

# Understanding the exploration-exploitation dilemma: An fMRI study of attention control and decision-making performance

**Daniella Laureiro-Martinez**

Department of Management, Technology and Economics, ETH Zurich

**Stefano Brusoni**

Department of Management, Technology and Economics, ETH Zurich

**Nicola Canessa**

Center for Cognitive Neuroscience (Vita-Salute San Raffaele University) and Division of Neuroscience (San Raffaele Scientific Institute)

**Maurizio Zollo**

Center for Research on Innovation, Organization and Strategy (CRIOS)  
Department of Management and Technology, Bocconi University, and  
Department of Strategy and Innovation, WU Vienna School of Economics and Business

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## **Abstract**

This paper studies the cognitive processes that enable decision-makers to switch between exploitation and exploration. We use functional magnetic resonance imaging (fMRI) in a sample of expert decision-makers to make two main contributions. First, we identify and contrast the specific brain regions and cognitive processes associated with exploitation and exploration decisions. Exploitation activates regions associated with reward-seeking, which track and evaluate the value of *current* choices, while exploration relies on regions associated with attentional control, tracking the value of *alternative* choices. Second, we propose and test the idea that stronger activation of the brain circuits related to attentional control allows individuals to achieve better decision-making performance as a result. We discuss the implications of these results for strategic management research and practice.

## Introduction

Adapting to complex and changing environments requires managers to explore novel knowledge domains while simultaneously exploiting existing knowledge (Abelson, 1976; Eisenhardt, Furr, and Bingham, 2010; Levinthal and March, 1993; March, 1991). Strategy scholars have identified a range of options for handling this trade-off. Structural ambidexterity scholars suggest assigning exploration and exploitation to different units (Benner and Tushman, 2003; Tushman and O'Reilly, 1996). Others propose inter-temporal separation (Burgelman, 2002; Siggelkow and Levinthal, 2003). Yet others argue that ambidexterity is best achieved through individuals' abilities to make decisions about exploration and exploitation cycles (Gibson and Birkinshaw, 2004). All researchers agree that key decision-makers play a critical role (Gibson *et al.*, 2004; Lubatkin *et al.*, 2006; O'Reilly and Tushman, 2011).

Considerable progress has been made in understanding how firms tackle the ambidexterity problem, but relatively little is known about individual decision-makers. Several authors discuss managers' ability to switch between different 'thought worlds' (Kostova and Zaheer, 1999; Raisch *et al.*, 2009). However, the antecedents of individual ambidexterity remain a critical gap in the literature (Eisenhardt *et al.*, 2010; Gupta, Smith, and Shalley, 2006). Proponents of the structural view, such as O'Reilly and Tushman, recognize that 'one of the most important lessons is that ambidextrous organizations need ambidextrous senior teams and managers' (2004, p. 81). For example, in the well-known study of Polaroid by (Tripsas and Gavetti, 2000), managers could not reframe the firm's business model in the context of new digital imaging technology. Understanding individual ambidexterity will show us the origins of organizational ambidexterity.

This paper offers a new response to this conceptual and empirical challenge, which aims to build on, and contribute to, the emerging behavioral theory of strategy (Gavetti, 2005 and 2012). It leverages recent neuroscientific work in both its theoretical (Aston-Jones and Cohen, 2005; Laureiro-Martínez, Brusoni, and Zollo, 2010) and empirical (Cohen, McClure, and Yu, 2007; Daw *et al.*, 2006) dimensions to improve our understanding of the micro-foundations of strategically relevant decision-making. According to Gavetti (2012), organizational performance is fundamentally influenced by leaders' superior ability to manage the mental processes necessary to pursue cognitively distant opportunities. Without losing, we might add, the ability to attend to cognitively closer tasks. However, the study of these abilities to manage mental processes has been so far limited in its theoretical foundations, based primarily on cognitive psychology, and in the use of related methods to infer, rather than directly and objectively observe, the variation across individuals of cognitive control capabilities. We use functional magnetic resonance imaging (fMRI) in a sample of expert decision-makers. There are two key reasons for choosing a neuroscientific approach based on brain imaging data (fMRI). First, there are robust findings from brain imaging studies that guide our discussion about the micro-level cognitive processes underpinning exploitation and exploration.

