EXPLORATION VERSUS EXPLOITATION DECISIONS IN THE HUMAN BRAIN: A SYSTEMATIC REVIEW OF FUNCTIONAL NEUROIMAGING AND NEUROPSYCHOLOGICAL STUDIES.

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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, the heterogeneity of experimental protocols and paradigms used to study these choice behaviours, as well as the predominance of reinforcement learning studies to study the neurocomputational basis of choice behaviours. We conducted a systematic review of functional neuroimaging (fMRI) studies of exploration- versus exploitation- based decision-making in healthy adult humans during reinforcement learning, information search, and foraging. Eleven fMRI studies met inclusion criterion. 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. Building from these findings in typical adult development, we next surveyed exploration-exploitation behaviours in neurodevelopmental, neuropsychological, and neuropsychiatric disorders, as well as lifespan development, and neurodegenerative disease. Findings revealed differing exploration and exploitation decision-making biases across populations. Taken together, our review highlights the need for precision-mapping of the neural circuitry and behavioural correlates associated with exploitation and exploration in humans. Characterizing exploration versus exploitation decisionmaking biases may offer a novel, trans-diagnostic approach to assessment, surveillance, and intervention for cognitive decline and dysfunction in normal development and clinical populations.

Keywords: Decision-making, reinforcement learning, foraging, information search, fMRI, attention network, default network

Dedication

This thesis is dedicated to John Angus Wyatt, my late grandfather who died at the age of 106 and who never stopped exploring.

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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 & 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 studied extensively across species and contexts, from hummingbirds (Melhorn et al., 2015; Nonacs, 2010) to humans (Algermissen et al., 2019; Cogliati Dezza et al., 2019; Domenech et al., 2020; Pajkossy et al., 2017; Pezzulo et al., 2016; Rich & Gureckis, 2018; Tomov et al., 2020; Walker et al., 2019; Zajkowski et al., 2017), and from ecology (Berger-Tal & 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 & Gershman, 2018; Spreng & Turner, 2021). There have been several reviews of exploration and exploitation as a decision-making framework (Hills et al., 2015; Mata & von Helversen, 2015; Melhorn et al., 2015; Spreng & 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. First, we review the most common behavioural approaches to measure the trade-off in human decision-making. Next, we report the results of a systematic review of the extant literature examining the functional neuroanatomy of the

exploration-exploitation trade-off in typically developing adults using functional brain imaging (fMRI) methods. Finally, we integrate these findings with studies examining the exploration-exploitation trade-off in neurotypical lifespan development as well as psychological and neurological disorders.

1.2 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 Helverson 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, where 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). As such, 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 & 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. As such, 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). As such, 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 & Turner, 2021).

Foraging can occur extra-personally, in the environment or intra-personally, referred to as 'foraging in mind' (Todd & 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 & 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-

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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 & Jones, 1979; Katehakis & 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 & Jones, 1979; Hogeveen et al., 2022; Katehakis & Veinott, 1987)

In early reinforcement learning studies involving the *n*-bandit tasks (Daw et al., 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 et al., 2017; Hogeveen et al., 2022; Horvath et al., 2021; Wilson et al., 2021). Common approaches used to characterize the behavioural and neural correlates of reinforcement learning include manipulations that disentangle the information from the reward value of a choice (Horvath et al., 2021), changing the time horizon for realizing choice gains (Cogliati Dezza et al., 2017), and altering the balance between risk versus information gain (Cogliati Dezza et al., 2017; Hogeveen et al., 2022; Wilson et al., 2014).

1.4 Information Search

Information search tasks measure how resources are accumulated from multiple sources (Blanchard & Gershman, 2018; O'Bryan et al., 2018). An example of this form of explorationexploitation paradigm might be searching for the best vitamin supplement. In seeking options do you stay with one relevant and empirical website, or do you search more broadly to seek information from multiple sources? (Chin et al., 2015). In these search paradigms, exploration is defined as the continued search across information sources whereas exploitation is defined as the decision to land upon (and exploit) the information from a selected source. A typical real-world information search task would be our seemingly unquenchable thirst to scour the internet searches for target information (Chin et al., 2015; Sharit et al., 2008). Most experimental information search tasks involve 'optimal stopping' behaviour, where exploration yields information gains across a linearly decreasing value threshold, with exploitation defined as the realization of those gains (minus the search costs). Information search has been most commonly studied through the lens of the classic Secretary Problem (Ferguson, 1989). Personnel hiring decisions (e.g., for a new Secretary), involve screening and then interviewing a series of candidates (i.e., exploring) to find the optimal choice. However, the choice to stop the search and select a candidate ("exploit") forestalls any further exploration, leaving the optimality of the choice ambiguous.

