.01.026.

Pynn, L.K., DeSouza, J.F., 2013. The function of efference copy signals: implications for symptoms of schizophrenia. Vis. Res. 76, 124–133. https://doi.org/10.1016/j.visres.2012.10.019.

Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. 98 (2), 676–682. https://doi.org/10.1073/pnas.98.2.676.

Rosenthal, R., 1979. The file drawer problem and tolerance for null results. Psychol. Bull. 86 (3), 638–641.

Saji, K., Ikeda, Y., Kim, W., Shingai, Y., Tateno, A., Takahashi, H., Suzuki, H., 2013. Acute NK1 receptor antagonist administration affects reward incentive anticipation processing in healthy volunteers. Int. J. Neuropsychopharmacol. 16, 1461–1471. https://doi.org/10.1017/S1461145712001678.

Sang, L., Qin, W., Liu, Y., Han, W., Zhang, Y., Jiang, T., Yu, C., 2012. Resting-state functional connectivity of the vermal and hemispheric subregions of the cerebellum with both the cerebral cortical networks and subcortical structures. Neuroimage 61, 1213–1225. https://doi.org/10.1016/j.neuroimage.2012.04.011.

Schlagenhauf, F., Juckel, G., Koslowski, M., Kahnt, T., Knutson, B., Dembler, T., Heinz, A., 2008. Reward system activation in schizophrenic patients switched from typical neuroleptics to olanzapine. Psychopharmacology 196, 673–684. https://doi.org/10.1007/s00213-007-1016-4.

Schmahmann, J.D., 2019. The cerebellum and cognition. Neurosci. Lett. 688, 62–75. https://doi.org/10.1016/j.neulet.2018.07.005.

Schmahmann, J.D., Weilburg, J.B., Sherman, J.C., 2007. The neuropsychiatry of the cerebellum – insights from the clinic. *Cerebellum*, 6, 254–267. https://doi.org/10.1080/14734220701490995.

Schmahmann, J.D., Guell, X., Stoodley, C.J., Halko, M.A., 2019. The theory and neuroscience of cerebellar cognition. Annu. Rev. Neurosci. 42, 337–364. https://doi.org/10.1146/annurev-neuro-070918-050258.

Schneider, M., Leuchs, L., Czisch, M., Sämann, P.G., Spoormaker, V.I., 2018. Disentangling reward anticipation with simultaneous pupillometry/fMRI. NeuroImage 178, 11–22. https://doi.org/10.1016/j.neuroimage.2018.04.078.

Schott, B.H., Niehaus, L., Wittmann, B.C., Schütze, H., Seidenbecher, C.I., Heinze, H.J., Düzel, E., 2007. Ageing and early-stage Parkinson's disease affect separable neural mechanisms of mesolimbic reward processing. Brain 130, 2412–2424. https://doi.org/10.1093/brain/awm147.

Schouw, M.L.J., De Ruiter, M.B., Kaag, A.M., Van den Brink, W., Lindauer, R.J.L., Reneman, L., 2013. Dopaminergic dysfunction in abstinent dexamphetamine users: results from a pharmacological fMRI study using a reward anticipation task and a methylphenidate challenge. Drug Alcohol Depend. 130, 52–60. https://doi.org/10.1016/j.drugalcdep.2012.10.010.

Schreiter, S., Spengler, S., Willert, A., Mohnke, S., Herold, D., Erk, S., Bermpohl, F., 2016. Neural alterations of fronto-striatal circuitry during reward anticipation in euthymic bipolar disorder. Psychol. Med. 46, 3187–3198. https://doi.org/10.1017/S0033291716001963.

Schutter, D.J.L.G., 2022. The cerebellum and disorders of emotion. Adv. Exp. Med. Biol. 1378, 273–283.

Scult, M.A., Knodt, A.R., Hanson, J.L., Ryoo, M., Adcock, R.A., Hariri, A.R., Strauman, T. J., 2017. Individual differences in regulatory focus predict neural response to reward. Soc. Neurosci. 12 (4), 419–429. https://doi.org/10.1080/17470919.2016.1178170.