Second, most established approaches rely on indirect measures, e.g. surveys and interviews, observation, experiments, and eye-tracking. Neuroscientific methods allow us to observe the relevant cognitive processes directly, as they unfold, and therefore without the possibility of intentional decision-making biases.

At the individual level, neuroscience offers great ‘observational’ advantages by allowing us to break down macro processes into their constituent parts, observe how those parts operate, and associate their activations with a well-defined performance indicator. Its disadvantage is that, at this stage, we can only draw conclusions about individual decision-making. However, the quest for robust microfoundations has generated some recent publications that support the use of neuroscience in strategic, organizational, and management studies more broadly (Kable, 2011; Powell, 2011; Volk and Köhler, 2012).

Our definitions of ‘exploration’ and ‘exploitation’ are consistent with work in management (March, 1991) and neurosciences (Daw *et al.*, 2006). Exploration entails disengaging from the current task to enable experimentation, flexibility, discovery, and innovation. Exploitation aims at optimizing the performance of a certain task, and is associated with high-level engagement, selection, refinement, choice, production, and efficiency. Decision-making performance is defined as the reward an individual obtains as a consequence of their decision.

Our study is built on two logical steps. First, we identify which brain regions and associated cognitive processes are activated when expert managers make exploitation vs. exploration decisions, and when they switch from one to the other. We show that the ability to change learning strategies is related to attentional control, i.e. the ability to refocus attention and select actions in relation to internal goals (Koechlin and Hyafil, 2007; Koechlin, Ody, and Kouneiher, 2003). While the general role of attention is to allocate cognitive processing power to stimuli, ‘attentional control’ refers to a separate, higher-level, ‘executive’ branch of the attentional system that focuses attention on selected aspects of the environment (Posner and Petersen, 1990; Posner and Snyder, 1975). Second, we link that neural activity to dependent variables related to strategic management. Superior attentional control highlights foregone alternatives, indicating when to move from exploitation to exploration. We test this argument by correlating the increased activation of brain areas associated with attentional control with decision-making performance in an exploration/exploitation task.

## **Theoretical framework and hypotheses**

What makes someone ambidextrous? Mom and colleagues (2007) found that the more a manager acquires top-down and bottom-up knowledge flows, or top-down and horizontal knowledge flows, the higher the levels of exploration and exploitation activity they could undertake. Others have shown that ambidextrous

managers have both a short-term and a long-term orientation (O'Reilly *et al.*, 2004; Probst and Raisch, 2005), and that ambidextrous individuals can perform tasks involving conflicting requirements or time horizons (Probst *et al.*, 2005; Raisch *et al.*, 2009; Smith and Tushman, 2005). However, none of these studies explains what makes someone better at both exploration and exploitation. Answering this requires analysis of managers' personal and cognitive characteristics (Raisch *et al.*, 2009).

Recent neuroscientific findings have shed some light on the neural mechanisms behind exploration and exploitation (Aston-Jones *et al.*, 2005; Cohen *et al.*, 2007; Daw *et al.*, 2006). Neuroscientists have identified several brain regions associated with either exploitation or exploration, and made some progress towards identifying the regions that control the switch to exploration (Boorman *et al.*, 2009). However, most of these studies rely on very small samples of inexperienced participants, or animals whose brains are similar to humans'. In this paper, we develop an explicit link between neuroscientific findings and social scientific research on ambidexterity and innovation, relying on a sample of expert decision-makers.

The management and neurosciences literatures propose various models of decision-making. We use the simplest: a stimulus-response framework centered on a value-based decision-making process (Rangel, Camerer, and Montague, 2008). We omit discussion of how stimuli are perceived, encoded, retrieved, and so on, for reasons of focus and simplicity.

