Meta-Analysis Reveals That Explore-Exploit Decisions are Dissociable by Activation in the Dorsal Lateral Prefrontal Cortex, Anterior Insula, and the Dorsal Anterior Cingulate Cortex

Daniel Sazhin, Abraham Dachs, & David V. Smith

Department of Psychology & Neuroscience, Temple University, Philadelphia, PA, USA

Acknowledgments
This work was supported in part by a grant from the National Institute on Drug Abuse (R03-DA046733). We thank Chelsea Helion, Vishnu Murty, and Michael McCloskey for feedback on prior versions of this manuscript. We thank Amanda Nguyen for help with data collection.

Conflict of interest statement
The authors declare no conflicts of interest.

Data availability
Data is available on OSF at: https://osf.io/86kp9/. Thresholded and unthresholded statistical maps are located on https://neurovault.org/collections/17882/.

Author Contribution Statement: Daniel Sazhin formulated the pre-registration, conducted analyses, and prepared the manuscript with contributions from all coauthors. Abraham Dachs collected the data and contributed to the manuscript. David Smith oversaw the project and contributed to the manuscript.

Correspondence
David V. Smith (david.v.smith@temple.edu)
Department of Psychology & Neuroscience
Temple University

Word Count: 12537
Figure Count: 5

Abstract

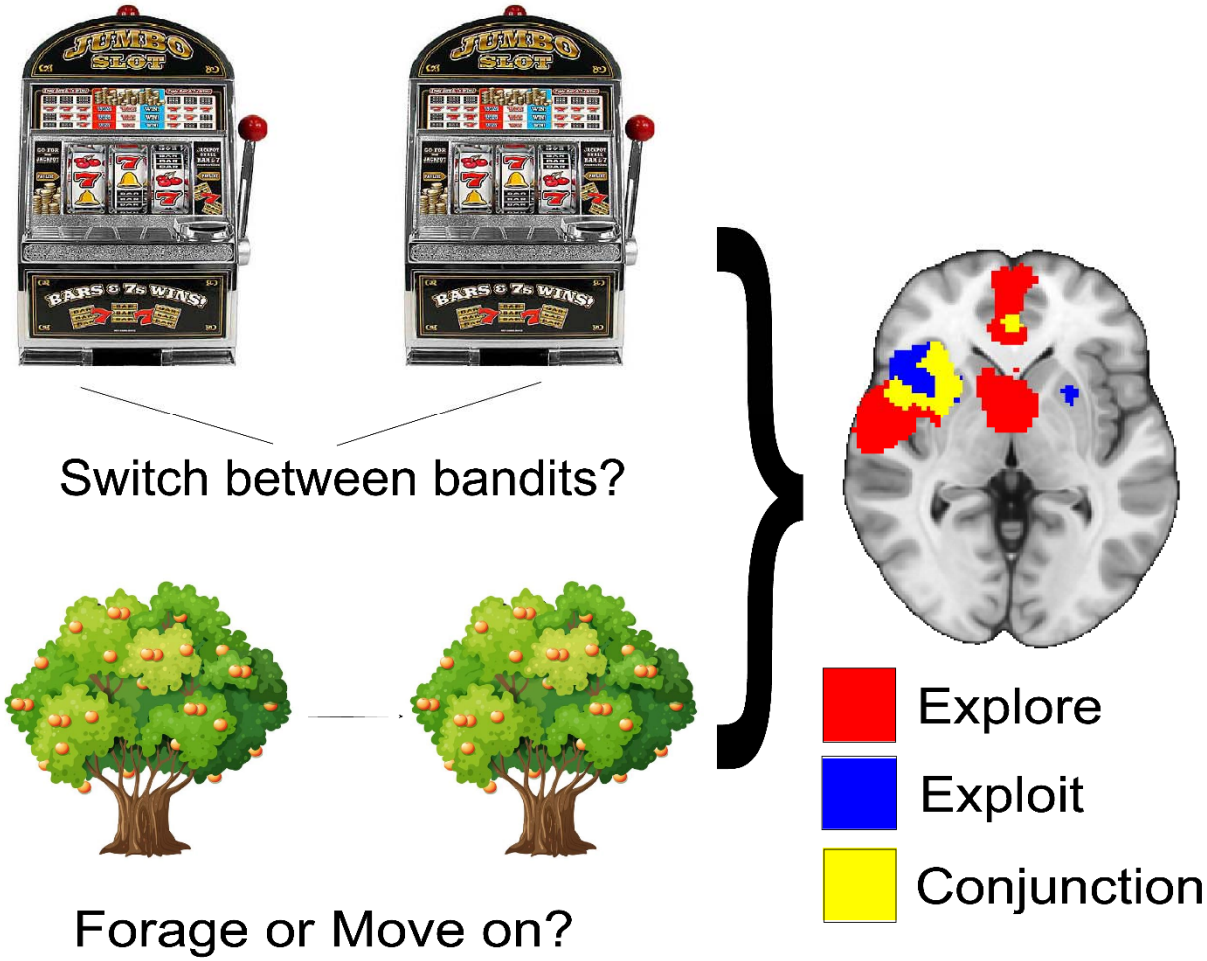
Explore-exploit research faces challenges in generalizability due to a limited theoretical basis for exploration and exploitation. Neuroimaging can help identify whether explore-exploit decisions involve an opponent processing system to address this issue. Thus, we conducted a coordinate-based meta-analysis (N=23 studies) finding activation in the dorsal lateral prefrontal cortex, anterior insula, and anterior cingulate cortex during exploration versus exploitation, which provides some evidence for opponent processing. However, the conjunction of explore-exploit decisions was associated with activation in the dorsal anterior cingulate cortex and dorsal medial prefrontal cortex, suggesting that these brain regions do not engage in opponent processing. Furthermore, exploratory analyses revealed heterogeneity in brain responses between task types during exploration and exploitation respectively. Coupled with results suggesting that activation during exploration and exploitation decisions is generally more similar than it is different suggests that there remain significant challenges in characterizing explore-exploit decision making. Nonetheless, dorsal lateral prefrontal cortex, anterior insula, and dorsal anterior cingulate cortex activation differentiate explore and exploit decisions and identifying these responses can aid in targeted interventions aimed at manipulating these decisions.

Indexing: Exploration, Exploitation, Dynamic Decision Making, fMRI

Abbreviations:

fMRI: Functional Magnetic Resonance Imaging
dlPFC: Dorsal Lateral Prefrontal Cortex
AI: Anterior Insula
ACC: Anterior Cingulate Cortex
dACC: Dorsal Anterior Cingulate Cortex
MCC: Midcingulate Cortex
IPS: Intraparietal Sulcus
vmPFC: Ventromedial Prefrontal Cortex
dmPFC: Dorsomedial Prefrontal Cortex
VS: Ventral Striatum

Graphical Abstract



Graphical Abstract: We conducted a coordinate-based meta-analysis (N=23 studies) where we found activation in the dorsal lateral prefrontal cortex, anterior insula, and the anterior cingulate cortex during exploration versus exploitation. However, the conjunction of explore-exploit decisions was associated with activation in the dorsal medial prefrontal cortex, and the insula, suggesting that these brain regions do not engage in opponent processing. Nonetheless, activation that differentiates explore and exploit decisions and can help in targeted interventions aimed at manipulating these decisions.

1. Introduction

Explore-exploit problems are ubiquitous in many real-world situations such as staying in one line of employment or moving to another, keeping versus selling a stock, or trying out a new ice cream flavor versus sticking with what you know. In situations where a person does not have full knowledge of their opportunities and outcomes, there is a fundamental dilemma of whether to explore the space of possibilities available to them or to exploit what they already know. Due to their prevalence in naturalistic settings, explore-exploit dilemmas have been extensively investigated, with an emphasis on whether certain people are consistently likely to overexploit or underexploit. Over and under exploitation is especially interesting in psychological research as markers of psychopathology, such as among people with anxiety, compulsivity and smoking habits (Aberg and Paz 2022; Merideth A. Addicott et al. 2014; L. S. Morris et al. 2016).

Despite the interest in explore-exploit tasks, generating generalizable insights from decisions made in the lab presents several major challenges. The first challenge is that explore-exploit situations generally involve many independent variables that are difficult to control, such as the hidden payoffs of existing options, the number of options available to the participant, the strategies guiding exploration (random or directed), and the time horizons of the tasks (Wilson et al. 2014). Even simply understanding the payoffs of these choices include a multitude of decision variables such as risk, uncertainty, and ambiguity. Overall, the independent variables investigated, such as uncertainty (Payzan-LeNestour et al. 2013), task difficulty (Lee and Daunizeau 2021), information search (Drugowitsch et al. 2012) suggest explore-exploit decisions are a subset of within a value-based decision-making process. Controlling these independent variables is necessary to assess if exploration and exploitation can be construed as a consistent and useful psychological construct.

Second, is a lack of behavioral convergence across foraging and n-armed bandit tasks (von Helversen et al. 2018), which suggests that exploration and exploitation may not be guided by consistent attitudes. Third, there remains a lack of a unified theory of exploration and exploitation, behaviorally and neurally, as to whether exploration and exploitation are opponent processes, or the result of the interaction of multiple underlying systems. These major questions suggest that reviewing the common features of exploration and exploitation could yield clarity both theoretically and empirically regarding how the field should understand these decisions. Specifically, by assessing common and distinct patterns of activation between exploration and exploitation across n-armed bandit and foraging tasks, it may be possible to identify evidence for whether explore-exploit decisions are dissociable psychological constructs. To do so, we first review extant literature, followed by conducting a coordinate-based (CBMA) meta-analysis to understand which brain regions are involved in exploration and exploitation.

1.1 Understanding Explore-Exploit Decisions Behaviorally

Many tasks have been conceived to isolate explore-exploit decisions, though they mostly fall within two categories: foraging tasks (M. A. Addicott et al. 2017) and n-armed bandit tasks (Cohen, McClure, and Yu 2007; M. A. Addicott et al. 2017; Zhen et al. 2022). These tasks are highly prevalent in explore-exploit research because they have computationally optimal closed-form solutions. In foraging tasks, a participant selects whether to forage from a patch of resources such as an apple tree, or to travel to another patch at some distance from the current patch (Mobbs et al. 2018; Bernstein, Kacelnik, and Krebs 1988; Stephens and Krebs 1986). The optimal strategy is determined by a marginal value theorem (pMVT) which is based on the payoffs within a current patch and the distance to the next patch (Charnov 1976). Foraging

tasks can be modeled through Markov decision processes (Averbeck 2015). In n-armed bandit tasks, the participant decides which slot machine they would like to sample from (Bellman and Kalaba 1957). Explore-exploit decisions are classified through a variety of computational algorithms, such as Boltzmann exploration (softmax), reinforcement learning (Kuleshov and Precup 2000), and can be approximated through Partially Observable Markov Decision Processes (POMDP) (Krishnamurthy and Wahlberg 2009). Ultimately, when the participant chooses bandits higher expected value, the decisions are classified as exploitative and when they choose bandits with lower or unknown expected value, they are classified as explorative (Daw et al. 2006).

While there are canonical foraging and n-armed bandit tasks, there are many other variants of these tasks. One variation of the n-armed bandit task is the Horizon Task which runs for 15, 30, or 45 minutes and was developed to discern if task length affects behavior (Trudel et al. 2020). Another variation of the n-armed bandit is the Leapfrog task where two bandits' values are fixed until the lower value bandit 'leapfrogs' over the higher value bandit at random intervals (Blanco et al. 2016). Variations of foraging also include the Clock Task (Moustafa et al. 2008). Optimal stopping problems such as the Secretary Task (Freeman 1983) are also sometimes grouped as explore-exploit dilemmas. With such a variety of tasks, a critical question is whether the independent variables manipulated within these tasks guide exploration and exploitation, or if general tastes in exploration and exploitation tend to guide behavior. If choices are inconsistent between tasks, then exploration and exploitation should not be conceived as independent constructs, but rather as the interaction of the underlying independent variables. Recent evidence suggests that foraging tasks and n-armed bandits lack behavioral convergence (von Helversen et al. 2018) which suggests that how people explore and exploit in n-armed bandits does not predict how people will explore or exploit in a foraging task. The lack of behavioral convergence between tasks is a major challenge as this suggests that there is a lack of a unifying psychological mechanism underlying exploration and exploitation decisions.

Another approach may be to assess if economic or psychological differences can reliably differences in exploration or exploitation. Investigators have found that the explore-exploit tradeoff was associated information gain and the level of recent rewards (Cogliati Dezza et al. 2017), and that this effect was modulated based on the cognitive load experienced by the participant (Cogliati Dezza, Cleeremans, and Alexander 2019). In the context of temporal discounting problems there have been mixed findings, with one investigation finding associations between temporal discounting and directed exploration and no relationship between temporal discounting and random exploration (Sadeghiyeh et al. 2020) and another study suggesting inconsistent preferences for temporal discounting and exploration and exploitation across multiple studies (Meyers and Koehler 2021). In assessing effects of impulsive behaviors, or risk attitudes, there were no significant associations with foraging decisions though gamblers exhibited more exploratory behavior (Merideth A. Addicott et al. 2015).

