



Review article

Exploration versus exploitation decisions in the human brain: A systematic review of functional neuroimaging and neuropsychological studies.

Lindsay E. Wyatt^a, Patrick A. Hewan^a, Jeremy Hogeveen^b, R. Nathan Spreng^{c,d,e,f,*}, Gary R. Turner^{a,**}

^a Department of Psychology, York University, Toronto, ON, Canada

^b Department of Psychology, The University of New Mexico, Albuquerque, NM, USA

^c Montréal Neurological Institute, Department of Neurology and Neurosurgery, McGill University, Montréal, QC, H3A 2B4, Canada

^d Department of Psychology, McGill University, Montréal, QC, Canada

^e Department of Psychiatry, McGill University, Montréal, QC, Canada

^f McConnell Brain Imaging Centre, Montréal Neurological Institute, McGill University, Montréal, QC, Canada

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ABSTRACT

Thoughts and actions are often driven by a decision to either explore new avenues with unknown outcomes, or to exploit known options with predictable outcomes. Yet, the neural mechanisms underlying this exploration-exploitation trade-off in humans remain poorly understood. This is attributable to variability in the operationalization of exploration and exploitation as psychological constructs, as well as the heterogeneity of experimental protocols and paradigms used to study these choice behaviours. To address this gap, here we present a comprehensive review of the literature to investigate the neural basis of explore-exploit decision-making in humans. We first conducted a systematic review of functional magnetic resonance imaging (fMRI) studies of exploration-versus exploitation-based decision-making in healthy adult humans during foraging, reinforcement learning, and information search. Eleven fMRI studies met inclusion criterion for this review. Adopting a network neuroscience framework, synthesis of the findings across these studies revealed that exploration-based choice was associated with the engagement of attentional, control, and salience networks. In contrast, exploitation-based choice was associated with engagement of default network brain regions. We interpret these results in the context of a network architecture that supports the flexible switching between externally and internally directed cognitive processes, necessary for adaptive, goal-directed behaviour. To further investigate potential neural mechanisms underlying the exploration-exploitation trade-off we next surveyed studies involving neurodevelopmental, neuropsychological, and neuropsychiatric disorders, as well as lifespan development, and neurodegenerative diseases. We observed striking differences in patterns of explore-exploit decision-making across these populations, again suggesting that these two decision-making modes are supported by independent neural circuits. Taken together, our review highlights the need for precision-mapping of the neural circuitry and behavioural correlates associated with exploration and exploitation in humans. Characterizing exploration versus exploitation decision-making biases may offer a novel, trans-diagnostic approach to assessment, surveillance, and intervention for cognitive decline and dysfunction in normal development and clinical populations.

1. Introduction

The decision to initiate a volitional behaviour often involves arbitrating between the choice to explore new avenues with unknown and potentially risky outcomes or to exploit prior knowledge and pursue options with known outcomes (Hills, et al., 2015; Spreng and Turner,

2021). *Do we order our favorite meal or try a different one? Do we take the usual route to work or venture onto the new highway? Do we stay with the same romantic partner or chance it with someone new?* These discrete choice options create a behavioural tension, and its resolution necessitates an exploration-exploitation trade-off (Cohen et al., 2007; Hills et al., 2015). This fundamental decision to explore or exploit has been

* Corresponding author. Montréal Neurological Institute, Department of Neurology and Neurosurgery, McGill University, Montréal, QC, H3A 2B4, Canada.

** Corresponding author.

E-mail addresses: nathan.spreng@gmail.com (R.N. Spreng), gturner@yorku.ca (G.R. Turner).

studied extensively across species and contexts, from hummingbirds (Melhorn, et al., 2015; Nonacs, 2010) to humans (Algermissen et al., 2019; Cogliati Dezza, Cleeremans and Alexander, 2019; Domenech et al., 2020; Pajkosy et al., 2017; Pezzulo et al., 2016; Rich and Gureckis, 2018; Tomov et al., 2020; Walker et al., 2019; Zajkowski et al., 2017), and from ecology (Berger-Tal and Avgar, 2012; Eliassen et al., 2007) to social group and organizational behaviour (March, 1991; Nielsen et al., 2018). Maintaining a balance between exploration and exploitation, and flexibly shifting between these options in response to fluctuating environmental contingencies, is associated with adaptive decision-making outcomes (Cohen, et al., 2007; Hills et al., 2013; Melhorn et al., 2015).

The exploration-exploitation trade-off offers an important lens through which to study the behavioural and neural development of biological systems. In humans, the focus of the current review, this trade-off has been linked to reward and affective drives and associated neural circuitry (Cohen, et al., 2007). More recently, exploration-exploitation decisions have been related to large-scale cortical systems (Allegra, et al., 2020; Blanchard and Gershman, 2018; Spreng and Turner, 2021). There have been several reviews of exploration and exploitation as a decision-making framework (Hills, et al., 2015; Mata and von Helversen, 2015; Melhorn et al., 2015; Spreng and Turner, 2021). However, there has yet to be a comprehensive review of the neural basis for the exploration-exploitation trade-off explicitly focusing on human neuroscience research, incorporating human neuroimaging, neurodevelopmental disorders, typical aging research and neuropsychological investigations. Here, we present a synthesis of this literature with the goal of disambiguating its underlying neural mechanisms. As an introduction to the structure of the review, we first summarize the most common behavioural approaches to measure the trade-off in human decision-making. Next, we report the findings from a systematic review of the cognitive neuroscience literature examining the functional neuroanatomy of the exploration-exploitation trade-off in typically developing healthy adults using functional magnetic resonance imaging (fMRI) methods. Finally, we integrate these findings with our review of neuropsychological studies examining the exploration-exploitation trade-off in neurotypical lifespan development as well as psychological and neurological disorders. We have chosen to integrate results from both literatures to provide a comprehensive survey of the putative neural mechanisms underlying human decisions to explore versus exploit, drawing upon both cognitive neuroscience and neuropsychological research.

1.1. Determinants and measurement of the exploration-exploitation trade-off

Explore-exploit decisions are typically studied in the laboratory using three categories of behavioural choice paradigms: foraging, reinforcement learning, and information search (reviewed by Melhorn et al., 2015; Sang et al., 2020; and see Averbeck, 2015; von Helversen et al., 2018 for a discussion of putative differences across task categories). Foraging refers to search and accrual of resources by searching in resource patches in extra- or intra-personal space. Reinforcement learning refers to repeated choice tasks where there is a requirement to maximize resource gains or avoid losses by selecting from options with differing reward values, initially unknown to the decision-maker. Information search refers to sequential information seeking from multiple sources before realizing a final gain. We briefly review these categories of choice tasks below.

1.2. Foraging

Foraging paradigms mimic ecological studies examining non-human animal choice decisions. Searches for food, shelter, and mating partners within fluctuating, patchy, and resource-limited environments require shifts from exploiting to exploring (Nonacs, 2010; van Dooren et al.,

2021; Wolfe, 2013). Exploiting the current resource patch conserves energy and reduces risk. As resource availability decreases, the potential value in exploring for a new resource patch is increased (Nonacs, 2010). Optimal foraging requires flexible shifting between exploration and exploitation based decisions (Hills, 2006; Nonacs, 2010). Foraging tasks in the laboratory typically manipulate reward structures and involve the search and collection of resources within a patchy and changing environment. The trade-off occurs when deciding to exploit the current patch where rewards are known, or to shift to a new patch to seek new information, but where the reward outcomes are unknown.

Of particular importance in foraging are considerations of resource patchiness and variable reward distributions. Natural environments frequently contain “patches” of rewarding resources in clumped and dispersed distributions (Todd and Hills, 2020). Declining resource availability in a local patch promotes a shift in search strategy from resource exploitation to exploration for new resource stores, whereas non-depleting resource structures promote sustained exploitation. Optimal reward and information (i.e., resource) accrual depends on the interplay between resource depletion and replenishment rates, as well as the cost of exploring unknown areas of the resource distribution (Charnov, 1976; Melhorn et al., 2015; Nonacs, 2010). Critically, on foraging tasks the decision space can be observed, as distinct from other exploration-exploitation paradigms such as reinforcement learning, where states that drive exploration must be inferred (or learned) based on choice outcomes. Decisions to explore in a foraging context may be neurocomputationally distinct from exploration decisions during reinforcement learning or information search (Averbeck, 2015). However, a recent meta-analytic review failed to identify task differences in human brain activity (including foraging) during exploration decisions (Zhen et al., 2022). We remain agnostic with respect to potential task-based differences in the current review.