Information search can occur in environments of depleting resources, where continuing to explore comes with a cost of missing the best, but no longer available, option. Search can also occur in environments of non-depleting resources which encourage more exploration, such as a volatile stock market where a 'missed opportunity' may actually replenish or grow in value, which may be realized later. Another determinant of choice behavior on information search tasks is the reward value of exploration. In many common information search tasks, exploration conveys information, but is not explicitly rewarded. In these tasks, reward is only obtained when exploration ends and the selected option is 'exploited', described above as the 'stopping problem'. However, in the real-world exploration can be rewarding (e.g., a taste-testing menu, or sampling a flight of beers at your local microbrewery). More recently, information search paradigms have attempted to model ecologically valid forms of information search, avoiding the stopping problem and allowing flexible switching between exploitation and exploration options that are both informative and rewarding (Sang et al., 2020).

While few studies have investigated the impact of rewarding exploitation and exploration during information search (Melhorn et al., 2015), early evidence suggests that rewarding exploration results in greater and more front-end loaded exploratory choices. Similarly, reducing uncertainty through repeated task exposure also results in greater and earlier exploratory choices on sequential information search tasks (Navarro et al., 2004). Positive affect has also been shown to reduce exploration during information search (von Helversen & Mata, 2012). In contrast, longer

temporal horizons appear to increase exploration on these tasks (Wilson et al., 2021), although few studies have directly investigated these manipulations.

2. Systematic review of functional imaging studies of the exploration-exploitation trade-off

While the behavioural parameters of explore-exploit decision-making have been studied extensively, the underlying neural correlates in humans are less well defined. To address this gap, we conducted a comprehensive review of 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, limiting the total number of studies that could be included in our review (and see (Zhen et al., 2022)).

In the earliest published neuroimaging study explicitly framed within an explorationexploitation decision-making model, Daw et al. (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 & 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). 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). While most studies examine exploration or exploitation brain activation patterns separately, 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. As such, here we provide the first 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 (forag*) AND (humans) AND (fMRI). Keywords for the reinforcement learning search were: (decisi* OR decision making OR decision-making) AND (forag*) AND (humans) AND (fMRI). Keywords for the information search were: (decisi* OR decision making OR decision-making) AND (fMRI). Keywords for the information search were: (decisi* OR decision making OR decision-making) 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). Figure 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.



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

Author	Ν	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-Martínez et al. (2014)	50	34.35(6.6)	All	4-armed bandit	Whole brain
Laureiro-Martínez et al. (2015)	63	34.45(6.45)	All	4-armed bandit	Whole brain
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
Hogeveen 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 & Gershman	18	21-36*	All	Observe or Bet	ROI

Table 1. Summary of fMRI studies included in the systematic review

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.

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 analyzed the location and frequency of statistically significant neural activations across all studies for exploration>exploitation and exploitation>exploration contrasts. 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 Figure 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 et al., 2019) in the first instance, and then adopt standard network 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.

Figure 2 displays significant cortical activations reported across all studies. Montreal Neurological Institute (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 & Hyde, 1997; Saad & Reynolds, 2012).



Figure 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.

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

Anatomical Region	Core vs Secondary (cortical vs subcortical)	Papers
Frontopolar cortex	Core (cortical)	1, 4, 5, 6, 7, 10,
Middle frontal gyrus	Core (cortical)	R: 2, 6, 7, 10, 5
cortex)		L. 0, 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	Core (cortical)	1, 3, 5, 10
sulcus		
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)	6, 7, 5
Cerebellum	Secondary (subcortical)	1, 4, 5, 7, 10
Thalamus	Secondary (subcortical)	5, 7, 10
Locus coeruleus	Non-designated (subcortical)*	6, 7

Table 2A. Exploration > Exploitation Core and Secondary Regions

Note. Reported regions are bilateral unless otherwise specified.

*Locus coeruleus was reported in only 2 studies. It is commonly reported in non-human animal studies and reported here for comprehensiveness.

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

 Table 2B. Exploitation > Exploration Core and Secondary Regions

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 striking 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 Figure 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. However, the characterizations here must be considered preliminary, pending more direct network-neuroscience studies of 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.