Other kinds of individual difference measures have yielded somewhat more robust associations with exploratory or exploitative behaviors. Experiences of lifetime scarcity were related to decreased resource-maximizing decision-making (Chang, Jara-Ettinger, and Baskin-Sommers 2022) and individuals with adverse childhood experiences explored less in a foraging task (Lloyd, McKay, and Furl 2022). Contextual effects in foraging tasks affect the explore-exploit tradeoff, with greater acute stress yielding overexploitation (Lenow et al. 2017), increased arousal associated with increased levels of exploration, and increases in valence substantially increased exploitation (van Dooren et al. 2021). Further, there are associations between psychopathologies and explore-exploit decisions. Some examples include that smokers make less initial exploratory choices (Merideth A. Addicott et al. 2012), people with greater anxiety and depression use lower levels of directed exploration (R. Smith et al. 2021), subjects with alcohol use disorders or binge eating disorders showed decreased exploration

when confronted with losses (L. S. Morris et al. 2016), and people with schizophrenia overuse random exploration strategies (Speers and Bilkey 2023). Taken together, explore-exploit tasks have been applied in a variety of psychological domains, yielding little consistency in terms of economic decisions, though people with maladaptive psychological or psychiatric attributes have an attenuated ability to optimize these decisions.

1.2 Neurobiological Mechanisms of Exploration and Exploitation

Explore-exploit tasks lack behavioral convergence, contain a multitude of possible independent variables, and lack a coherent theory as to whether exploration and exploitation are products of disparate versus unified mechanisms. Given the lack of clarity regarding the constructs and behaviors guiding explore-exploit decisions, another approach could examine the neurobiological factors that are consistent across explore-exploit choices. One notable challenge that could be observed neurobiologically is if explore-exploit tasks elicit a consistent or disparate set of responses during exploration versus exploitation (Cohen, McClure, and Yu 2007) *(see Figure 1).* If exploration and exploitation elicit reliably different patterns of activation across various tasks, it could provide a window into the mechanisms may modulate explore-exploit decisions through an opponent processing system. Over the past two decades, the accumulation of neuroimaging studies conducted in explore-exploit tasks suggests that reviewing these common patterns may provide insight into explore-exploit decision making as a whole.

Explore-exploit decisions in neuroscience have identified several key cortical and subcortical brain regions that contribute to these choices (Dennison, Sazhin, and Smith 2022). In animal literature, the Anterior Cingulate Cortex (ACC) has been identified as a major modulator of explore-exploit decisions. Versions of the n-armed bandit task have been adapted for rats and mice using n-armed radial mazes (Ohta et al. 2021). ACC activation has been linked to foraging in rats through an adapted patch foraging task (Kane et al. 2022) and a two-armed bandit monkey lesion study (Kennerley et al. 2006). Similarly, the dACC is tied to both exploration and exploitation in a monkey foraging task (Ramakrishnan, Hayden, and Platt 2019; Hayden, Pearson, and Platt 2011). Nonetheless, other findings suggest that the ventral striatum (VS) and amygdala represent immediate and future value of exploratory choices respectively in rhesus monkeys (Costa, Mitz, and Averbeck 2019). In human neuroimaging studies, there are some commonly cited areas of activation in brain regions associated with cognitive control (dlPFC), reward (VS), and attention (ACC), which are often used in region of interest (ROI) analyses (Shenhav et al. 2014; Wiehler, Chakroun, and Peters 2021; Hogeveen et al. 2022).

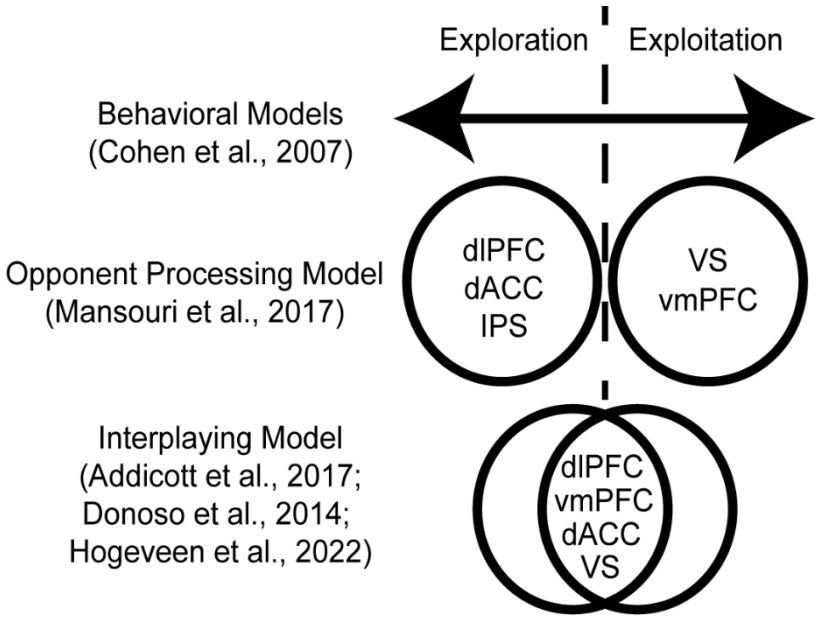


Figure 1: Models of exploration and exploitation. Behavioral models of explore-exploit decisions envision an optimal set of decisions, with people expressing tendencies to over or underexploit on a continuum of possible options. Nonetheless, the underlying mechanisms may be a binary or opponent processing model, where people are either exploring or exploiting, with corresponding brain activation. Another model suggests that exploration and exploitation is the product of the interplaying of underlying variables, where all the brain regions are involved in both exploration and exploitation, though may work together more or less depending on the explore-exploit situation.

1.3 Evidence for Models of Exploration and Exploitation

While it is known that an array of brain regions is involved in explore-exploit decisions, it remains a key challenge to understand how these brain regions respond to dynamic environments. Two major accounts explain explore–exploit behaviors, which are the interaction of several neural regions depending on contextual features of the explore-exploit decision (e.g., dACC, dorsal striatum, lateral PFC, and VS; Donoso et al., 2014), or a dual-system driven by opponent processes of exploration and exploitation in frontoparietal regions (e.g., dlPFC, **d**ACC, IPS vmPFC and VS; Mansouri et al. 2017; Hogeveen et al. 2022) (*see Figure 1)*. If exploration and exploitation are generally more context-dependent rather than dissociable constructs, there may be less consistency in activation across these decision phases and across tasks. Instead, clusters of brain regions may work together depending on the task or context resulting in exploration or exploitation behavior (Addicott et al., 2017, Donoso et al., 2014, Hogeveen et al., 2022). With this interpretation, exploration and exploitation behaviors may be more context specific, and could potentially better described by underlying variables such as the risk, uncertainty, information, time horizons or other variables involved in the decision-making process. Thus, an interplayed model may be the combination of underlying psychological constructs in a given situation. Nonetheless, one challenge of an interplayed model is that there could also be a more complex set of responses to exploration or exploitation, potentially represented through connectivity patterns in the brain. It is also plausible that exploration and exploitation can be construed as opponent processes with concrete neural markers that reliably

switch between exploration and exploitation (Mansouri et al., 2017). If this model has greater support, exploration and exploitation would be dissociable across tasks with consistent neural markers of activation. Furthermore, if there is evidence of opponent processing in exploration and exploitation this could allow for targeted interventions aimed at modulating these behaviors.

In trying to reconcile these accounts, studies tease apart how certain elements of explore-exploit dilemmas contribute to those decisions. For instance, understanding how environmental uncertainty and trends in information mediate this process may inform some of the underlying mechanisms in explore-exploit choices, with environmental uncertainty of new options (Badre et al. 2012; Navarro, Newell, and Schulze 2016; Tomov et al. 2020) seemingly largely processed in the PFC. Uncertainty in an environment has been represented in the brain in several ways, with relative uncertainty in the right rostrolateral PFC (Badre et al. 2012) and striatal dopamine function (Frank et al. 2009) driving directed exploration. The vmPFC was implicated in representing environmental uncertainty (Trudel et al. 2020), evidence accumulation in switching decisions (Blanchard and Gershman 2018), and determining the value of well-defined foraging options (Kolling et al., 2012). Taken together, these findings reinforce the importance of both frontopolar and subcortical regions in explore-exploit decisions, though it remains unclear to what degree an opponent process model driven by the frontoparietal cortex is supported by the weight of the evidence.

In sum, the current state of knowledge is limited in identifying consistent elements supporting neural circuitry associated with explore-exploit decisions, whether there are systematic biases in the literature, and if certain brain regions remain underemphasized in the reporting and interpretation of the data. One means of addressing these limitations is through quantitatively assessing patterns of activation across neuroimaging studies using coordinate-based meta-analyses (CBMA). We hypothesized that there would be convergence across explore-exploit studies in the activation of the vmPFC, dlPFC, VS, ACC, and IPS during explore-exploit decisions. These decisions are differentiated from the feedback phase where participants receive rewards based on their decision. While the feedback phase can provide important information for encoding the value of current and alternative outcomes while receiving feedback (Boorman, Rushworth, and Behrens 2013; Tsujimoto, Genovesio, and Wise 2011) the feedback phase does not completely capture the decision to shift choices on the following turn. Next, we expected that the exploitation versus exploration decision would be associated with greater vmPFC, VS, ACC activity in the exploration phase and that the exploration phase would be associated with greater activation in the IPS and dlPFC than in the exploitation phase. We speculated that the ACC could reflect an important role during exploitation through conflict monitoring (Weissman et al. 2003; Kim, Kroger, and Kim 2010; Mansouri et al. 2017) as exploitation involves decisions when to switch back to exploration. Thus, we expected that exploitation may reflect other processes beyond simply reward consumption since there is a routine opportunity to revert back to exploration. The act of monitoring this tradeoff and avoid over-exploiting could be a result of ACC conflict monitoring.

Since we began this investigation, two groups of researchers have conducted meta-analyses of explore decisions (Zhen et al. 2022), finding that exploration results in consistent activation of the dorsal medial prefrontal cortex and anterior insula, dorsolateral prefrontal cortex inferior frontal gyrus, and motor processing regions. (Wyatt et al. 2024). We extend these results by comparing exploration versus exploitation with a larger sample of studies and investigating task-based differences between exploration and exploitation using Seed-based D Mapping (SDM) software. Including the contrast between exploration and exploitation serves as a crucial means to subtract the effects of value-based decision making in order to understand activation that is unique to exploration and exploitation. Another group argued that prefrontal and parietal circuits integrate and switch between exploration and exploitation. Our approach differs from (Wyatt et al. 2024) in that we conducted a quantitative rather than qualitative meta-

analysis, with regions identified subsequent to conservative thresholding and permutation testing. Overall, our results aims to identify activation patterns that are unique to exploration and exploitation, thereby helping identify to what degree we can theoretically understand these choices within an opponent processing model. We also explore activation differences between n-armed bandits and other types of explore-exploit tasks while making exploration or exploitation decisions. In summary, we investigate the common patterns of activation across explore-exploit tasks, whether there are systematic biases in the literature, and if there are other regions that are underemphasized in the interpretation of the data.

2. Materials and Methods

2.1 Inclusion Criteria and Study Selection

The current coordinate-based meta-analysis primarily followed PRISMA guidelines for meta-analyses regarding inclusion criteria, filtering, and analyses (Moher et al. 2009). We incorporated a pre-registration (https://aspredicted.org/7hc7c.pdf), which detailed the hypotheses and analyses we intended to use. We conducted a systematic literature search to identify explore-exploit studies that used neuroimaging techniques. First, we identified search terms by examining task names from several existing explore-exploit literature reviews (Cohen, McClure, and Yu 2007; M. A. Addicott et al. 2017; Zhen et al. 2022). Potentially eligible studies published through 1/01/2023 were identified by searching the PUBMED using the grouped terms: (n-armed OR exploration-exploitation OR explore-exploit OR multi-armed OR forage OR foraging OR "reward rate" OR (explore AND exploit) OR "reward trend" OR "clock task" OR clock-task OR "temporal-difference" OR "patch leaving" OR patch-leaving OR leave-stay OR "time horizon" OR "horizon task" OR bandit OR MVT OR "marginal value theorem" OR leapfrog OR "leap frog" OR leap-frog OR prey model OR "diet breadth model" OR "web surfing task" OR "web-surfing task" OR trend-guided OR "uncertainty driven") AND (fMRI OR “functional magnetic resonance imaging” OR neuroimaging OR brain OR neural OR MNI OR “Montreal Neurological Institute” OR Tal OR coordinates). To enhance search sensitivity, the reference lists of the retrieved articles and review papers were further checked to identify potentially relevant articles. Additionally, we included studies that reported whole-brain analyses, as region of interest based analyses can bias coordinate-based meta-analyses (Moher et al. 2009) and were thus excluded. Finally, we incorporated studies that reported coordinates in a standard stereotactic space [i.e., Talairach or Montreal Neurological Institute (MNI) space]. The search process was conducted by Avi Dachs, with the first author identifying the studies accepted for final inclusion in the meta-analysis. For eligible studies that did not report whole-brain data, we contacted authors if the required information was unavailable in the published reports.