Beyond the foraging environment, additional determinants of search versus stay decisions have been proposed. These include the intrinsic motivation of the choice agent, value and uncertainty associated with choice options, as well as the relative value of the possible choice outcomes (e.g., information gain versus reward accumulation) (Melhorn, et al., 2015). While complex interactions among these factors are presumed to establish threshold criterion for shifts between exploration and exploitation, thresholds are also likely modulated by individual difference (e.g., personality, cognitive ability) as well as demographic (e.g., age, sex) factors (Spreng and Turner, 2021).

Foraging can occur extra-personally, in the environment or intra-personally, referred to as ‘foraging in mind’ (Todd and Hills, 2020). Internal foraging involves searching through one’s store of prior knowledge to either explore or exploit ‘patches’ of mental representations. For example, when asked to recall a list of semantically-related items such as animal names, staying within a single category (e.g., farm animals) would be considered exploiting whereas shifting among various categories (e.g., pets, jungle animals) would reflect a more exploratory search strategy (Hills, et al., 2015). Indeed, this capacity to forage in mind, to overcome prepotent, salient, or overlearned representations and flexibly search through one’s broader representational space has been theorized as the evolutionary basis for human free will (Todd and Hills, 2020).

1.3. Reinforcement learning

Reinforcement learning paradigms often involve an n -armed bandit task, kindred to a series of slot machines with variable probabilistic reward or loss distributions unknown to the decision-maker. Decision agents in these tasks must choose one of n slot machines with the goal of obtaining a reward and/or avoiding a loss (Gittins and Jones, 1979; Katehakis and Veinott, 1987). Once a machine is chosen, the value of the reward is revealed, and the decision-maker can then choose to remain at that bandit (exploit) or switch to a new machine (explore) for their next choice. Typically, the values and/or probabilities of reinforcement vary

independently across bandits and change gradually across trials, resulting in environmental uncertainty. Rewards on any individual trial are randomly obtained from a probability distribution that differs between bandits. To obtain the most rewards, the decision-maker must identify the machine with the highest expected payoff, which typically varies across the experiment. Within this shifting reward structure, exploration is thought to be driven by uncertainty about the relative future value of novel or under-sampled options (Averbeck, 2015), which might be higher than the learned value of options an agent has already experienced. As a result, decision-makers experience a tension between exploiting a bandit with more predictable outcomes or exploring novel or under-sampled bandits with uncertain outcomes (Addicott et al., 2017; Gittins and Jones, 1979; Hogeveen et al., 2022; Katehakis and Veinott, 1987).

In early reinforcement learning studies involving the n -bandit tasks (Daw, O'Doherty, Dayan, Seymour and Dolan, 2006) there was no theory-neutral method of distinguishing directed (i.e., intentional) exploration decisions from random choices. More recently, adapted bandit-type tasks manipulate the information value associated with the explore decision to create an explore bonus, making the distinction between directed exploration and random (non-directed) choice more explicit (Cogliati Dezza, Yu, Cleeremans and Alexander, 2017; Hogeveen et al., 2022; Horvath et al., 2021; Wilson et al., 2021). Several manipulations have been implemented to disambiguate the underlying psychological factors that drive exploration versus exploitation-based choice. Studies have distinguished the information gained from the reward value of a choice (i.e., rewards can be accrued without information gains, Horvath et al., 2021). Other paradigms have altered the time horizon for realizing gains (Cogliati Dezza, et al., 2017). Numerous studies have also manipulated the balance between risk versus information gain (Cogliati Dezza, et al., 2017; Hogeveen et al., 2022; Wilson et al., 2014). While such experimental manipulations hold significant potential for more precisely mapping brain and behavioural correlates of reinforcement learning, we have grouped these studies here as they are all assays of exploration versus exploitation-based decision-making (see Section 2).

1.4. Information search

Information search tasks measure how resources are accumulated from multiple sources (Blanchard and Gershman, 2018; O'Bryan et al., 2018). Across experimental paradigms of information search, exploration is defined as the continued search across information sources. In contrast, exploitation is operationalized as the choice to stop searching and choose one source of information (Chin et al., 2015). Perhaps the most common real-world exemplar of an information search task in the 21st century would be an internet search (Chin, et al., 2015; Sharit et al., 2008). For example, searching for a vacation destination may involve checking several online travel search engines to find the best vacation destination and price. One could explore numerous travel accumulator sites, visit specific airline and hotel sites, consult travel review blogs etc. Each decision to switch to a new website would be considered exploratory. However, once several sites have been explored, one ultimately lands on a site to 'exploit' the information by booking the vacation, and the search stops. Most experimental information search tasks involve 'optimal stopping' behaviour, where exploration decisions yield information gains. However, these explorations come at a cost (e.g., time spent on the internet) and these must be weighed against the ultimate value of exploiting a single information source. Typical modelling of information search tasks presumes a linearly decreasing value threshold for continuing to explore, allowing experimenters to calculate an 'optimal stopping point'. Early information search tasks were built upon the Secretary Task (Ferguson, 1989), wherein participants were confronted with hiring a secretary by screening and interviewing (exploring) and ultimately hiring (exploiting) a candidate. However, the choice to stop the search and select a candidate ("exploit") forestalls any

further exploration, leaving the optimality of the choice ambiguous.

To address this problem, recent information search paradigms have attempted to overcome the 'stopping problem' by not imposing a 'stop', allowing participants to choose (exploit) an option while continuing to search (explore) for a better choice (Sang, et al., 2020). On these tasks, experimenters are able to model explore-exploit behaviors across all choices, without imposing a terminal stop. This more closely models real-world search wherein the 'best' option is kept on-hold while exploration can continue. (For example, saving a search on one travel site, while continuing to explore other sites). As with reinforcement learning, several experimental manipulations have been introduced to better characterize decision-making performance on information search tasks. These include reducing uncertainty through repeated task exposure (Navarro, et al., 2004), and lengthening temporal horizons (Wilson, et al., 2021), both of which lead to greater exploration. In contrast, inducing positive mood states during information search reduces exploration in favor of exploitation based choice (von Helversen and Mata, 2012). Again, there are too few neuroimaging studies to parse these in our review. However, we note these behavioural manipulations here as context for mapping brain-behavioural associations in the following section as well as informing future research.

In this section we have provided a brief overview of the three primary categories of exploration and exploitation paradigms reported in the literature. As we have noted throughout, this is an expansive literature encompassing numerous studies with specific task manipulations across each category. In the next section we report the results of a systematic review of neuroimaging studies involving foraging, reinforcement learning and information search tasks. Given the relatively small number of studies meeting our inclusion criterion we have collapsed studies across task categories and provide task category-specific interpretations where relevant.

2. Systematic review of functional neuroimaging studies of the exploration-exploitation trade-off in healthy adults

While the behavioural parameters of explore-exploit decision-making have been studied extensively, the underlying neural correlates in humans are less well defined. We first conducted a comprehensive review of cognitive neuroscience research involving human neuroimaging studies directly contrasting exploration- and exploitation-based decision-making in healthy adults. We follow this quantitative review with a qualitative review of the comparatively fewer studies investigating explore-exploit decision-making in typical and atypical lifespan development as well as clinical syndromes. Here we focus on research in humans (comprehensive reviews of non-human animal studies may be found elsewhere, Hills, et al., 2015; Melhorn et al., 2015).

As we were interested in brain differences during exploration versus exploitation decisions, we explicitly focused our review on studies that included direct within-subject contrasts of exploration versus exploitation-based decisions. While this limited the total number of studies that could be included in our review, the primary rationale for our study was to directly contrast patterns of brain activity during exploration and exploitation. This requires within-subject and within-task comparisons of exploration versus exploitation-based choice. Several published studies have examined brain function during exploration, and to a lesser extent exploitation, (Zhen, et al., 2022). However, in the current review we explicitly focused on the trade-off or shifts between exploration and exploitation (or vice versa) within identical task contexts. Direct within-task contrasts, in which all non-relevant task features are matched across choice conditions, are essential to address our central question as to whether these two types of decisions are dissociable at the level of the brain.