### **Exploitation (H1)**

At the individual level, exploitation is defined as behavior that optimizes performance in the current task (Aston-Jones *et al.*, 2005). This definition is in line with March's (1991): 'The essence of exploitation is the refinement and extension of existing competences, technologies, and paradigms. Its returns are positive, proximate, and predictable.'

The literature also suggests that the objective of exploitation is to respond to current environmental needs. Exploitation involves bottom-up learning. At the organizational level, this generates the tendency to institutionalize reliable behaviors into routines (Harry and Schroeder, 2000). The organizational learning literature indicates that incremental refinements are achieved by internalizing or combining existing knowledge (Nonaka, 1994). This reinforces the tendency for individuals to implement behaviors that are suited to learning by doing, evaluate the rewards, and refine their behavior based on feedback. This last idea is consistent with recent findings in neurosciences.

Specific brain areas have been associated with a circuit involved in the assessment of rewards (gains) and punishments (costs) that lead to behavioral adjustments via reward-based learning. Neuroimaging studies consistently identify a circuit that is activated in response to the experience, anticipation, and seeking out of rewarding stimuli. This so-called mesocorticolimbic dopaminergic circuit is formed by the ventral midbrain (ventral tegmental area (VTA) and substantia nigra (SN)), ventral striatum (Str), nucleus accumbens (Acb), ventral caudate nucleus (VS), and ventro medial pre-frontal cortex (vmPFC) (Knutson *et*

*al.*, 2003; McClure, Berns, and Montague, 2003; O'Doherty *et al.*, 2001; Rolls, 2000) (figure 1). For a list of the names for regions of the brain, and their acronyms, please see table 1. In line with discussions in the neuroscientific and organizational learning literatures, we expect to find that experts' exploitative decisions activate brain regions associated with reward processing. We therefore hypothesize that:

H1. Compared to exploration, exploitation will involve stronger activations of the reward-related brain regions.

Figure 1 is a representation of the medial view of the brain. The main brain regions involved in exploitation are highlighted. The arrows describe the circuit involved in the assessment of rewards.

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## **Exploration (H2)**

In the neuroscientific literature, exploration has been defined as the behavior leading to 'disengagement from the current task and the search for alternative behaviors' (Aston-Jones *et al.*, 2005, p. 403). This definition fits with March's (1991, p. 81): 'The essence of exploration is experimentation with new alternatives. Its returns are uncertain, distant, and often negative.' There are two sides to this definition: the novelty of alternatives and the uncertainty of outcomes. While exploration includes both these elements, much of the research that followed (including March's own) separates them. For example, research based on NK models explains the difficulty of reaching a global optimum because of interdependencies (the K-element) across sub-problems (the N-element). The sub-problems per se are at least partially known, but the outcomes are hard to predict because of the difficulty of predicting the interaction effects of partial solutions (Ethiraj and Levinthal, 2004; Levinthal, 1997). Research in product design also stressed the strategic consequences of uncertainty in outcomes, caused by the unpredictability of the interdependencies among known components (Brusoni, Prencipe, and Pavitt, 2001). This line of reasoning is consistent with the broader discussion on complementarities in economics (Milgrom and Roberts, 1990).

What activates the search for better alternatives, despite the risks, is a basic mechanism of performance feedback (Cyert *et al.*, 1963; March *et al.*, 1958; Winter, 2000; Grève, 2003). Hence we focus our analysis on exploration decisions that entail uncertainty about outcomes, and are activated by unsatisfactory results. This is also consistent with individual-level findings in the neurosciences, where individuals have been found to shift focus from the current task when the utility of performing it falls below a certain threshold or aspiration level (Aston-Jones *et al.*, 2005). Hence, we expect that the brain regions involved in cognitive control will be strongly activated when managers revert to exploration. In particular, the dorsolateral prefrontal cortex (DLPFC) and frontopolar cortex (FPC) are responsible for top-

down control over attention, biasing attentional processes in favor of higher-level goals, especially when these must compete with otherwise prepotent behaviors (Miller and Cohen, 2001). Such top-down attentional control seems to be crucial for exploration, since it requires inhibition of the current choice in order to plan, search for, and select alternative choices. At the neural level, the process of controlling attention relies on activity in the locus coeruleus-norepinephrine circuit (LC-NE) (Sara, 2009). Changes in the activity of that circuit depend on inputs from the dopaminergic mesocorticolimbic brain regions in charge of the processing and anticipation of rewards, and on the striatal habituation mechanisms associated with learning by doing (Aston-Jones *et al.*, 2005).