Seeley, W.W., 2019. The salience network: a neural system for perceiving and responding to homeostatic demands. J. Neurosci. 39 (50), 9878–9882. https://doi.org/10.1523/JNEUROSCI.1138-17.2019.

Seeley, W.W., Menon, V., Schatzberg, A.F., Keller, J., Glover, G.H., Kenna, H., Greicius, M.D., 2007. Dissociable intrinsic connectivity networks for salience processing and executive control. *J. Neurosci.* 27 (9), 2349–2356. https://doi.org/10.1523/JNEUROSCI.5587-06.2007.

Sendhilnathan, N., Semework, M., Goldberg, M.E., Ipata, A.E., 2020. Neural correlates of reinforcement learning in mid-lateral cerebellum. Neuron 106, 188–198. https://doi.org/10.1016/j.neuron.2019.12.032.

Sescousse, G., Redouté, J., Dreher, J.C., 2010. The architecture of reward value coding in the human orbitofrontal cortex. J. Neurosci. 30 (39), 13095–13104. https://doi.org/10.1523/JNEUROSCI.3501-10.2010.

Sescousse, G., Caldú, X., Segura, B., Dreher, J.C., 2013. Processing of primary and secondary rewards: a quantitative meta-analysis and review of human functional neuroimaging studies. Neurosci. Biobehav. Rev. 37, 681–696. https://doi.org/10.1016/j.neubiorev.2013.02.002.

Seth, A.K., 2013. Interoceptive inference, emotion, and the embodied self. Trends Cogn. Sci. 17 (11), 565–573. https://doi.org/10.1016/j.tics.2013.09.007.

Seth, A.K., Suzuki, K., Critchley, H.D., 2012. An interoceptive predictive coding model of conscious presence. Front. Psychol. 2, 395. https://doi.org/10.3389/fpsyg.2011.00395.

Shadmehr, R., Smith, M.A., Krakauer, J.W., 2010. Error correction, sensory prediction, and adaptation in motor control. Annu. Rev. Neurosci. 33, 89–108. https://doi.org/10.1146/annurev-neuro-060909-153135.

Smith, S.M., Jenkinson, M., Woolrich, M.W., Beckmann, C.F., Behrens, T.E., Johansen-Berg, H., Matthews, P.M., 2004. Advances in functional and structural MR image analysis and implementation as FSL. NeuroImage 23, S208–S219. https://doi.org/10.1016/j.neuroimage.2004.07.051.

Spaniol, J., Bowen, H.J., Wegier, P., Grady, C., 2015. Neural responses to monetary incentives in younger and older adults. Brain Res. 1612, 70–82. https://doi.org/10.1016/j.brainres.2014.09.063.

Sprague, J.M., Chambers, W.W., 1954. Control of posture by reticular formation and cerebellum in the intact, anesthetized and unanesthetized and in the decerebrated cat. Am. J. Physiol. -Leg. Content 176, 52–64.

Sridharan, D., Levitin, D.J., Menon, V., 2008. A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. Proc. Natl. Acad. Sci. 105 (34), 12569–12574. https://doi.org/10.1073/pnas.0800005105.

Stoodley, C.J., Schmahmann, J.D., 2009. Functional topography in the human cerebellum: a meta-analysis of neuroimaging studies. NeuroImage 44, 489–501. https://doi.org/10.1016/j.neuroimage.2008.08.039.

Stoodley, C.J., Valera, E.M., Schmahmann, J.D., 2012. Functional topography of the cerebellum for motor and cognitive tasks: an fMRI study. NeuroImage 59 (2), 1560–1570. https://doi.org/10.1016/j.neuroimage.2011.08.065.

Strauss, G.P., Waltz, J.A., Gold, J.M., 2014. A review of reward processing and motivational impairment in schizophrenia. Schizophr. Bull. 40 (2), S107–S116. https://doi.org/10.1093/schbul/sbt197.