In the earliest published neuroimaging study explicitly framed within an exploration-exploitation decision-making model, Daw and colleagues (2006) reported that explore versus exploit-based decisions were associated with different patterns of brain activation. Numerous

investigations have since reported a dissociation between exploration and exploitation (Addicott et al., 2014; Amiez et al., 2012; Blanchard and Gershman, 2018; Chakroun et al., 2020; Cogliati Dezza et al., 2019; Hogeveen et al., 2022; Howard-Jones et al., 2010; Kolling et al., 2012; Laureiro-Martinez et al., 2015; Laureiro-Martinez, et al., 2013; O'Bryan, et al., 2018). However, beyond this broad agreement surrounding the dissociability of these two decision-types at the level of the brain, there has been limited consensus regarding the brain regions implicated in each form of choice behaviour.

Much of the inconsistency across neuroimaging studies of exploration and exploitation may be attributable to differences in experimental paradigms (von Helverson, et al., 2018). To our knowledge there has been only one published meta-analysis of neuroimaging studies in this area (Zhen, et al., 2022). However, the focus was restricted to exploration-based decision-making and did not include direct explore versus exploit contrasts. Here, we synthesize patterns of brain activity associated with exploration versus exploitation in foraging, reinforcement learning, and information search tasks. To identify consistencies in brain activation patterns across studies at a similar spatiotemporal scale, we limited our systematic review to those studies using fMRI methods.

2.1. Method

The present review was conducted in accordance with the guidelines of the 2009 Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) statement (Moher et al., 2009). These guidelines were introduced to enhance transparency and consistency in reporting the results of systematic reviews. Our search identified 11 studies that met inclusion criteria, below the suggested threshold of 17 studies necessary to conduct an inferential statistical meta-analysis (Eickhoff et al., 2017; Zhen et al., 2022). As described above, most studies examine exploration or exploitation brain activation patterns separately. However, we suggest that direct contrasts of brain activity during exploration versus exploitation-based choice offers a more precise delineation of brain regions uniquely engaged by these discrete choice behaviors. Here we provide a semi-quantitative review of the published studies that conducted and report these direct contrasts.

2.2. Literature search and article selection

To capture publications across the different domains of exploration-exploitation, we performed four literature searches on OVID and Web of Science (including PubMed and PsycINFO) in August 2022 for the following domains: 1) general exploration-exploitation, 2) foraging, 3) reinforcement learning, and 4) information search. Keywords for the general search were: (decisi* OR decision making OR decision-making) AND (exploration-exploitation OR exploration and exploitation) AND (humans) AND (fMRI). Keywords for the foraging search were: (decisi* OR decision making OR decision-making) AND (forag*) AND (humans) AND (fMRI). Keywords for the reinforcement learning search were: (decisi* OR decision making OR decision-making) AND (reinforc*) AND (humans) AND (fMRI). Keywords for the information search were: (decisi* OR decision making OR decision-making) AND (information search OR information-search) AND (humans) AND (fMRI). We also found additional eligible articles from relevant references and Google Scholar. The four searches yielded a total of 334 articles that were screened for eligibility.

Eligibility criteria included: a) healthy adult participants (including healthy controls), b) reported fMRI foci, c) reported stereotaxic coordinates in Talairach or Montreal Neurological Institute (MNI) space, and (d) the use of an exploration-exploitation paradigm as well as an exploration-exploitation contrast. Of note, studies reporting continuous or parametric manipulation of the exploration and exploitation trade-off (Mobbs, et al., 2013) did not report direct contrast activations and were not included in the review. Initially, eligibility criteria also included whole brain coverage. Given the limited number of studies in some task

domains we also included studies reporting only region of interest (ROI) analyses. Together the searches yielded 11 eligible articles, which included data from 301 participants across 11 different experiments. As expected, there was variability in specific experimental tasks, however all were easily mapped to the three primary task categories (foraging, reinforcement learning, information search). Fig. 1 depicts the steps taken to identify eligible articles from all four literature searches. Table 1 is a summary of the articles included in the systematic review.

2.3. Analysis

Patterns of neural activation are synthesized, interpreted, and reported at the omnibus level (i.e., across reinforcement learning, foraging and information search domains). This was necessary due to the comparatively few information search and foraging studies. All studies are categorized in Table 1. We report the location and frequency of statistically significant neural activations across all studies for exploration > exploitation and exploitation > exploration contrasts. As we were unable to conduct a quantitative meta-analysis, we provide a qualitative summary of our findings (in text, tables and figures) from the systematic review. Consistent with this approach, 'activated' regions were determined based on the statistical tests reported in the original papers. No further thresholding was applied in the current review. For clarity of interpretation, we refer to regions reported in over five studies as "core regions" and those identified in three to four studies as "secondary regions". Any regions reported in less than three of the 11 studies are not specifically interpreted due to low reliability. All cortical coordinates are displayed in Fig. 2.

In addition to identifying overlapping regions across studies, we also adopt a network neuroscience framework in our interpretation of the findings, ascribing reported activations to canonical largescale, cortical brain networks (Uddin et al., 2019; Yeo et al., 2011). For clarity and integration with previous literature, we report the anatomically based network labels and taxonomy proposed by Uddin and colleagues (Uddin et al., 2019) in the first instance, and then adopt Yeo's labels in subsequent text. It is important to note that the activations reported here were not analyzed, described, or discussed in a network context in the original papers.

Fig. 2 displays significant cortical activations reported across all studies. MNI coordinates from each study were converted to FreeSurfer surface space coordinates using Fusion (Wu, et al., 2018). Coordinates were then plotted on the fsaverage cortical surface with the seven-network cortical parcellation (Yeo, et al., 2011) overlap map using AFNI-SUMA (Cox and Hyde, 1997; Saad and Reynolds, 2012).

2.4. Exploration > exploitation related activation foci

Across the 11 studies, a total of 155 foci were more active during exploration than during exploitation. The frontopolar cortex and the dorsal anterior cingulate cortex were most frequently reported and met our operationalization threshold of 'core' regions, showing greater activity during exploration versus exploitation. Other core areas included right and left middle frontal gyrus, right precuneus and right and left intraparietal sulcus. Secondary regions showing greater exploration-related activation included bilateral anterior insula, left precentral gyrus, bilateral superior frontal gyrus, right inferior frontal gyrus, bilateral superior parietal lobule, bilateral cerebellum, and bilateral thalamus (Table 2A).

2.5. Exploitation > exploration related activation foci

A total of 95 foci were reported to be significantly more active during exploitation than during exploration. Ventromedial prefrontal and orbitofrontal cortex were most frequently reported and met our definition of 'core' exploitation regions. Secondary regions included left middle temporal gyrus, left angular gyrus, left posterior cingulate

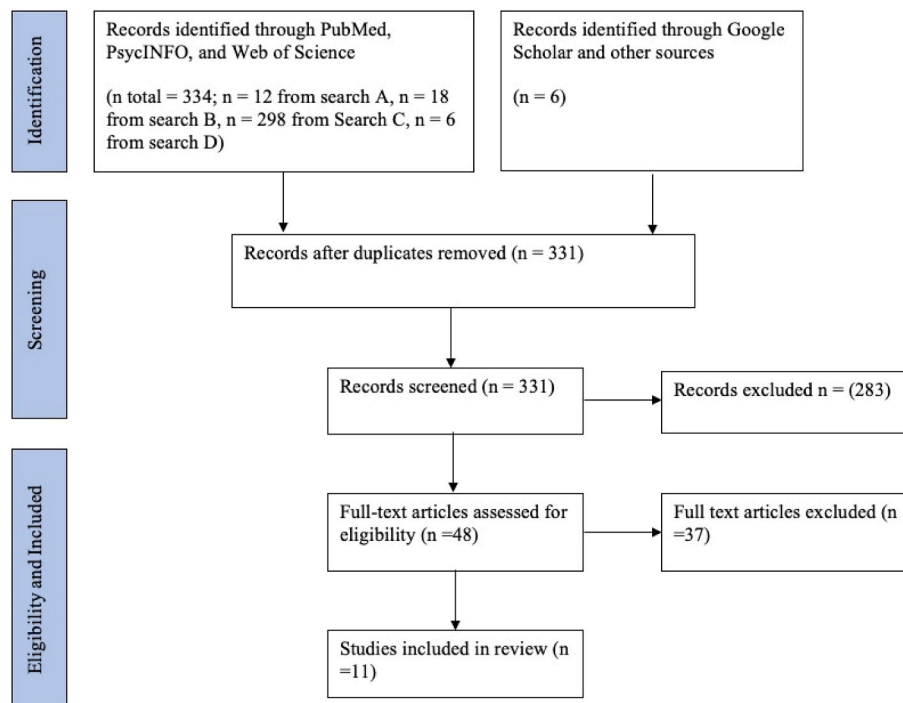


Fig. 1. PRISMA flowchart illustrating the steps taken to identify all eligible articles for systematic review on fMRI studies with exploration-exploitation contrasts.