Drawing on these studies, we predict that explorative choices will engage regions associated with the assessment of reward-related uncertainty and the circuit in charge of attentional control: the FPC and inferior parietal lobule (IPL) (Boorman *et al.*, 2009; Corbetta and Schulman, 2002; Daw *et al.*, 2006), and the LC-NE system (Cohen *et al.*, 2007). We therefore hypothesize that:

H2. Compared with exploitation, exploration will involve stronger activation of the regions involved with the assessment of reward-related uncertainty as well as cognitive and attentional control.

Figure 2 is a representation of the medial (left) and lateral (right) views of the brain. The main brain regions involved in exploration are highlighted (H2). The arrows describe the circuit responsible for processing reward-related uncertainty and for controlling attention.

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### **Switching and decision-making performance (H3)**

The ‘ambidexterity’ discussion, opened up by (Tushman *et al.*, 1996), revolves around the issue of how firms can ‘balance’ exploration and exploitation. However, there is little agreement on what ‘balance’ means. Is it doing equal amounts of exploration and exploitation, devoting the same time to each, or doing both at the same time? Or does it refer to switching between them as required? A crucial point, however, is that firms’ strategies ultimately arise from individual decision-makers, who must reconcile conflicting quests for efficiency and flexibility (Eisenhardt *et al.*, 2010; Gilbert, 2006; Smith *et al.*, 2005) by switching between exploration and exploitation (Laureiro-Martínez *et al.*, 2010). Thus, high performance relies on decision-makers resolving the fundamental tension between flexibility and efficiency (Brown and Eisenhardt, 1997; Tushman *et al.*, 1996).

Previous research suggests that when organizations operate in dynamic environments, flexibility is favored (Eisenhardt *et al.*, 2010). However, several authors show that, in practice, managers find it hard to know when to explore new opportunities, because they routinely discount threats and focus on short-term gains at the expense of less certain long-term returns (Bazerman and Watkins, 2004; Benner *et al.*, 2003;

Eisenhardt *et al.*, 2010). As a consequence, those individuals who are better at knowing when to switch from exploitation to exploration will achieve superior decision-making performance because they will capture the best opportunities and continue to exploit them until other, better possibilities arise.

However, switching to exploration, let alone doing it at the right time, is not simple. As reported by Sherman, Andy Grove notes: ‘... But success can trap you. The more successful we are as a microprocessor company, the more difficult it will be to become something else...’ (1993, para. 10)

This example illustrates the strategic importance of the explore-exploit decision, and the crucial role of senior individuals. In neurosciences, inter-individual differences in the level of activation of the FPC, one of the key areas for attentional control, have been shown to predict timely and effective switching to alternative choices (Boorman *et al.*, 2009).

We propose that inter-individual differences in attentional control might explain why some individuals are better at switching between exploitation and exploration. The logic underlying our argument is that the stronger activation of the brain regions associated with superior attentional control signals that the choice between exploitation and exploration is made with greater attention. In turn, this greater attention should lead to superior decision-making performance.

We test this argument by correlating the increased activation of the attention control regions with the performance obtained in an exploration/exploitation task. Here, we are not interested in identifying the cognitive processes and brain regions in charge of switching (the focus of Hypotheses 1 and 2). Rather, we want to see whether stronger activation of the brain regions involved in attentional control leads to better decision-making performance. By ‘stronger activation’, we mean a more powerful signal in the relevant brain regions. We can measure this by the brain oxygen level-dependent (‘BOLD’) signal, which is an indirect measure of neural activity underlying cognitive processes (for a brief review see (Logothetis, 2008) or (Logothetis and Wandell, 2004)).