The initial PUBMED search yielded 6,214 papers. Of these, 5,256 papers were then excluded based on title, leaving 958 papers to be excluded by abstract and full text contents. Of the 958 remaining papers, 762 papers were excluded for not covering explore and exploit tasks, 72 relevant papers were excluded for not collecting fMRI data, 45 animal studies were excluded, and 14 non-empirical papers were excluded, leaving only 65 papers for data extraction and coding (see Figure 2). In the coding phase, 47 more papers were excluded due to data that were incompatible with our analysis (i.e., not fMRI or whole-brain), leaving a total yield of 19 papers. Finally, our list of papers was cross-referenced with the papers included in a similar meta-analysis (Zhen, 2022) revealing 4 papers that had been wrongly excluded from our search. After these papers were added, our final corpus included 23 papers with a cumulative N of 602 participants (see Figure 2 and Table 1). In total, we included 13 n-armed bandit studies, which varied in the number of bandits presented to the participant. We identified foraging tasks and 3 other tasks, including a problem-solving task, clock hand task, web surf task, and an

observe-bet task. We grouped non-n-armed bandit tasks into an “other” category with a total of 10 studies to serve as a comparison group. Unlike n-armed bandits, the “other” tasks do not employ feedback about exploration or exploitation on each turn. Foraging, web-surf, and observe-or-bet tasks have clear shifts between exploration and exploitation based on observable changes in strategy. The clock hand task employs a fixed reward structure which is learned over time and exploration and exploitation is classified based on response times (M. A. Addicott et al. 2017). Thus, we classify tasks that do not have a continuous sequence of changing rewards as “other” types of exploration and exploitation tasks. Further, n-armed bandits involve *inferred* shifts to exploitation, whereas foraging tasks have distinct shifts from exploiting to traveling to other patches (Barack 2024). While both n-armed bandit and foraging tasks are grouped as explore-exploit tasks, they are sufficiently different to serve as potential comparison groups.

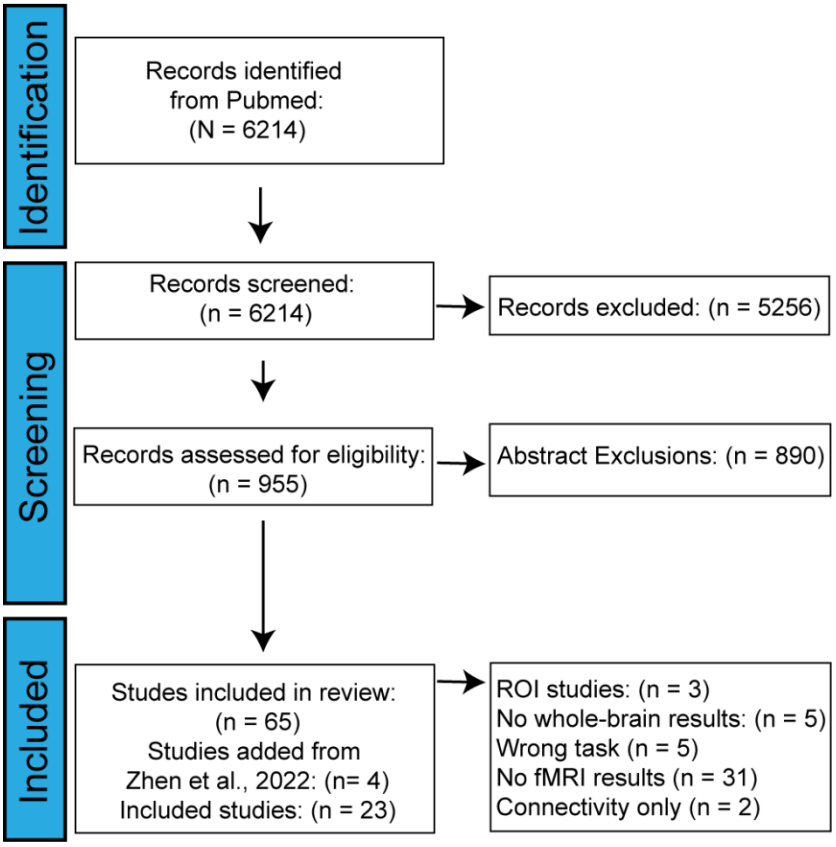


Figure 2: Inclusion criteria. Using the PRISMA flowchart system, we report the studies we identified, screened, and included in the meta-analysis. After we completed our initial search, four more studies identified by another meta-analysis (Zhen et al., 2022) that assessed activation during exploration. Starting from an initial search of 6,214 studies, we included n = 23 studies in our analyses.

Table 1: Included studies. N = 23 studies were included for the meta-analysis during explore-exploit decisions, and for the study of activation during exploration and exploitation specifically.

Paper	Program	Threshold	N	Age	Females	Task
Aberg et al., 2022	SPM	0.001	28	27.6	20	3-armed bandit
Abram et al., 2019	FSL	0.05	25	28.0	12	web-surf task
Addicott et al., 2014	SPM	0.005	22	36.0	NA	6-armed bandit
Amiez et al., 2012	AFNI	0.05	11	27.9	6	4-armed bandit
Badre et al., 2012	SPM	0.001	15	20.0	8	clock hand task
Blanchard & Gershman, 2018	SPM	0.001	18	26.0	11	observe-bet
Chakroun et al., 2020	SPM	0.05	31	26.9	0	4-armed bandit
Daw et al., 2006	SPM	0.001	14	NA	NA	4-armed bandit
Donoso et al., 2014	SPM	0.005	40	18-26	20	4-armed bandit
Dunne et al., 2016	SPM	0.005	17	23.3	9	2-armed bandit
Howard-Jones et al., 2020	SPM	0.001	16	25.5	8	4-armed bandit
Kolling et al., 2012	FSL	0.05	20	22-32	12	foraging
Korn et al., 2018	SPM	0.001	28	23.5	13	foraging
Korn et al., 2019	SPM	0.001	24	25.0	11	foraging
Laurerio-Martinez et al., 2014	SPM	0.05	50	35.1	11	4-armed bandit
Laurerio-Martinez et al., 2015	SPM	0.05	63	35.2	11	4-armed bandit
Mobbs et al., 2013	SPM	0.05	15	25.0	10	foraging
Seymour et al., 2012	SPM	0.001	30	NA	NA	4-armed bandit
Tomov et al., 2020	SPM	0.001	31	18–35	17	2-armed bandit
Trudel et al., 2020	FSL	0.05	24	25.6	14	2-armed bandit
Wang and Voss., 2014	AFNI	0.05	42	18-35	22	foraging
Wittman et al., 2016	FSL	0.05	20	21–32	8	foraging
Zacharopoulos 2018	SPM	0.001	18	18-37	11	foraging

2.2 Statistical Analysis

We conducted a CBMA meta-analysis using Seed-based d mapping software (SDM-PSI version 6.22). SDM was implemented using several steps to conduct analyses described in the SDM tutorial and manual. First, we imported the screened data by preparing folders with MNI text files that reported the clusters and t values for each coordinate. Files were named in accordance with SDM guidelines, which requires specifying if the coordinates were derived from FSL, SPM, or “other” software, and whether the coordinates were in MNI or Talairach space. For studies that reported Talairach coordinates, these results were automatically converted Talairach inputs into MNI space for subsequent analyses. Exploration and exploitation decisions were grouped based on the constructs reported in each study. 11 studies reported explore>exploit and exploit>explore contrasts and were coded as exploration and exploitation respectively (see Table 2). Other studies reported parametric effects for exploration and

exploitation decisions (see Table 2) through assessing several components underlying value-based decisions in uncertain environments. Studies modulated uncertainty (Badre et al. 2012; Trudel et al. 2020), relative value (Howard-Jones et al. 2010), task difficulty (Abram et al. 2019), search evidence, and search cost across decision stages (i.e.., exploration in Stage 1 and exploitation in Stage 2) (Zacharopoulos et al. 2018). We classified reinforcement learning associated with recent experience as exploration (Dunne, D'Souza, and O'Doherty 2016). Another variation of reinforcement learning included assessing exploitation as the last average reward rate, whereas exploration reflecting the expected values associated with learning past reward rates (Wittmann et al. 2016). Another study coded foraging value-decision value contrast for exploration and search value-decision value contrast for exploration (Kolling et al. 2012).

Another study varied the parametric value of staying with a foraging patch whereas exploration was classified as the difference in decision versus consumption (Abram et al. 2019). Switch-in events were classified as exploration and activation associated with actor absolute reliability as exploitation due to the behavioral design (Donoso, Collins, and Koechlin 2014). Other studies varied the presence or absence of newly available information (Wang and Voss 2014), and the advantageousness of the environment (Mobbs et al. 2013). In another study, the modeled choice kernel reflected exploratory decisions (Seymour et al. 2012). These classifications of exploration and exploitation reflect the coordinates selected for analysis and are accessible on OSF. Overall, the parametric effects generally reflected sensitivity to value, information, or uncertainty while exploring or exploiting an uncertain environment.

Table 2: Reported contrasts. Some studies reported explore>exploit and exploit>explore contrasts, which were coded as exploration and exploitation respectively. Others reported parametrically modulated effects. The classification of those modulators as exploration and exploitation is described in the methods section. The t-threshold identified for each study is reported, which was determined by the threshold identified in the analyses conducted by each study and their respective sample size.

Paper	T -threshold	Contrasts
Aberg et al., 2022	3.6459	Explore>Exploit
Abram et al., 2019	2.0639	Parametric Modulator
Addicott et al., 2014	3.1352	Explore>Exploit
Amiez et al., 2012	2.2282	Explore>Exploit
Badre et al., 2012	4.1404	Parametric Modulator
Blanchard & Gershman, 2018	3.9216	Explore>Exploit
Chakroun et al., 2020	2.0423	Explore>Exploit
Daw et al., 2006	4.2208	Explore>Exploit
Donoso et al., 2014	2.0227	Parametric Modulator
Dunne et al., 2016	3.252	Parametric Modulator
Howard-Jones et al., 2020	4.0728	Parametric Modulator
Kolling et al., 2012	2.093	Parametric Modulator
Korn et al., 2018	3.6896	Explore>Exploit
Korn et al., 2019	3.7921	Explore>Exploit
Laurerio-Martinez et al., 2014	2.0096	Explore>Exploit
Laurerio-Martinez et al., 2015	1.999	Explore>Exploit
Mobbs et al., 2013	2.1448	Parametric Modulator
Seymour et al., 2012	3.6594	Explore>Exploit
Tomov et al., 2020	3.6459	Parametric Modulator
Trudel et al., 2020	2.0686	Parametric Modulator
Wang and Voss 2014	1.68	Parametric Modulator
Wittman et al., 2016	2.093	Parametric Modulator
Zacharopoulos 2018	3.9651	Parametric Modulator

Next, we created an SDM table with all the respective peak coordinates. We noted t-stats in the SDM table with respect to effect sizes and converted reported p and z stats using the SDM "convert peaks" function (see Table 2). Then, we completed preprocessing using Functional MRI as its modality, with a gray matter correlation matter template following validated methods (Albajes-Eizagirre et al. 2019; J. Radua et al. 2012). We used a 1.0 anistropy setting, a 20 mm FWHM isotropic kernel, a gray matter mask, and a standard 2mm voxel size. This was followed by a mean analyses with 50 imputations (Joaquim Radua and Mataix-Cols 2009). To compare exploration and exploitation decisions, and n-armed bandit versus other tasks, we generated linear models respectively where we compared these groups by assigning a linear model analysis (Joaquim Radua et al. 2010). We used the SDM meta-regression tool with prediction dummy variable {exploit=1, explore=0} and {n-armed=1, other=0} for the positive side of the significance test. These models thus contrasted exploit with explore conditions and n-armed

bandit with other tasks respectively, with a 1 selected for the contrast of interest in the SDM model. Additionally, we included several nuisance regressors to control potentially confounding variables, specified as a “0” in the SDM linear model. Specifically, we included analysis type (parametrically modulated = 1, unmodulated = 0) and the smoothing kernel size (Sacchet and Knutson 2013). We included these nuisance regressors to ensure that analysis type was not a confounding variable and since the size of the smoothing kernel can move the observed activation anterior or posterior of the brain.