Table 1

Summary of fMRI studies included in the systematic review.

Author	N	Age (SD)	Handedness (R)	Paradigm	Analysis
				Reinforcement Learning	
Daw et al. (2006)	14	N/A	All	4-armed bandit	ROI
Howard-Jones et al. (2010)	16	25.5(3.8)	All	4-armed bandit	Whole brain
Addicott et al. (2014)	22	36(11)	All	6-armed bandit	Whole brain
Laureiro-Martinez et al. (2013)	50	34.35(6.6)	All	4-armed bandit	Whole brain
Laureiro-Martinez et al. (2015)	63	34.45(6.45)	All	4-armed bandit	Whole brain
Cogliati Dezza et al. (2019)	21	19-29*	All	Horizon Task	ROI
Chakroun et al. (2020)	31	26.85(4.01)	All	4-armed bandit	Whole brain
Hogveen et al. (2022)	37	26.6(7.24)	All	3-armed bandit	ROI
				Foraging	
Kolling et al. (2012)	18	22-32*	All	Foraging task	Whole brain
				Information Search	
Amiez et al. (2012)	11	27.9(3.6)	All	Problem solving	Whole brain
Blanchard and Gershman (2018)	18	21-36*	All	Observe or Bet	ROI

N sample size, R right-handed, SD standard deviation, N/A not available *Age range provided when mean is not reported, ROI region of interest.

cortex, left superior frontal gyrus, bilateral superior temporal gyrus, and bilateral hippocampus (Table 2B).

2.6. Exploration vs. exploitation: large-scale brain networks

Our systematic review revealed that exploration versus exploitation choice behaviours differ markedly with respect to the specific brain regions implicated. Given this dissociation we next examined the spatial coherence of these individual regions with the topographies of canonical large-scale brain networks (Yeo, et al., 2011) (see Fig. 2, Table 2, Table 3). We have chosen to review these data through a network neuroscience lens to highlight the correspondence between our findings and the large-scale network architecture of the brain. This approach is consistent with our recent model examining exploration versus exploitation in older adulthood (Spreng and Turner, 2021). In brief, the model posits that exploration-based decisions engage cognitive control regions of the brain associated with goal-directed attention. In contrast, exploitation-based decisions draw upon stored mnemonic representations, necessitating the involvement of default network brain regions

implicated in internally-directed cognition (Andrews-Hanna et al., 2014). However, it is important to emphasize that any network affiliations posited here must be considered preliminary, pending more direct empirical evidence using network-neuroscience methods to examine exploration versus exploitation-based decision-making. Table 3 reports the network-wise foci counts for all cortical activations for exploration > exploitation and exploitation > exploration contrasts.

We have selected the Yeo et al. (2011) cortical parcellation and network map as it represents the current gold standard for characterizing large-scale brain networks (see Uddin et al., 2019 for a discussion of network nomenclatures and associated anatomical labels). In brief, this cortical parcellation scheme was derived by analyzing fMRI data obtained at rest in 1000 subjects. A clustering approach was employed to identify and replicate networks of functionally-coupled regions across the cerebral cortex, revealing local networks confined to sensory and motor cortices as well as distributed networks of association regions (Yeo et al., 2011). Here we selected the canonical seven network solution (Fig. 2). Consistent with this network-based approach, we assign network labels to the activation foci based on their spatial overlap with

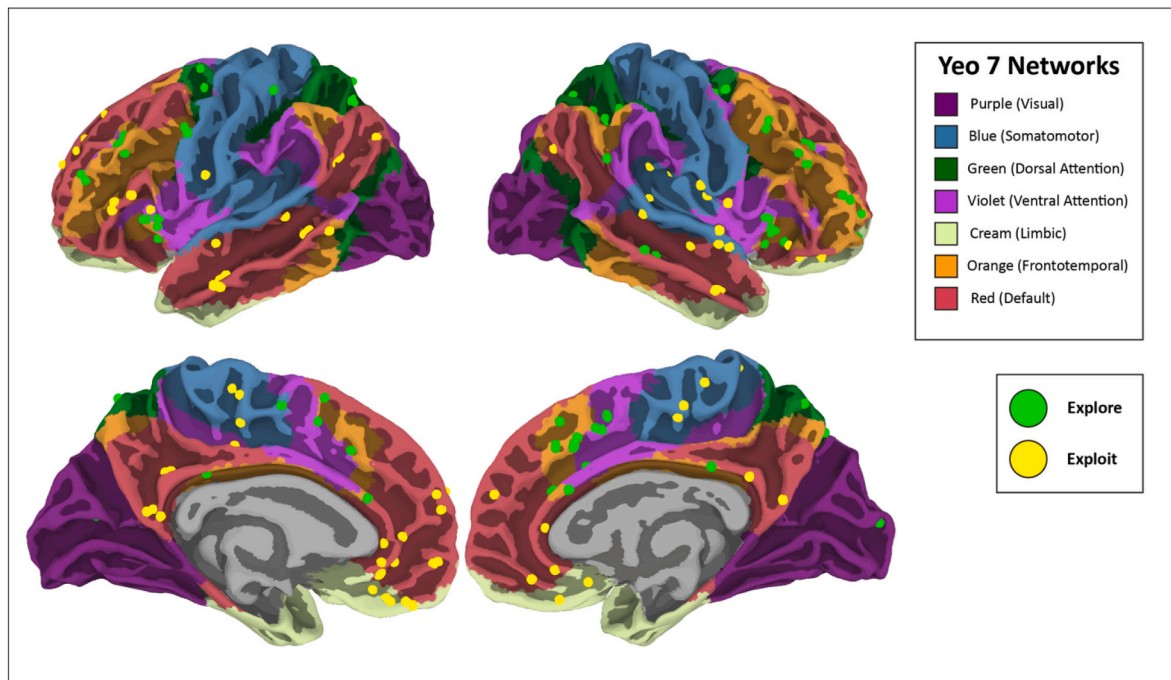


Fig. 2. Regions active during exploration-versus exploitation-based choice. All displayed foci are the maximal activation foci for each contrast, as reported in the original papers. Green spheres represent greater activation during exploration versus exploitation. Yellow spheres represent greater activation during exploitation versus exploration. [Note, 47 foci (40 explorative foci, 7 exploitative foci) subcortical activations are not observable in this cortical map. These are summarized in Table 2]. Foci were allocated to specific networks based on spatial alignment with the Yeo network maps.

Table 2A

Exploration > exploitation core and secondary regions.

Anatomical Region	Core vs Secondary (cortical vs subcortical)	Papers
Frontopolar cortex	Core (cortical)	1, 4, 5, 6, 7, 10, 11
Middle frontal gyrus (caudal to frontopolar cortex)	Core (cortical)	R: 2, 6, 7, 10, 5 L: 6, 7, 10, 5
Dorsal anterior cingulate cortex	Core (cortical)	3, 4, 5, 8, 10
Right precuneus	Core (cortical)	2, 4, 5, 6, 7
Bilateral Intraparietal sulcus	Core (cortical)	1, 3, 5, 10
Anterior insula	Secondary (cortical)	6, 7, 8, 10
Left precentral gyrus	Secondary (cortical)	5, 7, 10
Superior frontal gyrus	Secondary (cortical)	5, 6, 7
Right inferior frontal gyrus	Secondary (cortical)	2, 6, 7
Superior parietal lobule	Secondary (cortical)	5, 6, 7
Cerebellum	Secondary	1, 4, 5, 7, 10
Thalamus	Secondary (subcortical)	5, 7, 10
Locus coeruleus	Non-designated (subcortical)*	6, 7

Note. Reported regions are bilateral unless otherwise specified.