We propose that inter-individual differences in the strength of brain activity associated with explorative choices, represent a direct test of the relationship between activation of the attentional-control regions and decision-making performance (figure 2, Ho. 3). Therefore, we hypothesize that:

H3. The stronger the activation of the attentional control regions, the better the decision-making performance.

Figure 3 is a representation of the medial (left) and lateral (right) views of the brain. The regions where stronger activation should lead to better decision-making performance (H3) are colored yellow.

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## **Method**

In this section we describe the sampling strategy, the task, and the experimental procedures deployed to generate data on exploitation, exploration, and decision-making performance. The detailed fMRI techniques used are presented in the 'Detailed Methods' section of the online supplementary materials.

## **Sample**

Our sample comprises 63 right-handed (Oldfield, 1971) healthy participants (11 females; females' mean age = 33.333 years, standard deviation [s.d.] = 6.020; males' mean age = 35.595 years, s.d. = 6.911). All the participants have at least four years' experience of making managerial decisions in areas such as marketing, human resources, production, R&D, or finance.

All participants fulfilled all the requirements to participate in a neuroscientific study. None reported any history of psychiatric or neurological disorders, nor current use of psychoactive medications. They gave their written informed consent to the experimental procedure, which was approved by the local Ethics Committee. All participants were highly motivated to perform at their best by the promise of detailed feedback on their performance when the research project was concluded.

Our sample (N=63) is large compared to the norm in the field of cognitive neuroscience, where a typical study averages 15 participants (Yarkoni and Braver, 2010). Our sample size allows us to be very precise about the neuropsychological processes that underpin exploration and exploitation, and to identify decision-making performance differences across individuals. Also, our reliance on a sample of expert decision-makers is unique and constitutes the first 'empirical' bridging between strategic management and neuroscience: work in the latter domain builds on the collaboration of patients, laypersons, and even monkeys (Aston-Jones *et al.*, 2005; Cohen, McClure, and Yu, 2007; Daw, Niv, and Dayan, 2005; Daw *et al.*, 2006).

## **Task**

All participants engaged in a 'four-armed bandit' task where they had to choose among slot machines with uncertain odds (DeGroot, 1970). This task belongs to the broader category of bandit problems, a group of dynamic decision-making tasks well-suited to controlled laboratory studies and representative of a broad class of real-world problems (Steyvers, Lee, and Wagenmakers, 2009). It has been used in neuroimaging studies on the neural bases of explorative vs. exploitative choice (Boorman *et al.*, 2009; Daw *et al.*, 2006; Kovach *et al.*, 2012; Seymour *et al.*, 2012). It is also frequently applied in organization studies, notably by Jim March and colleagues (Denrell and March, 2001; March, 2003; Posen and Levinthal, 2012) to explain the antecedents and consequences of the same types of decisional outcomes. Although clearly simplified, this task nevertheless captures the key ingredients of a broad class of settings in which individuals are faced with the problem of choosing among options with uncertain outcomes, during a period of learning (Meyer and Shi, 1995).

## Experimental procedures

We replicated the study design in (Daw *et al.*, 2006). Participants were observed individually in one of our institution's brain imaging research laboratories. On arrival, they were welcomed by two of the co-authors. They were then seated at computers and told that they would be playing a game with the aim of accumulating as many points as possible, and that points could be exchanged for money at the end of the game. They were asked to read the instructions and then play a short training round. Following this participants were asked to play the game while lying inside the fMRI scanner, which took thousands of images of their brain as they played. After several processing steps, the information captured in the images was translated into a measure called the BOLD signal, which is used as an indirect indicator of the neural activity underpinning cognitive processing (Bandettini, 2006).