2.6.1 Exploration-based choice: Frontoparietal control and salience networks

Brain regions showing greater activation for exploration versus 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 midcinguloinsular 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 (Spreng et al., 2010; Vincent et al., 2007). Within the frontal-parietal control network, the

frontal polar cortex was the most consistently reported region during exploration-based decisionmaking (Addicott et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Hogeveen et al., 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 et al., 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 from exploration- to exploitation-based choice.

The middle frontal gyrus, a core frontal-parietal control network hub region, 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 & 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 core node of the dorsal attention network) 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; Signaling (Addicott et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Laureiro-Martinez et al., 2015; Laureiro-Martinez et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Laureiro-Martinez et al., 2015; Laureiro-Martinez et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Laureiro-Martinez et al., 2014; Chakroun et al., 2020; Daw et al., 2006; Laureiro-Martinez et al., 2015; 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, including dorsal anterior cingulate cortex and the anterior insula (Addicott et al., 2014; Amiez et al., 2012;

Blanchard & 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 exploration (Seeley, 2019; Uddin, 2015). The dorsal anterior cingulate cortex has been hypothesized to track the value of unchosen options (Blanchard & 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 & 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 also closely functionally connected to the noradrenergic system of the brain, including the locus coeruleus located in the brainstem (Mather & 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 & 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 frontal-parietal control network and the dorsal attention network (Vincent et al., 2007), and internally-directed cognitive processes, mediated by the default network (strongly 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 multimodal imaging approaches including neuromelanin and high-resolution structural brain stem imaging will be required to more reliably identify the role of the locus coeruleus in exploration and exploitation (Mather & Harley, 2016).

2.6.2 Exploitation-based choice: Default network

Regions active during exploitation-based choice closely overlap the medial frontal parietal brain network (default network) (Bartra et al., 2013; Clithero & Rangel, 2014; Daw et al., 2006; Laureiro-Martinez et al., 2015; Laureiro-Martinez et al., 2013). The default network has been associated with internally-directed cognitive processes including reward valuation, motivation, and memory (Andrews-Hanna et al., 2014).

A core hub of the anterior aspect of the default network, the ventromedial prefrontal cortex, was reliably observed during exploitation-based decisions (Amiez et al., 2012; Blanchard & 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 et al., 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 & 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 & 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 & Rolls, 2004; Laureiro-Martinez et al., 2015; O'Doherty, 2011; Peters & 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. The posterior cingulate cortex, a core node of the posterior default network (Andrews-Hanna, et al., 2014) was associated with exploitation in three studies (Chakroun et al., 2020; Laureiro-Martinez et al., 2015; Laureiro-Martinez et al., 2013). Within the realm 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 intrapersonal (mnemonic, affective) as well as contextual factors (Bartra et al., 2013; Grueschow et al., 2015; Lebreton2009; 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). This region has been implicated in the storage of activated long term memory representations (Cowan et al., 2005) as necessary for online tracking of reward values (Gobel et al., 2001). Consistent with the crucial role of mnemonic representations in exploitation-driven choice (Dombrovski et al., 2020), the hippocampus, a core node of the medial temporal default network subsystem (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 sensorymotor 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 (c.f. Haith & Krakauer, 2013).

2.6.3 Exploration versus exploitation: A network-based account

In a recent theoretical review, we proposed a network-based account of the exploration versus exploitation trade-off in late life development (Spreng & 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 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 largely dissociable neural network substrates. Extrapolating from these results, flexibly shifting between exploring and exploiting, as necessary for optimal resource accumulation in dynamic and resource-depleting environments, may critically depend on the integrity and interactivity of these large-scale brain systems. Further, thresholds for an exploration-exploitation trade-off may critically depend on the integrity and the dynamic functional coupling (and decoupling) of brain networks, suggesting a putative neural mechanism of the behavioural decision 'to seek or to stay' as a core driver of human thought and action.

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

Table 3. Spatial overlap between activation foci for Explore > Exploit and Exploit > Explore contrasts and canonical large-scale brain networks (Yeo et al., 2011)

2.7 Systematic review summary

While much work remains, identifying neural mechanisms associated with the explorationexploitation 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 exploitation, 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. Exploration and exploitation in normative and non-normative neurodevelopment

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 & Turner, 2021). In contrast, risk aversion and stores of prior knowledge and lived experiences increase with age (Mata & von Helversen, 2015; Mata et al., 2013; Spreng & Turner, 2021). The exploration-exploitation tradeoff 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.

3.1 Exploration-exploitation in early development

We were unable to identify any studies directly investigating exploration and exploitation in 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 explorationexploitation 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.