* Locus coeruleus (LC) was a non-designated region as it was only referenced in two studies. However, LC is theoretically important in exploration- and exploitation-based decision-making. Reliably imaging the LC remains a challenge with fMRI. methods.

the Yeo network mask. In the following sections we characterize the observed patterns of activation in terms of their most common network affiliation, and discuss putative functional associations. However, we note that the network affiliations reported here are ascribed post-hoc and were not reported within a network framework in the original papers.

2.6.1. Exploration-based choice: frontoparietal control, dorsal attention, and salience networks

Brain regions showing greater activation for exploration versus

Table 2B

Exploitation > exploration core and secondary regions.

Anatomical Region	Core vs Secondary	Papers
Ventromedial prefrontal cortex	Core (cortical)	1, 3, 5, 6, 7, 8, 9, 10
Orbitofrontal cortex	Core (cortical)	1, 4, 7, 9
Left middle temporal gyrus	Secondary (cortical)	4, 5, 7, 10
Left angular gyrus	Secondary (cortical)	5, 7, 10
Left posterior cingulate cortex	Secondary (cortical)	4, 7, 10
Left superior frontal gyrus	Secondary (cortical)	6, 7, 10
Superior temporal gyrus	Secondary (cortical)	7, 10, 4
Hippocampus	Secondary (subcortical)	4, 6, 7

Note. Reported regions are bilateral unless otherwise specified.

Numbered Reference List.

1. Daw et al. (2006).
2. Howard-Jones et al. (2010).
3. Kolling et al. (2012).
4. Amiez et al. (2012).
5. Addicott et al. (2014).
6. Laureiro-Martinez et al. (2013)
7. Laureiro-Martinez et al. (2015)
8. Blanchard and Gershman (2018).
9. Cogliati Dezza et al. (2019).
10. Chakroun et al. (2020).
11. Hogeveen et al. (2022).

exploitation closely cohere to the spatial topography of brain networks implicated in externally-focused and goal-directed processes, including the lateral frontal-parietal network (frontal-parietal control network), dorsal frontal parietal network (dorsal attention network) and mid-cinguloinsular network (salience network). The frontal-parietal control network is associated with goal-directed cognitive processes that require attentional allocation, and modulation of ongoing mental processes based on goal states (Niendam et al., 2012). Within the frontal-parietal control network, the frontal polar cortex was the most consistently reported region during exploration-based decision-making (Addicott, et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Hogeveen et al.,

Table 3
Network foci counts for Explore > Exploit and Exploit > Explore contrasts.

Network	Explore > Exploit	Exploit > Explore
Fronto-parietal control	56	2
Dorsal attention	32	0
Saliency	16	3
Default	5	53
Somatomotor	2	21
Limbic	1	8
Visual	3	0

Note. Subcortical foci excluded. Please see Fig. 2 for graphical representations of each network.

2022; Howard-Jones, et al., 2010; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013). This region has been implicated in decision uncertainty (Badre et al., 2012) and predictions about the expected exploration 'bonus', or the relative potential reward for making a directed exploratory versus an exploitation-based choice (Hogeveen, et al., 2022). More specifically, frontal polar cortex has been suggested to perform a role in exploration-based decisions through biasing and ultimately redirecting attention towards competing, but unchosen, options in response to shifting environmental contingencies (Badre, et al., 2012; Boorman et al., 2011; Cavanagh et al., 2012). Consistent with this idea, modulating activity in frontal polar cortex using transcranial magnetic stimulation has been shown to elicit greater exploratory behaviour during reinforcement learning (Raja Beharelle, Polania, Hare and Ruff, 2015). Notably, a recent meta-analysis of exploration failed to find frontal polar cortex activity during exploratory behaviour (Zhen, et al., 2022). However, this review focused on exploration-based responses and may not have captured the processing demands involved in shifting between exploration and exploitation.

The middle frontal gyrus (a fronto-parietal control network region, Yeo et al., 2011), was also reported across a number of studies as demonstrating greater activity during exploration versus exploitation (Addicott, et al., 2014; Chakroun et al., 2020; Hogeveen et al., 2022; Howard-Jones, et al., 2010; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013). This region is robustly associated with executive control processes in working memory, necessary to temporally bridge the gap from intention to action (Lemire-Rodger et al., 2019; Smith and Jonides, 1997) or reconcile past experiences with (unpredictable) future choice outcomes before implementing an exploratory search. The intraparietal sulcus was also consistently observed during exploration-based decisions (Addicott, et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013). This region (a region of the dorsal attention network, Yeo et al., 2011) is hypothesized to be a connector node between frontal and visuomotor regions, potentially facilitating exploratory actions in response to increased noradrenergic and decreased dopaminergic signaling (Addicott, et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013).

Exploration was also associated with core hubs of the salience network (Seeley, 2019; Uddin et al., 2019), including dorsal anterior cingulate cortex and the anterior insula (Addicott, et al., 2014; Amiez et al., 2012; Blanchard and Gershman, 2018; Chakroun et al., 2020; Kolling et al., 2012; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013). The salience network is involved in behavioural and attentional allocation towards meaningful stimuli. This may promote the switch from exploitation to exploration by signaling the appearance of an unexpected or novel stimulus of uncertain value, thereby promoting exploration over ongoing exploitation (Seeley, 2019; Uddin, 2015). The dorsal anterior cingulate cortex has been hypothesized to track the value of unchosen options (Blanchard and Hayden, 2014; Boorman et al., 2013; Hayden et al., 2011; Kolling et al., 2012), signalling when the predicted value of unknown alternatives exceeds that of previously exploited options, again biasing behaviour towards

exploration. While the precise computational role of the anterior insula remains uncertain in the context of exploration and exploitation, monitoring of potential reward outcomes may serve as a key function in the exploration circuit, putatively linking dorsal anterior cingulate and frontal polar cortices to trigger exploratory decisions when high value (but uncertain) outcomes are predicted (Addicott, et al., 2014; Amiez et al., 2012; Blanchard and Gershman, 2018; Chakroun et al., 2020; Kolling et al., 2012; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013; Li et al., 2006).

Dorsal anterior cingulate cortex and anterior insula are modulated by the noradrenergic system of the brain, including the locus coeruleus, located in the brainstem (Mather and Harley, 2016). The locus coeruleus is thought to play a role in attention modulation via noradrenergic signaling. Phasic locus coeruleus activity serves to sustain exploitation while tonic activity orients goal-directed attention and triggers exploration (Aston-Jones and Cohen, 2005; Cohen et al., 2007; Domenech et al., 2020; Dubois et al., 2021). Crucially, the salience network is thought to play a central role in toggling from externally-focused goal-directed attention, mediated by the fronto-parietal control network and the dorsal attention network (Uddin, 2015), and internally-directed cognitive processes, mediated by the default network (implicated in exploitation-based choice, see below). While locus coeruleus was only reported in two studies (Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013), reliably imaging locus coeruleus activity in human fMRI studies is challenging due to its size and location among other deep brainstem structures. Advanced imaging approaches including neuromelanin and other high-resolution structural brain stem imaging will be required to more reliably identify the role of the locus coeruleus in exploration and exploitation (Mather and Harley, 2016).

2.6.2. Exploitation-based choice: default network

Regions active during exploitation-based choice closely overlap with the medial frontal parietal brain network (default network, see Fig. 2, Table 3). The default network is associated with internally-directed cognitive processes including memory, social cognition and self-related processing (Andrews-Hanna et al., 2014). This includes the subjective valuation of rewards (Bartra et al., 2013; Clithero and Rangel, 2014), which is considered a key aspect of exploitation-based choice (Aston-Jones and Cohen, 2005; Cohen et al., 2007).