When lying inside the scanner, participants saw the stimuli on a screen positioned in front of the scanner using an angled mirror placed above their eyes. The game consisted of four slot machines that paid off points noisily, around four different means that changed from trial to trial. This feature, developed by (Daw *et al.*, 2006), allowed us to study exploratory and exploitative decisions under uniform conditions, in the context of a single task that could be performed inside the scanner. Participants were not told about the changing means; they only could learn about the current worth of a slot by active sampling. In each time period, participants had to resolve the dilemma of whether to choose an uncertain but familiar option (exploitation) or investigate a new one in the hope of a higher payoff (exploration). The options were known; the uncertainty was over outcomes.

Figure 4, from left to right, shows that the task followed the same sequence of events in each trial. First, the participants were presented with the four machines. Second, they chose one (by pressing one of four buttons on a keyboard). Third, within a few seconds, the number of points they had won by choosing that slot was displayed. Finally, and as is usual in neuroimaging studies, a fixation cross appeared signaling the end of one trial and the beginning of a new one. If no choice was made within the slots-presentation period, a red X was displayed for 4.2 seconds and a new trial was started. Participants played a total of 300 trials divided into four sessions (of 75 trials each). After each session, they were given a break, for as long as they wanted.

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The first four trials of each session were eliminated from our analyses so participants could start with a minimum amount of information (all participants, except one, explored the four slots in the first four trials). As it is commonly the case, in order to use the brain imaging method, we adopted a perspective based on a dichotomy. From the fifth trial on, participants' response to each trial was classified

as an exploitative or an exploratory choice. Choosing the same machine as in the previous trial was classified as an *exploitation* choice; choosing a different one was classified as *exploration*. In this simple definition, any change is exploration. *Decision-making performance* was measured by the total number of points accumulated over the 300 trials.

## Results

This section is split into three sub-sections presenting results to test hypotheses 1, 2, and 3. We identified the specific brain regions and cognitive processes associated with exploitation and exploration decisions, and the system in charge of change from exploitation to exploration. Exploitation is associated with reward seeking and tracks and evaluates the value of *current* choice (H1). Exploration relies on regions associated with attentional control and tracking the value of *alternative* choices (H2). The stronger activation of the attentional control circuit allows to achieve better decision-making performance (H3).

### Exploitation (H1)

As hypothesized, we found that exploitative choices elicited significantly stronger activations than explorative ones, in dopaminergic mesocorticolimbic regions associated with reward anticipation (Tobler *et al.*, 2007), namely the medial prefrontal cortex (mPFC) and the hippocampus (Hip) bilaterally. These brain regions are depicted in Figure 5. The exact locations of the brain regions in our findings are presented in Table 3.

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Based on the neuroscientific literature, our findings reflect anticipation of the safe, predictable reward implicit in an exploitative choice. The mPFC is the target of the mesocorticolimbic dopaminergic circuit, a neural system involved in reward-related behavioral adaptations (Ikemoto, 2007; Schultz, 2006). The functional role of this circuit arises from the release of dopamine from the VTA and SN in the ventral midbrain. These structures are bidirectionally connected to the striatal complex in the basal ganglia (BG), ventral Str (including the sub region Acb) as well as dorsal striatum (DS) (Ikemoto, 2007). The crucial role of dopamine transmission within these neural structures in the experience and anticipation of and search for *rewards* is highlighted in classical studies of drug self-administration and electrical self-stimulation (Olds and Milner, 1954). However, the roles of the VTA and VS necessarily result from their interactions with other brain structures along the dopaminergic circuit. Projections to the neocortex mainly reach the orbitofrontal cortex (OFC), that is, the ventral part of the frontal lobes located above the orbits, and particularly its medial portion, i.e. the mPFC.