Subsequently, we performed family wise error corrections and using n=1000 permutations (Albajes-Eizagirre et al. 2019). This correction controls for multiple comparisons by randomly swapping the effect-sizes between the voxels for each study, recalculating the means of the studies for each voxel and saving the maximum of the means (Albajes-Eizagirre et al. 2019). The results were then thresholded using threshold-free cluster enhancement (TFCE) with a corrected probability threshold of $p < 0.05$ (S. M. Smith and Nichols 2009). TFCE has also been shown to have a sensitivity comparable to a Family Wise Error correction and yield valid results with only about five percent of significant clusters based on spurious convergence across 200,000 simulated meta-analyses (Frahm et al. 2022). TFCE statistics are generally neither too liberal or conservative and have been used across many meta-analyses (Albajes-Eizagirre et al. 2019; Masson et al. 2021; Sheng et al. 2020). Masks were created and their values were extracted for reporting. For the conjunction of explore and exploit conditions, we conducted a CBMA of explore and exploit conditions respectively, and then used the multimodal function provided by SDM to produce the conjunction map.

To assess potential heterogeneity and potential bias in the CBMA results, we extracted funnel plots. We report the strength of evidence through multiple robustness considerations, study heterogeneity (I^2 statistic), effect of small studies on the results (metabias) with resulting funnel plot asymmetry, and excess significance. The funnel plots are constructed through assessing the residual, or the weight each study has in the meta-analysis, with the size of its treatment effect, identified as precision on the y axis, though these tests must be interpreted with caution as publication bias can arise from multiple sources (Sterne et al. 2011). All analyses were completed in Montreal Neurological Institute (MNI) space. To report consistent results across human brains (Mazziotta et al. 1995), we show probabilistic anatomical labels for clusters of activation using the Harvard–Oxford cortical and subcortical atlases (Desikan et al. 2006).

3. Results

We completed meta-analyses that assessed activation across explore-exploit tasks, followed by activation specific to exploration and exploitation. All meta-analyses controlled the size of the smoothing kernel, as well as whether the analyses reported were parametrically modulated or unmodulated. The first meta-analysis investigated activation pooling across both exploration and exploitation conditions and is reported in *Supplementary Results.* Next, we assessed the contrast between exploration and exploitation. Subsequently, we report activation that is consistent across both exploration and exploitation. Lastly, we show exploratory results revealing activation that is greater among n-armed bandit tasks versus other tasks during exploitation and exploration.

3.1 Neural Responses Between Exploration versus Exploitation Phases

We conducted a CBMA contrasting the exploration and exploitation conditions across all the explore-exploit tasks. We hypothesized that the exploitation phase would be associated with greater vmPFC, VS, ACC activity than the exploration phase. We did not find any significant clusters for exploitation versus exploration that exceed a threshold of $p < .05$. Next, we hypothesized that the exploration phase would be associated with greater activation in the IPS and dlPFC than in the exploitation phase. Our results indicated five significant clusters of activation in the dorsolateral prefrontal cortex, right dorsal anterior cingulate cortex, anterior insula, and superior temporal gyrus *(see Figure 3, Table 3)*. Using the Harvard-Oxford Atlas, our results were consistent with our hypotheses in finding stronger activation in the dlPFC during exploration versus exploitation. NeuroSynth was used to confirm anatomical localization, in conjunction with direct anatomical references from prior literature. We verified our anatomical labels for the centroids of the clusters using NeuroSynth with the first cluster (24,2,60) being associated with the term “dorsal premotor” (z = 7.55), second cluster (10,22,40) associated with the term “anterior cingulate cortex” (z = 7.96) and “dacc” (z= 4.96), the third cluster (34,22,6) being associated with the term “anterior insula” (z = 10.39), the fourth cluster (58,0,0) term associated with “superior temporal” (z = 7.13) and the fifth cluster (32,36,26) associated with the term “dorsolateral” (z=4.19). We followed up with analyses of metabias and excess significance, finding no significant metabias or excess significance for this CBMA.

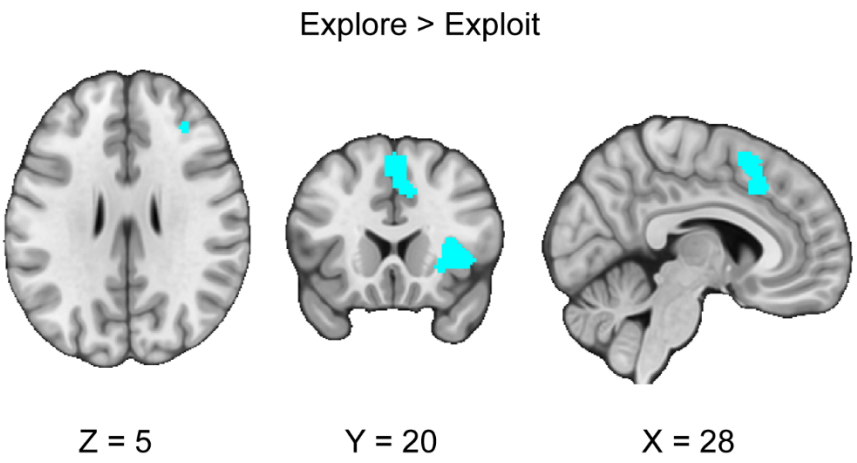


Figure 3. Clusters of activation in the contrast between explore versus exploit phases. Our results indicated that during the exploration versus exploitation phases, we found stronger activation in the dlPFC, AI and dACC, and the superior temporal gyrus. Maps were thresholded using TFCE at *p*=.05 and rendered in MRIcroGL. Thresholded (https://neurovault.org/images/888157/) and unthresholded (https://neurovault.org/images/888156/) images are available at Neurovault.

Table 3: Reported clusters of activation across meta-analyses conducted. Confirmatory analyses conducted according to the pre-registration include the explore and exploit conditions and assessing their respective conjunctions and contrasts. Exploratory analyses were conducted on n-armed bandit versus other tasks. Coordinates are reported in Montreal Neurological Institute (MNI) space.

Analysis Type	MNI coordinate	SDM-Z	P	Voxels	Cluster Location
Confirmatory					
Explore > Exploit	24,2,60	-4.784	0.001	1310	Right superior frontal gyrus, dorsolateral, BA 6
	10,22,40	-3.03	0.012	838	Right median cingulate / paracingulate gyri, BA 32
	34,22,6	-2.994	0.013	596	Right insula, BA 48
	58,0,0	-2.882	0.24	266	Right superior temporal gyrus, BA 48
	32,36,26	-4.205	0.02	41	Right middle frontal gyrus, BA 46
Exploit < Explore	Null				
Exploratory					
N-armed > Other (Exploit)	Null				
Other > N-armed (Exploit)	4,34,44	-4.296	0.003	475	Right superior frontal gyrus, medial, BA 8
	30,24,4	-4.468	0.003	352	(undefined), BA 47
N-armed > Other (Explore)	Null				
Other > N-Armed (Explore)	Null				

3.2 Neural Responses to the Conjunction Between Exploration and Exploitation Phases

We conducted a conjunction analysis across exploration and exploitation in the sample of studies we collected. We hypothesized that the conjunction of explore and exploit phases would be associated with activation in the IPS, dACC, and dlPFC. Supporting our hypothesis, we found common activation in the dACC in the conjunction between exploration and exploitation decisions *(see Figure 4).* Activation in exploration and exploitation elicits common activation across multiple regions with a correlation of r = .62 across the unthresholded explore and exploit images. These results suggest that areas of common activation should in the future be closely examined using multivariate and connectivity methods to understand how they are involved in exploration and exploitation. In contrast to our hypothesis, we did not find convergence in the IPS or dlPFC. We also found conjunctive patterns of activation in the dmPFC and anterior insula.

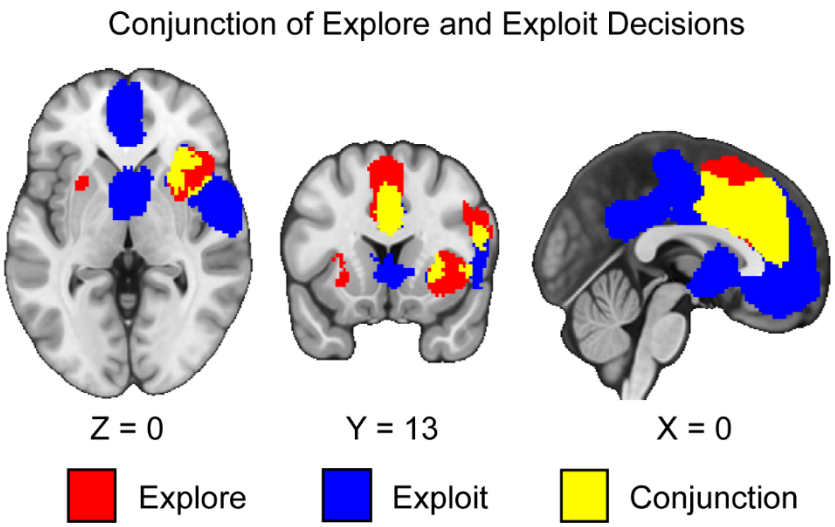


Figure 4. Clusters of activation in the conjunction of explore and exploit decisions. Our results indicate that during both explore and exploit phases, there is activation in the ACC, dmPFC, and the insula. Maps were thresholded using TFCE at *p*=.05 and rendered in MRIcroGL. Red corresponds to activation during exploration, blue during exploitation, and yellow for the conjunction between both decisions. Thresholded images are available at https://neurovault.org/images/888159/, https://neurovault.org/images/888160/, and https://neurovault.org/images/888161/. Unthresholded images are available at https://neurovault.org/images/888167/, https://neurovault.org/images/888168/, and https://neurovault.org/images/888169/.

3.3 Differential Activation Between N-Armed versus Other tasks During Exploration and Exploitation

We followed up our pre-registered hypotheses by assessing if there are differences between activation in n-armed bandit tasks compared to other tasks during exploration and exploitation. If there are activation differences between tasks, this may suggest that these tasks are not eliciting consistent patterns of activation in exploration and exploitation as may be expected. During exploration, we did not find any activation differences between n-armed bandits and other tasks. During the exploitation phase, we found that other tasks versus n-armed bandits resulted in two significant clusters (*see Table 3, Figure 5*). There was no reported excess significance, or metabias in the results ($p > .001$).

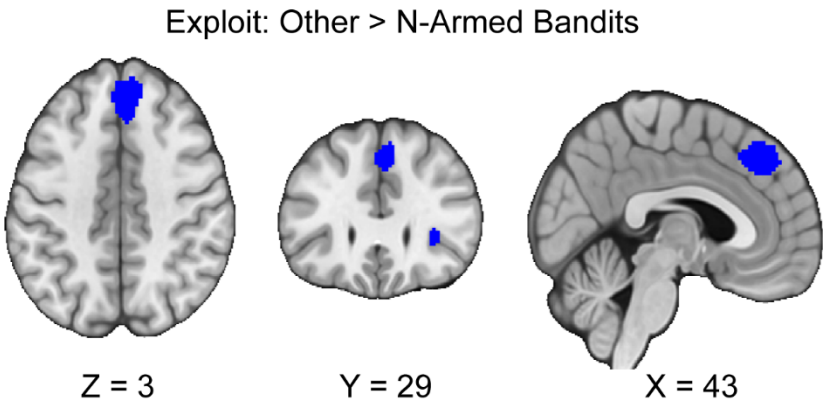


Figure 5. Clusters of activation during exploitation, between other tasks and n-armed bandits. Our results indicate that there are differences in activation between tasks during exploitation. We found that there was greater activation in the dmPFC and AI when participants exploited in other tasks versus n-armed bandits. Maps were thresholded using TFCE at *p*=.05 and rendered in MRIcroGL. Thresholded images are available at Neurovault: https://neurovault.org/images/888163/. Unthresholded images are available at Neurovault: https://neurovault.org/images/888162/, https://neurovault.org/images/888164/, https://neurovault.org/images/888165/, and https://neurovault.org/images/888166/.