Ventromedial prefrontal cortex, a default network region (Yeo et al., 2011), was reliably observed during exploitation-based decisions (Amiez, et al., 2012; Blanchard and Gershman, 2018; Chakroun et al., 2020; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013; O'Bryan, et al., 2018). The ventromedial prefrontal cortex codes reward anticipation (Tobler, O'Doherty, Dolan and Schultz, 2007), tracking the value of choice options (Boorman et al., 2009; Kolling et al., 2012; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013; O'Doherty, 2011). Anticipation and tracking of reward valuation is crucial for decoding whether choice outcomes are signals to continue exploiting or potential triggers to explore (Domenech, et al., 2020). Another closely adjacent and putative default network region, orbital frontal cortex, was also frequently associated with exploitation (Addicott, et al., 2014; Blanchard and Gershman, 2018; Chakroun et al., 2020; Daw et al., 2006). Both the ventromedial prefrontal cortex and orbital frontal cortex are involved in the subjective valuation of attainable rewards (Levy and Glimcher, 2012). Anticipated and subsequently realized rewards (i.e., those with low prediction errors) are related to increased activity in these regions which form part of the dopaminergic, mesocorticolimbic reward system (Bartra et al., 2013; Kringelbach and Rolls, 2004; Laureiro-Martinez, et al., 2015; O'Doherty, 2011; Peters and Buchel, 2010). Low prediction errors drive sustained exploitation as the drive to seek choice options with more uncertain outcomes (exploration) is reduced.

Secondary exploitation regions also cohere to the topography of the default network. Posterior cingulate cortex (a region of the default network, Andrews-Hanna, et al., 2014; Yeo et al., 2011) was associated

with exploitation in three studies (Chakroun, et al., 2020; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013). Within the context of decision-making behaviours, posterior cingulate cortex is thought to weigh the subjective value of the present choice relative to alternative choices, shaping reward-guided behaviour based on intra-personal (mnemonic, affective) as well as contextual factors (Bartra, et al., 2013; Grueschow et al., 2015; Lebreton et al., 2009; Lebreton et al., 2009; Bartra et al., 2013; Grueschow et al., 2015).

Exploitation was also associated with other default network regions including bilateral angular gyrus (Addicott, et al., 2014; Chakroun et al., 2020; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013). The angular gyrus has been implicated in long-term memory representations (Cowan, et al., 2005) and involved in the online tracking of reward values (Gobel et al., 2001), perhaps guiding exploitation decisions. Consistent with the crucial role of mnemonic representations in exploitation-driven choice (Dombrovski et al., 2020) the hippocampus, a region of the default network (Andrews-Hanna, et al., 2014), was also implicated in exploitation in several studies (Chakroun, et al., 2020; Laureiro-Martinez, et al., 2015; Laureiro-Martinez, et al., 2013).

A significant number of foci emerging from the exploit > explore contrasts also overlapped with the somatomotor network. Activation in this network has been associated with the retrieval of conceptual knowledge, such as the semantic attributes of word meaning which activate sensory-motor regions, consistent with embodied theories of concept representation (Fernandino, et al., 2016). This idea is also reminiscent of a recently proposed network model wherein default and somatomotor networks interact to integrate incoming sensory information with prior knowledge representations, generating prediction signals to guide future behaviour (Katsumi et al., 2022). Such integration may ultimately support exploitation-based decision-making which is associated with low prediction error in a given environment. An alternative explanation for somatomotor activations for exploit > explore decisions emerges from the model-free motor learning framework. In this account, exploitation reinforcement directly shapes the recruitment of medial and lateral premotor regions involved in selecting a reward-maximizing action (Haith and Krakauer, 2013).

2.6.3. Exploration versus exploitation: a network-based account

In a theoretical review, we proposed a network-based account of the exploration versus exploitation trade-off in late life development (Spreng and Turner, 2021). Results from the present review of empirical studies in young adults provides converging support for an interacting network model of explore-exploit decision-making. Across studies, direct contrasts of brain activity during exploration versus exploitation revealed multiple, non-overlapping regions implicated in either exploration or exploitation. Perhaps even more striking than the spatial dissociations among the specific foci is the spatial coherence between the patterns of activation for exploration and exploitation and the topographies of canonical large-scale brain networks (Table 3). Specifically, exploration-related activations aligned with networks related to the control of externally-directed attentional processing (frontal-parietal control network, dorsal attention network, salience network). In contrast, exploitation-related activations cohered to the default network, which is implicated in attentional processing of internal mnemonic, affective and motivational (reward) representations.

These findings suggest that exploration- and exploitation-based decision-making is mediated by dissociable large-scale functional brain networks. Early non-human and human animal studies of exploration and exploitation trade-offs posited that these choice behaviors critically depend on dynamic shifts in brain circuits that mediate attention, reward, and prediction-monitoring processes (Aston-Jones and Cohen, 2005; Cohen et al., 2007). Here we propose an expansion of this model, implicating large-scale brain networks in the flexible shifting between exploration and exploitation. We propose that flexibly shifting between exploring and exploiting, as necessary for optimal resource accumulation in dynamic and resource-depleting environments, may involve

interactions among these large-scale brain systems. Thresholds for shifting from exploration-to exploitation-based choice (or vice-versa) may be associated with dynamic coupling (and decoupling) of functional brain networks. Network interactivity is increasingly considered to be a neural mechanism supporting complex human cognition (Sporns, 2022; Spreng et al., 2010; Williams et al., 2022). Here we suggest such interactions may also be a putative neural mechanism underpinning the decision 'to seek or to stay', a core driver of human thought and action. However, network neuroscience methods are essential to test these claims. Further, future research using neurostimulation may be necessary to test causal models.

2.7. Systematic review summary (healthy adults)

While much work remains, identifying neural mechanisms associated with the exploration-exploitation trade-off, a fundamental driver of human behaviour, will have significant implications for our understanding of both normative and non-normative decision-making. Alterations in the integrity and interactivity of large-scale brain networks have been associated with atypical development as well as numerous psychological and neurological disorders (Andrews-Hanna, et al., 2014; Fox et al., 2014). This leads to the intriguing idea that the balance between exploitation and exploration, and the flexible shifting between decision-making modes, may be a transdiagnostic feature of these conditions, anchored in the dynamic network architecture of the brain.

In the next sections of the review, we explore this idea further, surveying evidence for alterations in the exploration-exploitation trade-off in normal lifespan development, as well as in neurological and neuropsychiatric disorders.

3. Neuropsychological studies of exploration and exploitation in child development, aging, neurological disease and neuropsychiatric disorders

Building from the findings of our systematic review of the exploration-exploitation trade-off in typically developing adults, next we review neuropsychological studies examining these decision-making modes in children and older adults as well as in neurological disease and neuropsychiatric disorders.

3.1. Exploration-exploitation in childhood and late life development

In typically developing humans, exploration-exploitation choice behaviour shifts across the lifespan in tandem with a number of developmental factors. Novelty-seeking and cognitive control processes decline from younger to older adulthood (Spreng and Turner, 2021). In contrast, risk aversion and stores of prior knowledge and lived experiences increase with age (Mata and von Helversen, 2015; Mata et al., 2013; Spreng and Turner, 2021). The exploration-exploitation trade-off involves balancing the risks of exploring with the rewards of exploiting or, put another way, balancing the drive for new information with the reassurance and reward of certainty. The tension between information and reward seeking choices changes across the adult lifespan, tracking shifts in motivation, cognition, and associated brain changes. These changes suggest that the balance between exploration and exploitation driven decision-making may also shift from younger to older adulthood.

We were unable to identify any studies directly investigating exploration and exploitation in early childhood, however, this has been studied in adolescence (Kayser et al., 2016; Lloyd et al., 2021; Somerville et al., 2017). Somerville and colleagues (2017) administered an exploration-exploitation task to adolescents and young adults while manipulating reward value, information value, and time horizon (i.e., the usefulness of information for future choices). Young adolescents failed to demonstrate a strategic exploratory bias (i.e., favoring exploration over longer time horizons). However, more strategic exploration emerged by later adolescence and remained stable into early adulthood.