On the basis of its anatomo-functional connectivity, the OFC consists of a sensory and a limbic circuit, located in its lateral and medial portions respectively (Ongur and Price, 2000). The sensory circuit receives mainly sensory information that reaches distinct subregions of the lateral OFC, and projections from the posterior Str (Carmichael and Price, 1995b). The limbic (medial) network centered in the vmPFC is strictly connected to the limbic structures (Hip and amygdala (Amg)) (Carmichael and Price, 1995a), posterior cingulate cortex (poCC) (Cavada *et al.*, 2000) and the VS. With regard to its function, there is a large body of data suggesting the role of the vmPFC in goal-directed behavior, through flexible processing of rewards and punishments that finally results in adjustments to behavior (see Kringelbach and Rolls (2004) for a review). Indeed, different lines of research associate the vmPFC with related but not completely overlapping functional roles, such as behavioral inhibition, emotional control, moral reasoning, social functioning, and, broadly, integration of the emotional and cognitive facets of relevant stimuli for behavior adaptations (Bechara, Damasio, and Damasio, 2000; Kringelbach *et al.*, 2004; Rolls, 2004). These different facets of the vmPFC's role in goal-directed behavioral adaptation can be explained by a general role of this region in representing the reward and punishment value of reinforcing stimuli. As such, the vmPFC would be crucially involved in the rapid (re)learning and reversal of associations between previous neutral stimuli and reinforcers (e.g. the association between a given slot machine and an imminent monetary reward). This role is likely also to involve the Hip associated with memory encoding. Indeed, as already mentioned, the mesocorticolimbic dopaminergic circuit is connected to the rostral portion of the Hip (Friedman, Aggleton, and Saunders, 2002). In particular, the subiculum (Sub), by connecting the Hip and the reward circuitry, activates the dopamine system to highlight the reinforcing properties of rewarding stimuli (Cooper *et al.*, 2006). In this functional framework the medial and lateral areas of the OFC will be involved respectively in ongoing monitoring of the reward value of reinforcers, or in evaluating the punishment value of reinforcers that might lead to a change in current behavior (Kringelbach *et al.*, 2004).

Confirming this view, previous data show the vmPFC to be more strongly activated by exploitation than exploration choices (Dayan, 2009). An interpretation of this result in relation to monitoring the reward value of reinforcers is supported and refined in recent work on neural systems showing that tracking the value of current vs. alternative choices enables adjustments to behavior. Boorman *et al.* (2009) employ fMRI and a Bayesian reinforcement-learning model (implemented in a two-armed bandit task) to investigate the neural precursors to decisional switching in uncertainty — that is, when a behavioral adjustment is not explicitly cued by features of the external environment, but rather is implied by the accumulated evidence on the utility associated with different choice options. They observed that, while making sequential choices, the vmPFC encodes the value of the *current* decision, namely a signal reflecting comparison between the current choice and alternative actions. This finding is consistent with evidence

showing involvement of the same region in exploitation choices (Daw *et al.*, 2006) and in coding of the expected value (or other variables) related to the chosen option (Behrens *et al.*, 2008; Daw *et al.*, 2006; Hampton, Bossaerts, and O'Doherty, 2006; Hare *et al.*, 2008; Kable and Glimcher, 2007; Knutson *et al.*, 2005; Tanaka *et al.*, 2004).

Based on the above evidence, the conjoint involvement of the vmPFC and the Sub in the formulation of an exploitation choice supports the role of the former in encoding the value of the current decision during the making of a new choice. Supporting this interpretation, focused analyses (called 'regions-of-interest analyses' or 'ROIs analyses'; see the Detailed Methods section in the online supplementary materials) confirm that the vmPFC region previously associated with tracking the value of the current choice by (Boorman *et al.*, 2009) is more strongly activated by exploitation than exploration (Table 2). These findings provide support for our first hypothesis about the involvement of the reward brain circuitry in charge of a bottom-up learning process that results in repetition of current behavior. Note also that ongoing work by the authors found the same results as presented here, using a computational rather than a behavioral definition of exploitation (as in (Daw *et al.*, 2006)).