Synofzik, M., Thier, P., Leube, D.T., Schlotterbeck, P., Lindner, A., 2010. Misattributions of agency in schizophrenia are based on imprecise predictions about the sensory consequences of one's actions. Brain 133, 262–271. https://doi.org/10.1093/brain/awp291.

Thakkar, K.N., Mathalon, D.H., Ford, J.M., 2021. Reconciling competing mechanisms posited to underlie auditory verbal hallucinations. . *Philos. Trans. R. Soc. B* 376, 20190702. https://doi.org/10.1098/rstb.2019.0702.

Treadway, M.T., Buckholtz, J.W., Zald, D., 2013. Perceived stress predicts altered reward and loss feedback processing in medial prefrontal cortex. Front. Hum. Neurosci. 7, 180. https://doi.org/10.3389/fnhum.2013.00180.

Tseng, Y.W., Diedrichsen, J., Krakauer, J.W., Shadmehr, R., Bastian, A.J., 2007. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. J. Neurophysiol. 98, 54–62. https://doi.org/10.1152/jn.00266.2007.

Vaidya, J.G., Knutson, B., O'Leary, D.S., Block, R.I., Magnotta, V., 2013. Neural sensitivity to absolute and relative anticipated reward in adolescents. PLoS One 8 (3), e58708. https://doi.org/10.1371/journal.pone.0058708.

Van de Steen, F., Krebs, R.M., Colenbier, N., Almgren, H., Marinazzo, D., 2020. Effective connectivity modulations related to win and loss outcomes. NeuroImage 207, 116369. https://doi.org/10.1016/j.neuroimage.2019.116369.

Van Leeuwen, J.M., Vink, M., Joëls, M., Kahn, R.S., Hermans, E.J., Vinkers, C.H., 2019. Increased responses of the reward circuitry to positive task feedback following acute stress in healthy controls but not in siblings of schizophrenia patients. NeuroImage 184, 547–554. https://doi.org/10.1016/j.neuroimage.2018.09.051.

Voss, M., Moore, J., Hauser, M., Gallinat, J., Heinz, A., Haggard, P., 2010. Altered awareness of action in schizophrenia: a specific deficit in predicting action consequences. Brain 133, 3104–3112. https://doi.org/10.1093/brain/awq152.

Vrieze, E., Pizzagalli, D.A., Demyttenaere, K., Hompes, T., Sienaert, P., de Boer, P., Claes, S., 2013. Reduced reward learning predicts outcome in major depressive disorder. Biol. Psychiatry 73, 639–645. https://doi.org/10.1016/j.biopsych.2012.10.014.

Wagner, M.J., Kim, T.H., Savall, J., Schnitzer, M.J., Luo, L., 2017. Cerebellar granule cells encode the expectation of reward. Nature 544 (7648), 96–100. https://doi.org/10.1038/nature21726.

Weissman, D.H., Roberts, K.C., Visscher, K.M., Woldorff, M.G., 2006. The neural bases of momentary lapses in attention. Nat. Neurosci. 9 (7), 971–978. https://doi.org/10.1038/nn1727.

Welniarz, Q., Worbe, Y., Gallea, C., 2021. The forward model: a unifying theory for the role of the cerebellum in motor control and sense of agency. Front. Syst. Neurosci. 15, 644059 https://doi.org/10.3389/fnsys.2021.644059.

Wen, Y.Q., Zhu, J.N., Zhang, Y.P., Wang, J.J., 2004. Cerebellar interpositus nuclear inputs impinge on paraventricular neurons of the hypothalamus in rats. Neurosci. Lett. 370, 25–29. https://doi.org/10.1016/j.neulet.2004.07.072.

Werner, N.S., Schweitzer, N., Meindl, T., Duschek, S., Kambeitz, J., Schandry, R., 2013. Interoceptive awareness moderates neural activity during decision-making. Biol. Psychol. 94, 498–506. https://doi.org/10.1016/j.biopsycho.2013.09.002.