Adolescents also displayed adaptive exploratory behaviour in a resource foraging paradigm where exploration was the optimal strategy, resulting in greater resource accrual (Lloyd, et al., 2021). Evidence of an exploration-bias is consistent with cognitive and brain changes known to occur post-puberty (Spear, 2000; Steinberg, 2008). Synaptic pruning and myelination of the prefrontal cortex, a hub region responsible for executive functions and cognitive control processes such as risk assessment and decision-making, continues into late adolescence, with some evidence that this neurodevelopmental trajectory may continue into the third decade of life (Spear, 2000; Steinberg, 2008; Tamm et al., 2002; Yurgelun-Todd, 2007). In contrast, development of ventral limbic regions, associated with affect, motivation, and reward processes is mostly complete by early adolescence (Casey, 2015). This developmental imbalance in adolescence results in a drive for novelty and experience-seeking, in the context of low control processes, as necessary to adjudicate between decision outcomes (underpinned by the lead-lag development of reward versus control circuits). Together these trajectories may establish a propensity for exploration and experiential learning in adolescence (Casey et al., 2008; Romer et al., 2017) that begins to show an age-related decline even in early adulthood, continuing across the adult lifespan into late-life development.

While research is only beginning to be conducted in this area, there is early evidence that exploration decreases with age; with older adults showing a bias towards exploitation of prior knowledge to make decisions (Chin, et al., 2015; Hills, 2019; Mata and von Helversen, 2015; Mata et al., 2009; Mata et al., 2013; Qiu and Johns, 2020; Spreng and Turner, 2019, 2021). Older adults allocate more time to exploiting fewer sources in information search tasks. In contrast, younger adults tend to explore more sources while spending less time at each source (Chin, et al., 2015). The older age-related exploitation bias is also evident in both externally and internally directed foraging tasks (Mata and von Helversen, 2015; Mata et al., 2009), suggesting that the predictability of relying on prior knowledge to gain more certain rewards is prioritized (exploitation) over the less certain value of new information (exploration).

Age differences in the exploration-exploitation trade-off have also been associated with subcortical and cortical brain changes occurring over the course of late life development. Older adults show reduced sensitivity to negative future outcomes (Samanez-Larkin, et al., 2007), mediated by dopaminergic signalling (Samanez-Larkin and Knutson, 2015) and increased attention to positively valenced information (Charles and Carstensen, 2010), associated with noradrenergic signalling (Mather and Harley, 2016). Although speculative, age-related changes to these subcortically mediated neurotransmitter systems may shift attention towards affectively valenced goals, while positive expectancies may bias older adults to favor the more certain rewards of exploitation over uncertain outcomes associated with exploration-based decisions. Further, exploration- and exploitation-based decisions in younger adults are associated with dissociable large scale cortical systems implicated in attentional control processes and access to prior knowledge stores (see section 2 above). With age, these networks become less segregated, resulting in greater and less flexible between-network coupling (Chan et al., 2014; Setton et al., 2023; Spreng and Schacter, 2012; Turner and Spreng, 2015). We have argued that shifts in network interactivity and flexibility with increasing age, may provide a neural mechanism favouring greater dependence on prior knowledge over cognitive control processes, an idea we have labelled the Default-Executive Coupling Hypothesis of Aging (DECHA, Spreng and Turner, 2019; Turner and Spreng, 2015). In brief, we posit that greater, and less flexible, coupling between default network brain regions, implicated in internally-directed mnemonic processes, and frontal executive regions, implicated in cognitive control, may be associated with greater engagement of – and reliance on – prior knowledge during complex cognitive processes. Building from these ideas we have recently argued that greater infusion of prior knowledge into goal-directed cognitive processes (e.g., decision-making) may ultimately lead to the

emergence of an exploitation bias in older adulthood (Spreng and Turner, 2019, 2021).

3.2. Exploration-exploitation in atypical development (neurological & neuropsychiatric disorders)

Research investigating differences in exploration- and exploitation-based decision-making associated with neurological and psychiatric disorders also remains in its infancy. However, a growing number of studies are beginning to reveal the nature of these differences, and their relationship to clinical symptom profiles, as well as alterations in brain structure and function. Characterizing differences in exploration and exploitation in clinical populations will advance our understanding of behavioural phenotypes, potentially improving early surveillance and intervention approaches, as well as expanding knowledge of the neural mechanisms associated with exploration- and exploitation-based decision-making as a trans-diagnostic feature of these disorders.

Exploitation-biases have been reported in Alzheimer's disease (AD) and Mild Cognitive Impairment. This is evidenced by reduced semantic switching during a verbal fluency task, a marker of exploitation bias (Auriacombe, et al., 2006; Gomez and White, 2006; Henry et al., 2004; Pakhomov et al., 2016; Raoux et al., 2008; Troger et al., 2019). The capacity for random number generation is also reduced in AD (Brugger et al., 1996). This inability to suppress well-learned number sequences is consistent with an exploitation bias that continues from normal aging into neurodegenerative disease. Similar difficulties have also been observed following brain injury in younger adults (Spatt and Goldenberg, 1993). Fluency and generative tasks are known to engage cognitive control processes to overcome the prepotency of exploiting prior knowledge. These neurological findings implicate damage to lateral prefrontal cortices, dopaminergic signalling, and connectivity to posterior and subcortical regions, including medial temporal lobe memory systems in biasing search towards greater reliance on prior knowledge (Auriacombe, et al., 2006; Brugger et al., 1996; Gomez and White, 2006; Henry et al., 2004; Pakhomov et al., 2016; Raoux et al., 2008; Troger et al., 2019). Further, AD is associated with tauopathy, a neurodegenerative process characterized by abnormalities in tau, the protein responsible for maintaining the structural integrity of neurons (Avila et al., 2004). The earliest tau pathology originates in the locus coeruleus (Mather and Harley, 2016), a brain region thought to mediate shifting between exploration-exploitation by altering noradrenergic signaling (Aston-Jones and Cohen, 2005). As noted above, the emergence of exploitation-biases in AD may reflect reduced attentional flexibility, secondary to altered noradrenergic signaling.

Frontotemporal Dementia (behavioural variant) is a neurodegenerative disease characterized by marked atrophy in the anterior insula as well as the frontal and anterior temporal lobes (Seeley, 2019). Frontotemporal dementia patients show altered stimulus-reinforcement learning and decreased exploration compared to healthy controls (Strenziocck, et al., 2011). These differences are positively associated with the degree of atrophy in the orbitofrontal cortex, a region associated with the integration of rewards and risks of choice options, as necessary to arbitrate exploration-exploitation trade-offs.

Parkinson's disease (PD) is a neurodegenerative condition characterized by the loss of dopamine producing neurons in the substantia nigra, resulting in a variety of motor and cognitive deficits (Emanzadeh and Surguchov, 2018). PD patients show decreased sensitivity to risk and loss (Gescheidt, et al., 2013), as well as an increase in exploratory behaviours after treatment with a dopamine agonist (Bodi, et al., 2009). This exploratory bias is more pronounced in PD patients with impulsive compulsive behaviours (Djamshidian, O'Sullivan et al., 2011), a sub-population of PD with higher levels of ventral-striatal dopamine compared to non-impulsive patients (Evans et al., 2005; O'Sullivan, et al., 2011). This suggests a putative neural mechanism associating ventral-striatal dopamine availability with exploration and risk-seeking behaviours (Djamshidian, et al., 2010; Voon et al., 2010).

Biases have also been observed in neurodevelopmental disorders. Information foraging is impaired in both autism spectrum disorder and attention deficit (hyperactivity) disorder (ADHD). However foraging patterns differ between these two conditions. ASD is characterized by exploitation as well as a desire for “sameness” and consistency on decision-making tasks (Elison et al., 2012; Gliga et al., 2018; Pellicano et al., 2011; Pierce and Courchesne, 2001). In contrast, ADHD is characterized by heightened exploration and novelty seeking (Addicott, et al., 2021; Gliga et al., 2018; Salgado et al., 2009; Ziegler et al., 2016). Both autism spectrum disorder and ADHD have been associated with atypical dopaminergic (Kriete and Noelle, 2015; Solanto, 2002) and noradrenergic functioning (Biederman and Spencer, 1999; Blaser et al., 2014), again implicating both neurotransmitter systems in shaping choice behaviours in these neurodevelopmental disorders.