4. Discussion

This investigation conducted a coordinate-based meta-analysis of explore-exploit tasks. We included both n-armed bandit and other types of explore-exploit tasks and analyzed them to assess patterns of activation that are consistent across explore-exploit decisions, as well as unique to exploration and exploitation decisions respectively, and differences in activation between tasks. First, we found consistent activation unique to exploration and exploitation decisions, with activation in the dlPFC, vmPFC, ACC, IPS, dmPFC, and VS. These results suggest that exploration and exploitation generally evoke activation associated with value-based decision-making (Bartra, McGuire, and Kable 2013; Rangel, Camerer, and Montague 2008), although it does not control for activation unique to these individual decision phases. This suggests that while these regions are commonly recruited, their precise role may differ between exploration and exploitation. Second, we found greater activation in the dlPFC, dACC, and the AI during exploration versus exploitation. Third, we conducted an exploratory analysis to assess differences between n-armed bandits and foraging tasks during exploration and exploitation respectively. We found differences in activation in the AI and dmPFC between other tasks and n-armed bandit tasks during exploitation. Overall, our meta-analytic results support previous findings that have identified critical regions involved in exploration and exploitation.

4.1 Opponent Processing versus Interplaying Models of Exploration and Exploitation

When we investigated the contrast between exploration and exploitation, we found stronger activation in the dlPFC, AI, and dACC during exploration compared to exploitation, suggesting that these regions are part of opponent processes in explore-exploit decisions. These results are consistent with past findings (Laureiro-Martínez et al. 2014), suggesting that the dlPFC may contribute to tracking the value of alternative choices (Laureiro-Martínez et al. 2015; Raja Beharelle et al. 2015), attending to risk (Obeso et al. 2021), tracking uncertainty (Chakroun et al. 2020; Tomov et al. 2020), and guiding directed exploration (Zajkowski, Kossut, and Wilson 2017). Additionally, as the dlPFC is implicated in cognitive control (Friedman and Robbins 2022), dlPFC activation may affect working memory as it relates to information gain and integrating recent rewards (Cogliati Dezza, Cleeremans, and Alexander 2019; Cogliati Dezza et al. 2017).

The AI subserves several notable computational mechanisms that are relevant for exploration and exploitation. Overall, the AI has been found to respond more strongly exploration versus exploitation (Kayser et al. 2016; Ohira et al. 2013; Tomov et al. 2020; Blanchard and Gershman 2018). Two recent accounts suggest that the AI could be processing risk (Zhen et al. 2022), or could serve as part of a broader salience network during exploration (Hogeveen et al. 2022). While the AI serves an important role within valuation processing (Bartra, McGuire, and Kable 2013), other studies have indicated that the AI is stronger activated with the sudden introduction of reward structures rather than stable reward systems (Li et al. 2006). Thus, while the AI is involved in risk processes (Preuschoff et al., 2011; Smith et al., 2014), its role may involve orienting the dACC and dlPFC toward changes in valuations related to risk and uncertainty.

Contrary to our expectations, we found that the dACC was more activated during exploration versus exploitation. The dACC may contribute to exploration versus exploitation by tracking trends in foraging tasks (Wittmann et al. 2016; Kolling et al. 2012), feedback processing (Kolling et al., 2016) preparing movement away from disadvantageous foraging patches (Mobbs et al. 2013), with more self-focused individuals showing lower activity in dACC compared to

individuals who were foraging for others (Zacharopoulos et al. 2018), and evaluating salient feedback for learning optimal strategies (Amiez et al. 2012). The interpretations emphasizing the role of the dACC in foraging may be confounded as one investigation found that dACC engagement was explained by choice difficulty, and not the value of foraging (Shenhav et al. 2014). This account is further complicated by that recent in rhesus monkeys suggests that choice difficulty does not influence local field potentials in the dACC (Goussi-Denjean et al. 2023).These mixed findings suggest that the role of the dACC is difficult to categorize precisely given its heterogeneity in function across many cognitive processes. We judge that our results are consistent with the prefrontal and parietal circuits integrating and switching between exploration and exploitation (Hogeveen et al. 2022; Wyatt et al. 2024). Integrating the roles of the dlPFC, AI and dACC in regulating exploration versus exploitation is also consistent with recent findings suggesting that these regions could be part of a circuit that modulates strategic decisions (Jahn et al. 2023). Overall, our results broadly support the account that greater dlPFC, AI, and dACC activation during exploration versus exploitation can be characterized through opponent processes, though there are challenges in inferring the precise functions of each region during explore-exploit decisions.

We further acknowledge that while the center of the second cluster described captures the dACC, it also extends into the midcingulate cortex, and supplementary motor areas (Wagera et al. 2016). While the spatial resolution of CBMAs using FWER correction is relatively low, the cluster may potentially be reflecting activation and resulting processes outside of the dACC. Some studies indicate that the MCC is involved in attention processing (Touroutoglou et al. 2020), feedback processing, pain, salience, action-reward association, premotor functions, and conflict monitoring (Procyk et al. 2016). Additionally, SMA or dmPFC function could facilitate state change decisions by tracking reward rate over time (Kolling and O'Reilly 2018), and tracking reward magnitudes (Vural, Katruss, and Soutschek 2024). Thus, while the second cluster is consistent with past studies that have indicated the role of the dACC during exploration versus exploitation, this cluster may also be capturing several additional processes involved in explore-exploit decisions.

In contrast to recent meta-analyses (Wyatt et al. 2024; Zhen et al. 2022), our results suggest that many brain regions involved in value-based decision making are coactivated across both exploration and exploitation rather than evoking distinct patterns of activation. For example, our results suggested that the dorsal medial prefrontal cortex and premotor cortex (Zhen et al., 2022) were involved in both exploration and exploitation. While these brain regions may be involved in exploration, by subtracting activation related to exploitation we show that these other brain regions may be simply involved in the overall value-based decision process (Rangel, Camerer, and Montague 2008) rather than being unique to exploration. Additionally, while the qualitative approach taken by Wyatt and colleagues indicated that the IPS and Precuneus have greater activation during exploration and exploitation, our quantitative analyses indicate that many of these regions fail to survive thresholding and are generally sensitive to both exploration and exploitation. Thus, while we agree with a recent empirical work that control and attention networks are involved in exploration (Hogeveen et al. 2022), our results suggest that more precisely that greater activation in the dACC, AI, and dlPFC differentiates exploration and exploitation decisions.

However, there remain two large issues in interpreting exploration and exploitation through the lens of the opponent process model. The first is that there are more similarities than differences in activation across our results. Even when controlling for the effects of exploration and exploitation decisions specifically, our conjunction analyses reveal that exploration and exploitation generally elicit similar patterns of activation, particularly in the dACC and dmPFC.

These results suggest that areas of common activation should closely examined on the future using multivariate and connectivity methods to understand how they are involved in exploration and exploitation. Extending a previous meta-analysis suggests that these regions are not unique to exploration (Zhen et al. 2022), but are also involved in exploitation. As a result, when differences are reported in these regions, they may be due to the interplaying of more complex underlying variables modulating these brain processes rather than a product of a general opponent processing system for exploration versus exploitation decisions.

Secondly, our exploratory analyses suggest that there remains substantial heterogeneity between tasks. This issue may speak to the lack of behavioral convergent validity between these tasks (von Helversen et al. 2018), which is to say that a participant exploiting in a foraging task does not predict how they will exploit in an n-armed bandit task. During exploitation, we found differences in activation in the insula and dmPFC between other tasks and n-armed bandits. In theory, we would not expect to see differences in activation if exploitation across tasks reliably elicit similar responses, we would not expect to see differences between these tasks. Nonetheless, the differences in AI and dmPFC could reflect differences in how people perceive risk and uncertainty (ie: Zhen et al. 2022) or salient features (ie: (Hogeveen et al. 2022) while exploiting in n-armed bandits versus foraging tasks. Thus, while our results suggest that while the dACC, AI and dlPFC differentiate exploration and exploitation, these constructs remain fragile to the context of the decision based on task, and that most of the activation associated with these decision processes is indistinguishable and is modulated based on context. As such, the interplaying model of exploration and exploitation is generally a better descriptor of these constructs, though the dlPFC, AI, and dACC can act as opponent processes between these types of decisions.

4.2 Limitations

Although our work has found that exploration and exploitation can be dissociated by dlPFC, AI, and dACC activation, we acknowledge our study has several notable limitations. First, while we included N=23 studies, this quantity is fairly low for a CBMA type meta-analysis, with a common benchmark suggesting a minimum of 17–20 Experiments (Yeung et al. 2019). However, the exploratory CBMA of n-armed bandits versus other tasks during exploration and exploitation contrasted 13 versus 10 studies. Since this sample size is below the benchmark, it should be considered exploratory. Nonetheless, there is a lack of clear guidance as to what constitutes acceptable sample sizes for SDM, as this highly depends on the effects measured, the number of participants, and whether thresholded images are included or not. Second, while we found substantial areas of coactivation between explore-exploit conditions, we cannot conclude that these areas are consistently involved with both types of decisions. For example, prior studies have shown that a region may appear to be involved in different processes despite having patterns of activation and connectivity profiles (Woo et al. 2014; D. V. Smith, Sip, and Delgado 2015). Further analyses could disentangle the involvement of these brain regions and show distinct connectivity with other brain regions to better understand their involvement in explore-exploit decisions. Third, we acknowledge that CBMA has relatively low spatial resolution, limiting precise anatomical interpretations (Radua et al. 2012).

Other limitations extend beyond meta-analytic methods when assessing exploration and exploitation more generally. Explore-exploit tasks limit the manner in which information is presented, and a latent variable that may bias switching decisions includes the trend in information. Some studies have started to explore the effects of trends in information (Wittmann et al. 2016; Kolling et al. 2012; Vestergaard and Schultz 2020), though it remains underexplored

how these trends bias people to act too soon or too late. Further, brain connectivity (Friston 2011; Utevsky et al. 2017) may reveal patterns of explore-exploit decision making, yet few connectivity studies (S. Morris et al. 2015; Tardiff et al. 2021) have been completed in this domain. Since the default mode network (DMN) is implicated in executive function and cognitive control (Fox et al. 2005), and the executive control network (ECN) serves to rapidly instantiate new task states (Marek and Dosenbach 2018), both the DMN and ECN could interact to drive exploiting versus exploring decisions. Future studies may reconcile the gap that remains in understanding how explore-exploit decisions are associated with brain connectivity patterns.

While acknowledging limitations for generalizing both behavioral and neural results resulting from exploration and exploitation, the finding that the dlPFC, AI, and dACC reliably distinguish exploration and exploitation could inspire important future directions. First, a fruitful future direction includes modulating dlPFC responses, which are quite common in transcranial stimulation studies. Since there are many links between the dlPFC and psychopathology such as schizophrenia (Wu et al. 2017), anxiety (Balderston et al. 2020), and substance use (Goldstein and Volkow 2011), regulating dlPFC activation may reliably modulate explore-exploit decisions. Specific to substance use, while there has been extensive research into the neural mechanisms of addiction, it remains underexplored how individual differences in decision making serve as risk factors for increasing consumption of substances. Past investigations revealed that smokers explore less and learn faster (Merideth A. Addicott et al. 2012) and require greater cognitive control when exploring (Merideth A. Addicott et al. 2014). People with greater alcohol use tend to avoid uncertainty (L. S. Morris et al. 2016) and explore less. Brain responses may be modulated by substance use and mediated by social context (Sazhin et al. 2020). Sharing rewards with friends decreases connectivity between VS and dorsomedial prefrontal cortex (Wyngaarden et al. 2023), suggesting that social contexts are an important feature of understanding substance use decisions. Future investigations could also study the role of trends in decision making and assess whether substance users forecast future trends worse than non-substance users. Using explore-exploit dilemmas, researchers can assess how people make predictions, and whether substance users have an impaired cognitive ability to predict future outcomes.

5. Conclusion

In summary, we conducted a coordinate-based meta-analysis of neuroimaging studies using explore-exploit tasks. We found that areas associated with executive control (dlPFC), attention (IPS, dACC), and reward (VS) are reflected in exploration and exploitation decisions. Exploration versus exploitation can be distinguished by greater activation in the dlPFC, AI, and dACC. Nonetheless, there remains substantial heterogeneity in brain responses due to task types, modulated by activation in the AI and the dmPFC while exploiting. Further, exploration and exploitation are associated with more similar than dissimilar patterns of activation in the AI, dmPFC, dACC, and VS. These results suggest that exploration and exploitation are not reliable opponent processes but are more of a product of the interplaying of underlying physiological and psychological features guiding these decisions. Nonetheless, the finding that the dlPFC, AI, and dACC distinguish exploration and exploitation could serve as an important area of future research in cognitive neuroscience and psychopathology, as modulating these brain regions could shift how people explore and exploit.

References

Aberg, Kristoffer C., and Rony Paz. 2022. "Average Reward Rates Enable Motivational Transfer across Independent Reinforcement Learning Tasks." *Frontiers in Behavioral Neuroscience* 16:1041566. https://doi.org/10.3389/fnbeh.2022.1041566.