3.2 Exploration-exploitation in older adults

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 & von Helversen, 2015; Mata et al., 2009; Mata et al., 2013; Qiu & Johns, 2020; Spreng & 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). This exploitation bias is also evident both in externally and internally directed foraging tasks (Mata & 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 & Knutson, 2015) and increased attention to positively valanced information (Charles & Carstensen, 2010), associated with noradrenergic signalling (Mather & Harley, 2016). Although speculative, age-related changes to these subcortically mediated neurotransmitter systems may shift attention towards affectively valanced 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., 2022; Spreng & Schacter, 2012; Turner & Spreng, 2015). We have argued that shifts in network interactivity and flexibility may provide a neural mechanism favouring greater dependence on prior knowledge over cognitive control processes, ultimately leading to the emergence of an exploitation bias in older adulthood (Spreng & Turner, 2019, 2021).

3.3 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.

3.4 Neurological and neurodevelopmental disorders

Exploitation-biases have been reported in Alzheimer's disease (AD) and Mild Cognitive Impairment (MCI). This is evidenced by reduced semantic switching during a verbal fluency task which is considered to be a marker of exploitation bias (Auriacombe et al., 2006; Gomez & 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 & Goldenberg, 1993). Fluency and generative tasks are known to engage cognitive control processes to overcome the prepotency of exploiting prior knowledge. As such, 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 & 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 & Harley, 2016), a brain region thought to mediate shifting between exploration-exploitation by altering noradrenergic signaling (Aston-Jones & 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 (Strenziock 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 (Emamzadeh & 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 et al., 2011), a subpopulation 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 (ASD) 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 & 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 ASD and ADHD have been associated with atypical dopaminergic (Kriete & Noelle, 2015; Solanto, 2002) and noradrenergic functioning (Biederman & Spencer, 1999; Blaser et al., 2014), again implicating both neurotransmitter systems in shaping choice behaviours in these neurodevelopmental disorders.

3.5 Psychiatric Disorders

Differences in exploration-exploitation trade-offs have been reported in schizophrenia, with biases toward exploration or exploitation dependent 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 & 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.

3.6 Summary: Normative and non-normative development

While scant, 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 & 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 non-normative development and clinical populations, elevated levels of endogenous dopamine in neurological disorders such as PD have been linked to an exploratory decisionmaking bias (Djamshidian et al., 2010; Evans et al., 2005; O'Sullivan et al., 2011; Voon et al., 2010). In contrast low dopamine availability results in 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 & Mathews, 2012), and atypical neurodevelopment (Addicott et al., 2021; Elison et al., 2012; Pellicano et al., 2011; Pierce & Courchesne, 2001; Salgado et al., 2009) also implicate noradrenergic signaling, and attention network dysfunction 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 & White, 2006; Henry et al., 2004; Pakhomov et al., 2016; Raoux et al., 2008; Strenziock 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 nonnormative 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 reporting findings from a systematic review of functional neuroimaging studies directly contrasting brain activity during exploration and exploitation-based decision-making in younger adults. We also summarized evidence from a qualitative review of studies examining exploration and exploitation biases in younger and older adulthood, as well as in clinical disorders.

Our findings revealed reliably dissociable patterns of brain activity associated with exploration and exploitation-based decision-making in typically developing adults (Figure 2). Activation patterns during exploration-based choice closely cohered to the control and attention

networks of the brain as well as core nodes of the salience network. These associations strongly implicate both cognitive control and attentional orienting in decisions to explore versus exploit. In contrast, activation during exploitation-based decisions showed a striking overlap with the default network. This suggests that exploitation-based choice is linked to engagement of regions along the medial surface of the brain including limbic and paralimbic regions implicated in affective, reward, and mnemonic processing. Crucially, the salience network flexibly couples with these other networks (Seeley, 2019) suggesting that this ensemble of functionally connected brain regions may support switching between exploration and exploitation-based choice, as necessary for adaptive decision-making. We 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 largescale 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.

By also including studies investigating the exploration-exploitation trade-off across the lifespan and in clinical populations, the breadth of findings reviewed here provide strong support for considering the exploration-exploitation trade-off as a novel paradigmatic approach to study adaptive and maladaptive decision-making behaviour in humans. There is a clear dissociation between the neural instantiation of exploration- versus exploitation-based choice. As such, 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.

The present review also revealed considerable variability in experimental approaches to measuring exploration and exploitation. As highlighted recently (von Helverson et al., 2018) task-specific factors strongly influence choice decisions. 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 highly 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.

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