Differences in exploration-exploitation trade-offs have also been reported in several neuropsychiatric disorders. In persons diagnosed with schizophrenia, biases toward exploration or exploitation depend on symptom profiles. Greater negative symptoms are associated with lower uncertainty-driven exploration choices (and greater exploitation) during reinforcement learning (Martinelli et al., 2018; Strauss et al., 2011). In contrast, the presence of disorganized symptoms in schizophrenia is associated with less exploitation and more maladaptive and random exploration choices during reinforcement learning (Cathomas, et al., 2021). Further, during random number generation, individuals with schizophrenia (Artiges, et al., 2000; Salame et al., 1998) as well as those with pathological worry (Hirsch and Mathews, 2012) show a reduced ability to generate random sequences (exploration), providing sequential number strings, again consistent with an exploitation bias in this population.

The exploration-exploitation trade-off has also been studied in the context of addiction and substance use disorder. Individuals who are dependent on tobacco (Addicott, et al., 2014), alcohol (Morris, et al., 2016), methamphetamine (Harle, et al., 2015) and ecstasy (Koester, et al., 2013) tend to make more exploitative decisions and show impaired strategic exploration on decision-making tasks. Chronic intake of addictive substances diminishes natural dopamine and results in dopamine hypofunction, thus dampening sensitivity to natural rewards (Thiruchselvam et al., 2017). This suggests that those experiencing substance-dependency have an over-reliance on exploitative search to obtain immediate known rewards, further implicating the dopaminergic reward system in shaping exploration and exploitation biases.

3.3. Summary: neuropsychological studies of exploration and exploitation

Lifespan development and clinical studies provide additional insights into the behavioural and neural correlates of the exploration-exploitation trade-off. In normative lifespan development, there is converging evidence that age-related declines in control processes, tethered to increases in affectively-based goal hierarchies, shorter temporal horizons, and reduced drive towards novelty-seeking result in an exploitation-bias in later life (Spreng and Turner, 2021). However, as most published research has focused on younger adulthood, there remains little evidence characterizing the slope of change or possible inflection points occurring over the life course.

In clinical populations elevated levels of endogenous dopamine in neurological disorders such as PD have been linked to an exploratory decision-making bias (Djamshidian, et al., 2010; Evans et al., 2005; O’Sullivan, et al., 2011; Voon et al., 2010). In contrast low dopamine availability promotes an exploitative bias (Addicott, et al., 2014; Bodi et al., 2009; Harle et al., 2015; Morris et al., 2016; Thiruchselvam et al., 2017). Altered decision-making biases associated with schizophrenia (Artiges, et al., 2000; Cathomas et al., 2021; Martinelli et al., 2018; Salame et al., 1998; Strauss et al., 2011), pathological worry (Hirsch and Mathews, 2012), and atypical neurodevelopment (Addicott, et al., 2021; Elison et al., 2012; Pellicano et al., 2011; Pierce and Courchesne, 2001; Salgado et al., 2009) also implicate noradrenergic signaling in altered

exploration-exploitation trade-offs. Further, deficits on fluency and generative tasks in neurodegenerative disorders (Auriacombe, et al., 2006; Brugger et al., 1996; Gomez and White, 2006; Henry et al., 2004; Pakhomov et al., 2016; Raoux et al., 2008; Strenziocck et al., 2011; Troger et al., 2019) implicate anterior and ventromedial prefrontal regions as well as cortical-cortical and cortico-subcortical connectivity as putative mechanisms underpinning exploration and exploitation biases in non-normative development.

4. Conclusions and future directions

Deciding whether to explore or exploit is at the core of all human mentation and action. Characterizing the neural basis of these choices, and trade-offs between them, offers a promising avenue of research into the nature of human volition, and changes in the context of normative and non-normative lifespan development. Here we advance this proposal by reviewing and summarizing study findings across two bodies of literature examining exploration- and exploitation-based decision-making in humans. We first conducted a systematic review of the cognitive neuroscience literature using fMRI methods to characterize patterns of brain activity during exploration and exploitation-based decision-making in healthy adults. Next, we integrated study findings from neuropsychological studies in childhood and late life development as well as in neurological disease and neuropsychiatric disorders.

Our review of fMRI studies revealed dissociable patterns of brain activity associated with exploration and exploitation-based decision-making in healthy adults (Fig. 2). Activation patterns during exploration-based choice cohered to the control and attention networks as well as regions of the salience network. Consistent with non-human (Aston-Jones and Cohen, 2005) and human (Cohen, et al., 2007) models of exploration and exploitation, these findings strongly implicate both cognitive control and attentional orienting in decisions to explore versus exploit. In contrast, activation patterns during exploitation-based decisions showed a striking overlap with the default network, engaging regions along the medial surface of the brain including limbic and paralimbic regions implicated in affective, reward, and mnemonic processing. Our review also revealed engagement of the ventral attention network/salience network (Uddin et al., 2019). The salience network mediates ‘switching’ between default network and frontoparietal control network activations to guide appropriate responses to salient stimuli. Here we posit that this network may support switching between exploration and exploitation-based choice as the salience of rewards shifts over time. We again caution that the original study findings were not presented within a network neuroscience framework. However, the dissociation between brain activity patterns attributed to exploration and exploitation-based choice, and the spatial coherence of these patterns with distinct large-scale brain networks (Table 3), suggest that examining exploration-exploitation trade-offs through a network neuroscience lens may reveal novel neural mechanisms, advancing our understanding of individual, lifespan and clinical differences in this fundamental aspect of human decision making.

To provide a more comprehensive characterization of putative brain regions and neural circuits implicated in exploration and exploitation, we also included a review of neuropsychological studies investigating the exploration-exploitation trade-off in children and older adults as well as clinical populations. The findings provide strong evidence implicating specific neurotransmitter systems in exploration versus exploitation-biased decision-making. Disruptions to the dopaminergic system, as observed in neuropsychiatric disorders including PD, schizophrenia and ADHD resulted in reduced exploration, suggesting that dopamine availability is necessary for exploratory drives, while its absence promotes greater exploitation. Similarly, alterations in norepinephrine signalling, possibly related to early tau accumulation in the locus coeruleus, may disrupt flexible coupling among large scale brain networks, mediated by the salience network. In the context of declining dopaminergic signalling, this may result in an emergent exploitation

bias. While speculative, we have argued that a loss of flexible network coupling, and associated reductions in attentional shifting in older adulthood, could result in a different threshold for exploration-exploitation trade-offs, and prepotent exploitation bias in aging (Spreng and Turner, 2021). These biases may well be present in neurological and neuropsychiatric disease, however future studies are necessary to test this prediction.

By integrating our reviews of cognitive neuroscience and neuropsychological studies we identified converging evidence for both the independence as well as the integration of large-scale brain systems in the exploration-exploitation trade-off. While functional neuroimaging investigations are necessary to map large-scale brain circuits, neurodevelopmental and neuropsychological studies provide additional insights into the chemoarchitecture underlying exploration and exploitation-based decision-making. Our integrated approach is consistent with recent efforts to characterize chemoarchitecture as a key feature of the multi-scale organization of the brain, with evidence for strong topographic alignment among neurotransmitter systems, functional network organization, cognitive function, and disease vulnerability (Hansen, et al., 2022). While future empirical studies are necessary to confirm and refine our conclusions, here we have provided preliminary evidence for such topographic specificity underpinning decisions to explore versus exploit. Precision mapping of the trade-off, or biases towards exploration or exploitation, holds significant potential as a behavioural assay of underlying brain changes (individually or collectively across networks) occurring in the context of normative and nonnormative lifespan development, brain injury, and neurological disease.

Finally, our review revealed considerable variability in experimental approaches to measuring exploration and exploitation. Task-specific factors can influence choice decisions (von Helverson, et al., 2018). This presents a significant challenge for measuring general differences in exploration and exploitation biases across individuals using a single behavioural measure or even across decision paradigms (foraging, reinforcement learning, information search). However, our findings, which revealed consistent results across studies dissociating neural activation patterns during exploration versus exploitation suggest that there are common processes, or constellations of processes, that underpin decisions to explore versus exploit that are generalizable across task contexts. To elucidate these processes, whether neural or behavioural, will require careful manipulation of task parameters (e.g., value, temporality, ambiguity, contingencies, and choice-outcome dependencies) using within-subject experimental designs. Such an approach will be necessary to promote our understanding of individual differences, and associated neural processes, as well as informing future investigations of fundamental decision-making differences in typical and atypical human development.

Declaration of competing interest

The authors of this work declare no conflicts of interest.

Data availability

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

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