Abram, Samantha V., Michael Hanke, A. David Redish, and Angus W. 3rd MacDonald. 2019. "Neural Signatures Underlying Deliberation in Human Foraging Decisions." *Cognitive, Affective & Behavioral Neuroscience* 19 (6): 1492–1508. https://doi.org/10.3758/s13415-019-00733-z.

Addicott, M. A., J. M. Pearson, M. M. Sweitzer, D. L. Barack, and M. L. Platt. 2017. "A Primer on Foraging and the Explore/Exploit Trade-Off for Psychiatry Research." *Neuropsychopharmacology* 42 (10): 1931–39. https://doi.org/10.1038/npp.2017.108.

Addicott, Merideth A., David A.A. Baranger, Rachel V. Kozink, Moria J. Smoski, Gabriel S. Dichter, and F. Joseph McClernon. 2012. "Smoking Withdrawal Is Associated with Increases in Brain Activation during Decision Making and Reward Anticipation: A Preliminary Study." *Psychopharmacology* 219 (2): 563–73. https://doi.org/10.1007/s00213-011-2404-3.

Addicott, Merideth A., John M. Pearson, Brett Froeliger, Michael L. Platt, and F. Joseph McClernon. 2014. "Smoking Automaticity and Tolerance Moderate Brain Activation during Explore-Exploit Behavior." *Psychiatry Research* 224 (3): 254–61. https://doi.org/10.1016/j.pscychresns.2014.10.014.

Addicott, Merideth A., John M. Pearson, Nicole Kaiser, Michael L. Platt, and F. Joseph McClernon. 2015. "Suboptimal Foraging Behavior: A New Perspective on Gambling." *Behavioral Neuroscience* 129 (5): 656–65. https://doi.org/10.1037/bne0000082.

Albajes-Eizagirre, Anton, Aleix Solanes, Eduard Vieta, and Joaquim Radua. 2019. "Voxel-Based Meta-Analysis via Permutation of Subject Images (PSI): Theory and Implementation for SDM." *NeuroImage* 186 (February):174–84. https://doi.org/10.1016/j.neuroimage.2018.10.077.

Amiez, Céline, Jérôme Sallet, Emmanuel Procyk, and Michael Petrides. 2012. "Modulation of Feedback Related Activity in the Rostral Anterior Cingulate Cortex during Trial and Error Exploration." *NeuroImage* 63 (3): 1078–90. https://doi.org/10.1016/j.neuroimage.2012.06.023.

Averbeck, Bruno B. 2015. "Theory of Choice in Bandit, Information Sampling and Foraging Tasks." *PLOS Computational Biology* 11 (3): e1004164. https://doi.org/10.1371/journal.pcbi.1004164.

Badre, David, Bradley B. Doll, Nicole M. Long, and Michael J. Frank. 2012. "Rostrolateral Prefrontal Cortex and Individual Differences in Uncertainty-Driven Exploration." *Neuron* 73 (3): 595–607. https://doi.org/10.1016/j.neuron.2011.12.025.

Balderston, Nicholas L., Emily M. Beydler, Camille Roberts, Zhi-De Deng, Thomas Radman, Tiffany Lago, Bruce Luber, Sarah H. Lisanby, Monique Ernst, and Christian Grillon. 2020. "Mechanistic Link between Right Prefrontal Cortical Activity and Anxious Arousal Revealed Using Transcranial Magnetic Stimulation in Healthy Subjects." *Neuropsychopharmacology* 45 (4): 694–702. https://doi.org/10.1038/s41386-019-0583-5.

Barack, David L. 2024. "What Is Foraging?" *Biology & Philosophy* 39 (1): 3. https://doi.org/10.1007/s10539-024-09939-z.

Bartra, Oscar, Joseph T. McGuire, and Joseph W. Kable. 2013. "The Valuation System: A Coordinate-Based Meta-Analysis of BOLD fMRI Experiments Examining Neural

Correlates of Subjective Value." *NeuroImage* 76 (August):412–27. https://doi.org/10.1016/j.neuroimage.2013.02.063.

Bellman, Richard, and Robert Kalaba. 1957. "Dynamic Programming and Statistical Communication Theory." *Proceedings of the National Academy of Sciences* 43 (8): 749–51. https://doi.org/10.1073/pnas.43.8.749.

Bernstein, Carlos, Alejandro Kacelnik, and John R. Krebs. 1988. "Individual Decisions and the Distribution of Predators in a Patchy Environment." *Journal of Animal Ecology* 57 (3): 1007–26. https://doi.org/10.2307/5108.

Blanchard, Tommy C., and Samuel J. Gershman. 2018. "Pure Correlates of Exploration and Exploitation in the Human Brain." *Cognitive, Affective & Behavioral Neuroscience* 18 (1): 117–26. https://doi.org/10.3758/s13415-017-0556-2.

Blanco, Nathaniel J., Bradley C. Love, Michael Ramscar, A. Ross Otto, Kirsten Smayda, and W. Todd Maddox. 2016. "Exploratory Decision-Making as a Function of Lifelong Experience, Not Cognitive Decline." *Journal of Experimental Psychology. General* 145 (3): 284–97. https://doi.org/10.1037/xge0000133.

Boorman, Erie D., Matthew F. Rushworth, and Tim E. Behrens. 2013. "Ventromedial Prefrontal and Anterior Cingulate Cortex Adopt Choice and Default Reference Frames during Sequential Multi-Alternative Choice." *Journal of Neuroscience* 33 (6): 2242–53. https://doi.org/10.1523/JNEUROSCI.3022-12.2013.

Chakroun, Karima, David Mathar, Antonius Wiehler, Florian Ganzer, and Jan Peters. 2020. "Dopaminergic Modulation of the Exploration/Exploitation Trade-off in Human Decision-Making." Edited by Samuel J Gershman, Michael J Frank, Samuel J Gershman, Bruno B Averbeck, and John Pearson. *eLife* 9 (June):e51260. https://doi.org/10.7554/eLife.51260.

Chang, Shou-An A., Julian Jara-Ettinger, and Arielle Baskin-Sommers. 2022. "Resource Scarcity Compromises Explore-Exploit Decision-Making." *Journal of Experimental Social Psychology* 98 (January):104254. https://doi.org/10.1016/j.jesp.2021.104254.

Charnov, Eric L. 1976. "Optimal Foraging, the Marginal Value Theorem." *Theoretical Population Biology* 9 (2): 129–36. https://doi.org/10.1016/0040-5809(76)90040-X.

Cogliati Dezza, Irene, Axel Cleeremans, and William Alexander. 2019. "Should We Control? The Interplay between Cognitive Control and Information Integration in the Resolution of the Exploration-Exploitation Dilemma." *Journal of Experimental Psychology. General* 148 (6): 977–93. https://doi.org/10.1037/xge0000546.

Cogliati Dezza, Irene, Angela J. Yu, Axel Cleeremans, and William Alexander. 2017. "Learning the Value of Information and Reward over Time When Solving Exploration-Exploitation Problems." *Scientific Reports* 7 (1): 16919. https://doi.org/10.1038/s41598-017-17237-w.

Cohen, Jonathan D, Samuel M McClure, and Angela J Yu. 2007. "Should I Stay or Should I Go? How the Human Brain Manages the Trade-off between Exploitation and Exploration." *Philosophical Transactions of the Royal Society B: Biological Sciences* 362 (1481): 933–42. https://doi.org/10.1098/rstb.2007.2098.

Costa, Vincent D., Andrew R. Mitz, and Bruno B. Averbeck. 2019. "Subcortical Substrates of Explore-Exploit Decisions in Primates." *Neuron* 103 (3): 533-545.e5. https://doi.org/10.1016/j.neuron.2019.05.017.

Daw, Nathaniel D., John P. O'Doherty, Peter Dayan, Ben Seymour, and Raymond J. Dolan. 2006. "Cortical Substrates for Exploratory Decisions in Humans." *Nature* 441 (7095): 876–79. https://doi.org/10.1038/nature04766.

Dennison, Jeffrey B., Daniel Sazhin, and David V. Smith. 2022. “Decision Neuroscience and Neuroeconomics: Recent Progress and Ongoing Challenges.” *Wiley Interdisciplinary Reviews. Cognitive Science* 13 (3): e1589. https://doi.org/10.1002/wcs.1589.

Desikan, Rahul S., Florent Ségonne, Bruce Fischl, Brian T. Quinn, Bradford C. Dickerson, Deborah Blacker, Randy L. Buckner, et al. 2006. “An Automated Labeling System for Subdividing the Human Cerebral Cortex on MRI Scans into Gyral Based Regions of Interest.” *NeuroImage* 31 (3): 968–80. https://doi.org/10.1016/j.neuroimage.2006.01.021.

Donoso, Maël, Anne G. E. Collins, and Etienne Koechlin. 2014. “Human Cognition. Foundations of Human Reasoning in the Prefrontal Cortex.” *Science (New York, N.Y.)* 344 (6191): 1481–86. https://doi.org/10.1126/science.1252254.

Dooren, Roel van, Roy de Kleijn, Bernhard Hommel, and Zsuzsika Sjoerds. 2021. “The Exploration-Exploitation Trade-off in a Foraging Task Is Affected by Mood-Related Arousal and Valence.” *Cognitive, Affective & Behavioral Neuroscience* 21 (3): 549–60. https://doi.org/10.3758/s13415-021-00917-6.

Drugowitsch, Jan, Rubén Moreno-Bote, Anne K. Churchland, Michael N. Shadlen, and Alexandre Pouget. 2012. “The Cost of Accumulating Evidence in Perceptual Decision Making.” *Journal of Neuroscience* 32 (11): 3612–28. https://doi.org/10.1523/JNEUROSCI.4010-11.2012.

Dunne, Simon, Arun D’Souza, and John P. O’Doherty. 2016. “The Involvement of Model-Based but Not Model-Free Learning Signals during Observational Reward Learning in the Absence of Choice.” *Journal of Neurophysiology* 115 (6): 3195–3203. https://doi.org/10.1152/jn.00046.2016.

Fox, Michael D., Abraham Z. Snyder, Justin L. Vincent, Maurizio Corbetta, David C. Van Essen, and Marcus E. Raichle. 2005. “The Human Brain Is Intrinsically Organized into Dynamic, Anticorrelated Functional Networks.” *Proceedings of the National Academy of Sciences of the United States of America* 102 (27): 9673–78. https://doi.org/10.1073/pnas.0504136102.

Frahm, Lennart, Edna C. Cieslik, Felix Hoffstaedter, Theodore D. Satterthwaite, Peter T. Fox, Robert Langner, and Simon B. Eickhoff. 2022. “Evaluation of Thresholding Methods for Activation Likelihood Estimation Meta□analysis via Large□scale Simulations.” *Human Brain Mapping* 43 (13): 3987–97. https://doi.org/10.1002/hbm.25898.

Frank, Michael J., Bradley B. Doll, Jen Oas-Terpstra, and Francisco Moreno. 2009. “The Neurogenetics of Exploration and Exploitation: Prefrontal and Striatal Dopaminergic Components.” *Nature Neuroscience* 12 (8): 1062–68. https://doi.org/10.1038/nn.2342.

Freeman, P. R. 1983. “The Secretary Problem and Its Extensions: A Review.” *International Statistical Review / Revue Internationale de Statistique* 51 (2): 189–206. https://doi.org/10.2307/1402748.

Friedman, Naomi P., and Trevor W. Robbins. 2022. “The Role of Prefrontal Cortex in Cognitive Control and Executive Function.” *Neuropsychopharmacology* 47 (1): 72–89. https://doi.org/10.1038/s41386-021-01132-0.

Friston, Karl J. 2011. “Functional and Effective Connectivity: A Review.” *Brain Connectivity* 1 (1): 13–36. https://doi.org/10.1089/brain.2011.0008.

Goldstein, Rita Z., and Nora D. Volkow. 2011. “Dysfunction of the Prefrontal Cortex in Addiction: Neuroimaging Findings and Clinical Implications.” *Nature Reviews. Neuroscience* 12 (11): 652–69. https://doi.org/10.1038/nrn3119.

Goussi-Denjean, Clément, Vincent Fontanier, Frederic M. Stoll, and Emmanuel Procyk. 2023. "The Differential Weights of Motivational and Task Performance Measures on Medial and Lateral Frontal Neural Activity." *Journal of Neuroscience* 43 (23): 4329–40. https://doi.org/10.1523/JNEUROSCI.0007-22.2023.

Hayden, Benjamin Y., John M. Pearson, and Michael L. Platt. 2011. "Neuronal Basis of Sequential Foraging Decisions in a Patchy Environment." *Nature Neuroscience* 14 (7): 933–39. https://doi.org/10.1038/nn.2856.

Helversen, Bettina von, Rui Mata, Gregory R. Samanez-Larkin, and Andreas Wilke. 2018. "Foraging, Exploration, or Search? On the (Lack of) Convergent Validity between Three Behavioral Paradigms." *Evolutionary Behavioral Sciences* 12 (3): 152–62. https://doi.org/10.1037/ebs0000121.