Whitton, A.E., Treadway, M.T., Pizzagalli, D.A., 2015. Reward processing dysfunction in major depression, bipolar disorder and schizophrenia. Curr. Opin. Psychiatry 28 (1), 7. https://doi.org/10.1097/YCO.0000000000000122.

Wilson, R.P., Colizzi, M., Bossong, M.G., Allen, P., Kempton, M., Bhattacharyya, S., 2018. The neural substrate of reward anticipation in health: a meta-analysis of fMRI findings in the monetary incentive delay task. Neuropsychol. Rev. 28, 496–506. https://doi.org/10.1007/s11065-018-9385-5.

Wolpert, D.M., Ghahramani, Z., Jordan, M.I., 1995. An internal model for sensorimotor integration. Science 269 (5232), 1880–1882.

Wolpert, D.M., Miall, R.C., Kawato, M., 1998. Internal models in the cerebellum. Trends Cogn. Sci. 2 (9), 338–347.

Xiao, N., Wu, G., Zhou, Z., Yao, J., Wu, B., Sui, J., Tin, C., 2023. Positive feedback of efferent copy via pontine nucleus facilitates cerebellum-mediated associative learning. Cell Rep. 42, 112072 https://doi.org/10.1016/j.celrep.2023.112072.

Yan, C., Wang, Y., Su, L., Xu, T., Yin, D.Z., Fan, M.X., Chan, R.C., 2016. Differential mesolimbic and prefrontal alterations during reward anticipation and consummation in positive and negative schizotypy. Psychiatry Res.: Neuroimaging 254, 127–136. https://doi.org/10.1016/j.pscychresns.2016.06.014.

Yang, X., Su, Y., Yang, F., Song, Y., Yan, J., Luo, Y., Zeng, J., 2022. Neurofunctional mapping of reward anticipation and outcome for major depressive disorder: a voxel-based meta-analysis. Psychol. Med. 1–14. https://doi.org/10.1017/S0033291722002707.

Yao, Y.W., Liu, L., Worhunsky, P.D., Lichenstein, S., Ma, S.S., Zhu, L., Yip, S.W., 2020. Is monetary reward processing altered in drug-naïve youth with a behavioral addiction? Findings from internet gaming disorder. NeuroImage: Clin. 26, 102202 https://doi.org/10.1016/j.nicl.2020.102202.

Yeo, B.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M., Buckner, R.L., 2011. The organization of the human cerebral cortex estimated by intrinsic functional connectivity. J. Neurophysiol. 106, 1125–1165. https://doi.org/10.1152/jn.00338.2011.

Zaki, J., Davis, J.I., Ochsner, K.N., 2012. Overlapping activity in anterior insula during interoception and emotional experience. NeuroImage 62, 493–499. https://doi.org/10.1016/j.neuroimage.2012.05.012.

Zeng, J., Yan, J., Cao, H., Su, Y., Song, Y., Luo, Y., Yang, X., 2022. Neural substrates of reward anticipation and outcome in schizophrenia: a meta-analysis of fMRI findings in the monetary incentive delay task. Transl. Psychiatry 12, 1–14. https://doi.org/10.1038/s41398-022-02201-8.

Zhornitsky, S., Dhingra, I., Le, T.M., Wang, W., Li, C.S.R., Zhang, S., 2021. Reward related responses and tonic craving in cocaine addiction: an imaging study of the monetary incentive delay task. Int. J. Neuropsychopharmacol. 24 (8), 634–644. https://doi.org/10.1093/ijnp/pyab016.

Zhu, J.N., Yung, W.H., Kwok-Chong Chow, B., Chan, Y.S., Wang, J.J., 2006. The cerebellar-hypothalamic circuits: potential pathways underlying cerebellar involvement in somatic-visceral integration. Brain Res. Rev. 52, 93–106. https://doi.org/10.1016/j.brainresrev.2006.01.003.