Hogeveen, Jeremy, Teagan S. Mullins, John D. Romero, Elizabeth Eversole, Kimberly Rogge-Obando, Andrew R. Mayer, and Vincent D. Costa. 2022. "The Neurocomputational Bases of Explore-Exploit Decision-Making." *Neuron* 110 (11): 1869-1879.e5. https://doi.org/10.1016/j.neuron.2022.03.014.

Howard-Jones, Paul A., Rafal Bogacz, Jee H. Yoo, Ute Leonards, and Skevi Demetriou. 2010. "The Neural Mechanisms of Learning from Competitors." *NeuroImage* 53 (2): 790–99. https://doi.org/10.1016/j.neuroimage.2010.06.027.

Jahn, Caroline I., Jan Grohn, Steven Cuell, Andrew Emberton, Sebastien Bouret, Mark E. Walton, Nils Kolling, and Jérôme Sallet. 2023. "Neural Responses in Macaque Prefrontal Cortex Are Linked to Strategic Exploration." *PLoS Biology* 21 (1): e3001985. https://doi.org/10.1371/journal.pbio.3001985.

Kane, Gary A., Morgan H. James, Amitai Shenhav, Nathaniel D. Daw, Jonathan D. Cohen, and Gary Aston-Jones. 2022. "Rat Anterior Cingulate Cortex Continuously Signals Decision Variables in a Patch Foraging Task." *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience* 42 (29): 5730–44. https://doi.org/10.1523/JNEUROSCI.1940-21.2022.

Kayser, Andrew S., Zdeňa Op de Macks, Ronald E. Dahl, and Michael J. Frank. 2016. "A Neural Correlate of Strategic Exploration at the Onset of Adolescence." *Journal of Cognitive Neuroscience* 28 (2): 199–209. https://doi.org/10.1162/jocn_a_00896.

Kim, Chobok, James K. Kroger, and Jeounghoon Kim. 2010. "A Functional Dissociation of Conflict Processing within Anterior Cingulate Cortex." *Human Brain Mapping* 32 (2): 304–12. https://doi.org/10.1002/hbm.21020.

Kolling, Nils, Timothy E. J. Behrens, Rogier B. Mars, and Matthew F. S. Rushworth. 2012. "Neural Mechanisms of Foraging." *Science (New York, N.Y.)* 336 (6077): 95–98. https://doi.org/10.1126/science.1216930.

Kolling, Nils, and Jill X. O'Reilly. 2018. "State-Change Decisions and Dorsomedial Prefrontal Cortex: The Importance of Time." *Current Opinion in Behavioral Sciences* 22 (August):152–60. https://doi.org/10.1016/j.cobeha.2018.06.017.

Krishnamurthy, Vikram, and Bo Wahlberg. 2009. "Partially Observed Markov Decision Process Multiarmed Bandits—Structural Results." *Mathematics of Operations Research* 34 (2): 287–302.

Kuleshov, Volodymyr, and Doina Precup. 2000. "Algorithms for Multi-Armed Bandit Problems." *Journal of Machine Learning Research*, no. 1–48 (October). https://www.semanticscholar.org/paper/Algorithms-for-multi-armed-bandit-problems-Kuleshov-Precup/bae1cec84407412a610fa8d11db063c71a3bf6a2.

Laureiro Martínez, Daniella, Stefano Brusoni, Nicola Canessa, and Maurizio Zollo. 2015. "Understanding the Exploration–Exploitation Dilemma: An fMRI Study of Attention Control and Decision-Making Performance." *Strategic Management Journal* 36 (3): 319–38. https://doi.org/10.1002/smj.2221.

Laureiro-Martínez, Daniella, Nicola Canessa, Stefano Brusoni, Maurizio Zollo, Todd Hare, Federica Alemanno, and Stefano F. Cappa. 2014. "Frontopolar Cortex and Decision-Making Efficiency: Comparing Brain Activity of Experts with Different Professional Background during an Exploration-Exploitation Task." *Frontiers in Human Neuroscience* 7 (January):927. https://doi.org/10.3389/fnhum.2013.00927.

Lee, Douglas G, and Jean Daunizeau. 2021. "Trading Mental Effort for Confidence in the Metacognitive Control of Value-Based Decision-Making." Edited by Tobias H Donner, Michael J Frank, and Andrew Westbrook. *eLife* 10 (April):e63282. https://doi.org/10.7554/eLife.63282.

Lenow, Jennifer K., Sara M. Constantino, Nathaniel D. Daw, and Elizabeth A. Phelps. 2017. "Chronic and Acute Stress Promote Overexploitation in Serial Decision Making." *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience* 37 (23): 5681–89. https://doi.org/10.1523/JNEUROSCI.3618-16.2017.

Li, Jian, Samuel M. McClure, Brooks King-Casas, and P. Read Montague. 2006. "Policy Adjustment in a Dynamic Economic Game." *PLOS ONE* 1 (1): e103. https://doi.org/10.1371/journal.pone.0000103.

Lloyd, Alex, Ryan Thomas McKay, and Nicholas Furl. 2022. "Individuals with Adverse Childhood Experiences Explore Less and Underweight Reward Feedback." *Proceedings of the National Academy of Sciences of the United States of America* 119 (4): e2109373119. https://doi.org/10.1073/pnas.2109373119.

Mansouri, Farshad Alizadeh, Etienne Koechlin, Marcello G. P. Rosa, and Mark J. Buckley. 2017. "Managing Competing Goals — a Key Role for the Frontopolar Cortex." *Nature Reviews Neuroscience* 18 (11): 645–57. https://doi.org/10.1038/nrn.2017.111.

Marek, Scott, and Nico U. F. Dosenbach. 2018. "The Frontoparietal Network: Function, Electrophysiology, and Importance of Individual Precision Mapping." *Dialogues in Clinical Neuroscience* 20 (2): 133–40.

Masson, Rémy, Geneviève Demarquay, David Meunier, Yohana Lévêque, Salem Hannoun, Aurélie Bidet-Caulet, and Anne Caclin. 2021. "Is Migraine Associated to Brain Anatomical Alterations? New Data and Coordinate-Based Meta-Analysis." *Brain Topography* 34 (3): 384–401. https://doi.org/10.1007/s10548-021-00824-6.

Mazziotta, J. C., A. W. Toga, A. Evans, P. Fox, and J. Lancaster. 1995. "A Probabilistic Atlas of the Human Brain: Theory and Rationale for Its Development. The International Consortium for Brain Mapping (ICBM)." *NeuroImage* 2 (2): 89–101. https://doi.org/10.1006/nimg.1995.1012.

Meyers, Ethan A., and Derek J. Koehler. 2021. "Individual Differences in Exploring versus Exploiting and Links to Delay Discounting." *Journal of Behavioral Decision Making* 34 (4): 515–28. https://doi.org/10.1002/bdm.2226.

Mobbs, Dean, Demis Hassabis, Rongjun Yu, Carlton Chu, Matthew Rushworth, Erie Boorman, and Tim Dalgleish. 2013. "Foraging under Competition: The Neural Basis of Input-Matching in Humans." *Journal of Neuroscience* 33 (23): 9866–72. https://doi.org/10.1523/JNEUROSCI.2238-12.2013.

Mobbs, Dean, Pete C. Trimmer, Daniel T. Blumstein, and Peter Dayan. 2018. “Foraging for Foundations in Decision Neuroscience: Insights from Ethology.” *Nature Reviews. Neuroscience* 19 (7): 419–27. https://doi.org/10.1038/s41583-018-0010-7.

Moher, David, Alessandro Liberati, Jennifer Tetzlaff, Douglas G. Altman, and PRISMA Group. 2009. “Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement.” *Annals of Internal Medicine* 151 (4): 264–69, W64. https://doi.org/10.7326/0003-4819-151-4-200908180-00135.

Morris, Laurel S., Kwangyeol Baek, Prantik Kundu, Neil A. Harrison, Michael J. Frank, and Valerie Voon. 2016. “Biases in the Explore–Exploit Tradeoff in Addictions: The Role of Avoidance of Uncertainty.” *Neuropsychopharmacology* 41 (4): 940–48. https://doi.org/10.1038/npp.2015.208.

Morris, Stephen, Kurinchi S. Gurusamy, Jessica Sheringham, and Brian R. Davidson. 2015. “Cost-Effectiveness Analysis of Endoscopic Ultrasound versus Magnetic Resonance Cholangiopancreatography in Patients with Suspected Common Bile Duct Stones.” *PloS One* 10 (3): e0121699. https://doi.org/10.1371/journal.pone.0121699.

Moustafa, Ahmed A., Michael X. Cohen, Scott J. Sherman, and Michael J. Frank. 2008. “A Role for Dopamine in Temporal Decision Making and Reward Maximization in Parkinsonism.” *Journal of Neuroscience* 28 (47): 12294–304. https://doi.org/10.1523/JNEUROSCI.3116-08.2008.

Navarro, Daniel J., Ben R. Newell, and Christin Schulze. 2016. “Learning and Choosing in an Uncertain World: An Investigation of the Explore–Exploit Dilemma in Static and Dynamic Environments.” *Cognitive Psychology* 85 (March):43–77. https://doi.org/10.1016/j.cogpsych.2016.01.001.

Obeso, Ignacio, Maria-Trinidad Herrero, Romain Ligneul, John C. Rothwell, and Marjan Jahanshahi. 2021. “A Causal Role for the Right Dorsolateral Prefrontal Cortex in Avoidance of Risky Choices and Making Advantageous Selections.” *Neuroscience* 458 (March):166–79. https://doi.org/10.1016/j.neuroscience.2020.12.035.

Ohira, H., M. Matsunaga, H. Murakami, T. Osumi, S. Fukuyama, J. Shinoda, and J. Yamada. 2013. “Neural Mechanisms Mediating Association of Sympathetic Activity and Exploration in Decision-Making.” *Neuroscience* 246 (August):362–74. https://doi.org/10.1016/j.neuroscience.2013.04.050.

Ohta, Hiroyuki, Kuniaki Satori, Yu Takarada, Masashi Arake, Toshiaki Ishizuka, Yuji Morimoto, and Tatsuji Takahashi. 2021. “The Asymmetric Learning Rates of Murine Exploratory Behavior in Sparse Reward Environments.” *Neural Networks : The Official Journal of the International Neural Network Society* 143 (November):218–29. https://doi.org/10.1016/j.neunet.2021.05.030.

Payzan-LeNestour, Elise, Simon Dunne, Peter Bossaerts, and John P. O’Doherty. 2013. “The Neural Representation of Unexpected Uncertainty during Value-Based Decision Making.” *Neuron* 79 (1): 191–201. https://doi.org/10.1016/j.neuron.2013.04.037.

Preuschoff, Kerstin, Bernard Marius ’t Hart, and Wolfgang Einhauser. 2011. “Pupil Dilation Signals Surprise: Evidence for Noradrenaline’s Role in Decision Making.” *Frontiers in Neuroscience* 5. https://doi.org/10.3389/fnins.2011.00115.

Procyk, Emmanuel, Charles R. E. Wilson, Frederic M. Stoll, Maïlys C. M. Faraut, Michael Petrides, and Céline Amiez. 2016. “Midcingulate Motor Map and Feedback Detection: Converging Data from Humans and Monkeys.” *Cerebral Cortex* 26 (2): 467–76. https://doi.org/10.1093/cercor/bhu213.

Radua, J., D. Mataix-Cols, M. L. Phillips, W. El-Hage, D. M. Kronhaus, N. Cardoner, and S. Surguladze. 2012. "A New Meta-Analytic Method for Neuroimaging Studies That Combines Reported Peak Coordinates and Statistical Parametric Maps." *European Psychiatry: The Journal of the Association of European Psychiatrists* 27 (8): 605–11. https://doi.org/10.1016/j.eurpsy.2011.04.001.

Radua, Joaquim, Odile A. van den Heuvel, Simon Surguladze, and David Mataix-Cols. 2010. "Meta-Analytical Comparison of Voxel-Based Morphometry Studies in Obsessive-Compulsive Disorder vs Other Anxiety Disorders." *Archives of General Psychiatry* 67 (7): 701–11. https://doi.org/10.1001/archgenpsychiatry.2010.70.

Radua, Joaquim, and David Mataix-Cols. 2009. "Voxel-Wise Meta-Analysis of Grey Matter Changes in Obsessive–Compulsive Disorder." *The British Journal of Psychiatry* 195 (5): 393–402. https://doi.org/10.1192/bjp.bp.108.055046.

Raja Beharelle, Anjali, Rafael Polanía, Todd A. Hare, and Christian C. Ruff. 2015. "Transcranial Stimulation over Frontopolar Cortex Elucidates the Choice Attributes and Neural Mechanisms Used to Resolve Exploration-Exploitation Trade-Offs." *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience* 35 (43): 14544–56. https://doi.org/10.1523/JNEUROSCI.2322-15.2015.

Ramakrishnan, Arjun, Benjamin Y. Hayden, and Michael L. Platt. 2019. "Local Field Potentials in Dorsal Anterior Cingulate Sulcus Reflect Rewards but Not Travel Time Costs during Foraging." *Brain and Neuroscience Advances* 3 (December):2398212818817932. https://doi.org/10.1177/2398212818817932.

Rangel, Antonio, Colin Camerer, and P. Read Montague. 2008. "A Framework for Studying the Neurobiology of Value-Based Decision Making." *Nature Reviews Neuroscience* 9 (7): 545–56. https://doi.org/10.1038/nrn2357.

Sacchet, Matthew D., and Brian Knutson. 2013. "Spatial Smoothing Systematically Biases the Localization of Reward-Related Brain Activity." *NeuroImage* 66 (February):270–77. https://doi.org/10.1016/j.neuroimage.2012.10.056.

Sadeghiyeh, Hashem, Siyu Wang, Maxwell R. Alberhasky, Hannah M. Kyllo, Amitai Shenhav, and Robert C. Wilson. 2020. "Temporal Discounting Correlates with Directed Exploration but Not with Random Exploration." *Scientific Reports* 10 (1): 4020. https://doi.org/10.1038/s41598-020-60576-4.

Sazhin, Daniel, Angelique M. Frazier, Caleb R. Haynes, Camille R. Johnston, Iris Ka-Yi Chat, Jeffrey B. Dennison, Corinne P. Bart, et al. 2020. "The Role of Social Reward and Corticostriatal Connectivity in Substance Use." *Journal of Psychiatry and Brain Science* 5:e200024. https://doi.org/10.20900/jpbs.20200024.

Seymour, Ben, Nathaniel D. Daw, Jonathan P. Roiser, Peter Dayan, and Ray Dolan. 2012. "Serotonin Selectively Modulates Reward Value in Human Decision-Making." *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience* 32 (17): 5833–42. https://doi.org/10.1523/JNEUROSCI.0053-12.2012.

Sheng, LiQin, PanWen Zhao, HaiRong Ma, Liang Qi, ZhongQuan Yi, YuanYuan Shi, JianGuo Zhong, HaiCun Shi, ZhenYu Dai, and PingLei Pan. 2020. "Gray Matter Alterations in Restless Legs Syndrome." *Medicine* 99 (29): e21374. https://doi.org/10.1097/MD.0000000000021374.

Shenhav, Amitai, Mark A. Straccia, Jonathan D. Cohen, and Matthew M. Botvinick. 2014. "Anterior Cingulate Engagement in a Foraging Context Reflects Choice Difficulty, Not Foraging Value." *Nature Neuroscience* 17 (9): 1249–54. https://doi.org/10.1038/nn.3771.

Smith, Ashley R., Laurence Steinberg, and Jason Chein. 2014. "The Role of the Anterior Insula in Adolescent Decision Making." *Developmental Neuroscience* 36 (3–4): 196–209. https://doi.org/10.1159/000358918.

Smith, David V., Kamila E. Sip, and Mauricio R. Delgado. 2015. "Functional Connectivity with Distinct Neural Networks Tracks Fluctuations in Gain/Loss Framing Susceptibility." *Human Brain Mapping* 36 (7): 2743–55. https://doi.org/10.1002/hbm.22804.

Smith, Ryan, Samuel Taylor, Robert C. Wilson, Anne E. Chuning, Michelle R. Persich, Siyu Wang, and William D. S. Killgore. 2021. "Lower Levels of Directed Exploration and Reflective Thinking Are Associated With Greater Anxiety and Depression." *Frontiers in Psychiatry* 12:782136. https://doi.org/10.3389/fpsyt.2021.782136.

Smith, Stephen M., and Thomas E. Nichols. 2009. "Threshold-Free Cluster Enhancement: Addressing Problems of Smoothing, Threshold Dependence and Localisation in Cluster Inference." *NeuroImage* 44 (1): 83–98. https://doi.org/10.1016/j.neuroimage.2008.03.061.

Speers, Lucinda J., and David K. Bilkey. 2023. "Maladaptive Explore/Exploit Trade-Offs in Schizophrenia." *Trends in Neurosciences* 46 (5): 341–54. https://doi.org/10.1016/j.tins.2023.02.001.

Stephens, David W., and John R. Krebs. 1986. *Foraging Theory*. Princeton University Press.

Sterne, Jonathan A. C., Alex J. Sutton, John P. A. Ioannidis, Norma Terrin, David R. Jones, Joseph Lau, James Carpenter, et al. 2011. "Recommendations for Examining and Interpreting Funnel Plot Asymmetry in Meta-Analyses of Randomised Controlled Trials." *BMJ* 343 (July):d4002. https://doi.org/10.1136/bmj.d4002.

Tardiff, Nathan, John D. Medaglia, Danielle S. Bassett, and Sharon L. Thompson-Schill. 2021. "The Modulation of Brain Network Integration and Arousal during Exploration." *NeuroImage* 240 (October):118369. https://doi.org/10.1016/j.neuroimage.2021.118369.

Tomov, Momchil S., Van Q. Truong, Rohan A. Hundia, and Samuel J. Gershman. 2020. "Dissociable Neural Correlates of Uncertainty Underlie Different Exploration Strategies." *Nature Communications* 11 (1): 2371. https://doi.org/10.1038/s41467-020-15766-z.

Touroutoglou, Alexandra, Joseph Andreano, Bradford C. Dickerson, and Lisa Feldman Barrett. 2020. "The Tenacious Brain: How the Anterior Mid-Cingulate Contributes to Achieving Goals." *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior* 123 (February):12–29. https://doi.org/10.1016/j.cortex.2019.09.011.

Trudel, Nadescha, Jacqueline Scholl, Miriam C. Klein-Flügge, Elsa Fouragnan, Lev Tankelevitch, Marco K. Wittmann, and Matthew F. S. Rushworth. 2020. "Polarity of Uncertainty Representation during Exploration and Exploitation in Ventromedial Prefrontal Cortex." *Nature Human Behaviour*, August, 1–16. https://doi.org/10.1038/s41562-020-0929-3.

Tsujimoto, Satoshi, Aldo Genovesio, and Steven P. Wise. 2011. "Frontal Pole Cortex: Encoding Ends at the End of the Endbrain." *Trends in Cognitive Sciences* 15 (4): 169–76. https://doi.org/10.1016/j.tics.2011.02.001.

Utevsky, Amanda V., David V. Smith, Jacob S. Young, and Scott A. Huettel. 2017. "Large-Scale Network Coupling with the Fusiform Cortex Facilitates Future Social Motivation." *eNeuro* 4 (5). https://doi.org/10.1523/ENEURO.0084-17.2017.

Vestergaard, Martin D., and Wolfram Schultz. 2020. "Retrospective Valuation of Experienced Outcome Encoded in Distinct Reward Representations in the Anterior Insula and

Amygdala." *Journal of Neuroscience*, October. https://doi.org/10.1523/JNEUROSCI.2130-19.2020.

Vural, Gizem, Natasha Katruss, and Alexander Soutschek. 2024. "Pre-Supplementary Motor Area Strengthens Reward Sensitivity in Intertemporal Choice." *NeuroImage* 299 (October):120838. https://doi.org/10.1016/j.neuroimage.2024.120838.

Wagera, Tor D., Lauren Y. Atlasc, Matthew M. Botvinicke, Luke J. Changf, Robert C. Coghillg, Karen Deborah Davish, Gian Domenico Iannettik, Russell A. Poldrackl, and Alexander J. Shackmanm. 2016. "The Importance of Respecting Variation in Cingulate Anatomy□: Comment on Lieberman & Eisenberger 2015 and Yarkoni." In . https://www.semanticscholar.org/paper/The-importance-of-respecting-variation-in-cingulate-Wagera-Atlasc/1ba6e3ced94a01e1adfa43b5c68dacd210a8463e.

Wang, Jane X., and Joel L. Voss. 2014. "Brain Networks for Exploration Decisions Utilizing Distinct Modeled Information Types during Contextual Learning." *Neuron* 82 (5): 1171–82. https://doi.org/10.1016/j.neuron.2014.04.028.

Weissman, D. H., B. Giesbrecht, A. W. Song, G. R. Mangun, and M. G. Woldorff. 2003. "Conflict Monitoring in the Human Anterior Cingulate Cortex during Selective Attention to Global and Local Object Features." *NeuroImage* 19 (4): 1361–68. https://doi.org/10.1016/s1053-8119(03)00167-8.

Wiehler, A., K. Chakroun, and J. Peters. 2021. "Attenuated Directed Exploration during Reinforcement Learning in Gambling Disorder." *The Journal of Neuroscience□: The Official Journal of the Society for Neuroscience* 41 (11): 2512–22. https://doi.org/10.1523/JNEUROSCI.1607-20.2021.

Wilson, Robert C., Andra Geana, John M. White, Elliot A. Ludvig, and Jonathan D. Cohen. 2014. "Humans Use Directed and Random Exploration to Solve the Explore-Exploit Dilemma." *Journal of Experimental Psychology. General* 143 (6): 2074–81. https://doi.org/10.1037/a0038199.

Wittmann, Marco K., Nils Kolling, Rei Akaishi, Bolton K. H. Chau, Joshua W. Brown, Natalie Nelissen, and Matthew F. S. Rushworth. 2016. "Predictive Decision Making Driven by Multiple Time-Linked Reward Representations in the Anterior Cingulate Cortex." *Nature Communications* 7 (August):12327. https://doi.org/10.1038/ncomms12327.

Woo, Choong-Wan, Leonie Koban, Ethan Kross, Martin A. Lindquist, Marie T. Banich, Luka Ruzic, Jessica R. Andrews-Hanna, and Tor D. Wager. 2014. "Separate Neural Representations for Physical Pain and Social Rejection." *Nature Communications* 5 (1): 5380. https://doi.org/10.1038/ncomms6380.

Wu, Shihao, Huiling Wang, Cheng Chen, Jilin Zou, Huan Huang, Peifu Li, Yilin Zhao, et al. 2017. "Task Performance Modulates Functional Connectivity Involving the Dorsolateral Prefrontal Cortex in Patients with Schizophrenia." *Frontiers in Psychology* 8 (February):56. https://doi.org/10.3389/fpsyg.2017.00056.

Wyatt, Lindsay E., Patrick A. Hewan, Jeremy Hogeveen, R. Nathan Spreng, and Gary R. Turner. 2024. "Exploration versus Exploitation Decisions in the Human Brain: A Systematic Review of Functional Neuroimaging and Neuropsychological Studies." *Neuropsychologia* 192 (January):108740. https://doi.org/10.1016/j.neuropsychologia.2023.108740.

Wyngaarden, James B., Camille R. Johnston, Daniel Sazhin, Jeff B. Dennison, Ori Zaff, Dominic Fareri, Michael McCloskey, Lauren B. Alloy, David V. Smith, and Johanna M.

Jarcho. 2023. “Reward Sensitivity and Corticostriatal Function during Social Rewards.” *bioRxiv*, June, 2023.01.17.524305. https://doi.org/10.1101/2023.01.17.524305.

Yeung, Andy Wai Kan, Michaela Robertson, Angela Uecker, Peter T. Fox, and Simon B. Eickhoff. 2023. “Trends in the Sample Size, Statistics, and Contributions to the BrainMap Database of Activation Likelihood Estimation Meta-Analyses: An Empirical Study of 10-Year Data.” *Human Brain Mapping* 44 (5): 1876–87. https://doi.org/10.1002/hbm.26177.

Zacharopoulos, George, Amitai Shenhav, Sara Constantino, Gregory R. Maio, and David E. J. Linden. 2018. “The Effect of Self-Focus on Personal and Social Foraging Behaviour.” *Social Cognitive and Affective Neuroscience* 13 (9): 967–75. https://doi.org/10.1093/scan/nsy057.

Zajkowski, Wojciech K., Malgorzata Kossut, and Robert C. Wilson. 2017. “A Causal Role for Right Frontopolar Cortex in Directed, but Not Random, Exploration.” *eLife* 6 (September). https://doi.org/10.7554/eLife.27430.

Zhen, Shanshan, Zachary A. Yaple, Simon B. Eickhoff, and Rongjun Yu. 2022. “To Learn or to Gain: Neural Signatures of Exploration in Human Decision-Making.” *Brain Structure & Function* 227 (1): 63–76. https://doi.org/10.1007/s00429-021-02389-3.