### **Exploration (H2)**

We find that compared with exploitation choices, exploration choices elicit significantly stronger activation of the attention control regions, i.e. the circuitry composed of bilateral parietal and frontal regions. In the parietal regions, we find that activation occurs in the temporo-parietal junction (TPJ) and intraparietal sulcus (IPS), as well as in the superior parietal lobule (SPL). In the frontal regions, activations involve bilaterally the frontal eye fields (FEF), middle frontal gyrus (MFG), and the FPC. These findings provide support for our second hypothesis. Further frontal activation was observed in the dorsal anterior cingulate cortex (dACC) (Picard and Strick, 1996) and pre-supplementary motor area (pre-SMA), in the medial surface of the brain. In line with *a priori* hypotheses (Aston-Jones *et al.*, 2005), the locus coeruleus (LC) is also more strongly activated by exploration than exploitation choice. Importantly, and in line with our initial hypothesis, we observed activation of the ventral frontoinsula cortex (VFC), discussed further in the Discussion and Conclusions section. The insula (Ins) is in charge of affective processing, signaling negative emotions, both physical and moral (Calder, Lawrence, and Young, 2001; Dalgleish, 2004; Sanfey *et al.*, 2003). In particular, in several studies, the Ins is consistently associated with feelings of disgust, a negative feeling that derives from disapproval of the current situation (for a review see (Murphy, Nimmo-Smith, and Lawrence, 2003)). Indeed, the crucial role of anterior Ins in signaling the affective/motivational significance of the probability of aversive outcomes was confirmed by a study of patients with anterior Ins lesions, who display impaired sensitivity to the odds of winning (Clark *et al.*, 2008). We argue that this is related to the anxiety and fear generated by choosing the most uncertain option (i.e. exploration). Most of these brain regions are depicted in figure 6.

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Due to intrinsic limitations in the evaluation of the measures of neural activity (BOLD signal responses) in the brainstem, the predicted involvement of the LC in exploration vs. exploitation was also assessed in areas defined on the basis of both functional (Astafiev *et al.*, 2010) and anatomical (Keren *et al.*, 2009) criteria, independent of the previous results (Table 3). This was done by means of ROIs analyses (see the Detailed Methods section in the online supplementary materials). We employed the same approach to directly compare the frontopolar and parietal activations observed in our study with those previously associated by Boorman *et al.* (2009) with tracking the value of alternative vs. current choices. The results confirm that the regions activated in that study, as well as the LC (Astafiev *et al.*, 2010; Keren *et al.*, 2009), are more strongly activated during exploration than exploitation choices. Table 3 presents the exact location of the brain regions that appear more active when participants are exploring rather than exploiting.

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The model that emerges from our data is strongly rooted in the extensive literature on the neural systems underlying attentional control and executive functioning, as well as recent evidence on the neural mechanisms that underpin behavioral flexibility in dynamic settings. The fronto-parietal brain regions that are more strongly activated by exploration choices are typically associated with executive functioning, a general and broad cognitive system that is considered to control and manage the execution of other cognitive processes (Botvinick *et al.*, 2001; Ridderinkhof *et al.*, 2004). The functions, components, and even definition of this system are the subject of ongoing debate. However, it is commonly accepted that its overall function is to manage novel situations that are beyond the scope of automatic processes implemented in learned behavioral schemas (Miller *et al.*, 2001).

It follows that this system is crucial for many cognitive processes, which while not completely overlapping, are all related to behavioral control and flexibility. These include, for instance, error detection and conflict monitoring, inhibition of inappropriate actions and initiation of appropriate ones, cognitive flexibility, planning, working memory, and attentional control. It is important to note that the executive functioning system has been associated with a network connecting the frontal and parietal regions. Within the frontal regions, the dACC is involved in conflict monitoring (Ridderinkhof *et al.*, 2004), and signals the need for increased attention control implemented by the DLPFC, via connections with both the parietal cortex (PL) (for attentional shifting see (Corbetta *et al.*, 2002)) and FPC to coordinate actions related to

internal goals, particularly complex tasks that require computation of higher-order relations (e.g. involving a tradeoff among different variables) (Koechlin *et al.*, 2003).

The process we have described is strictly connected to optimizing exploitation and exploration choices, aimed at maximizing the rewards via maintenance of a known (safe and reassuring) choice, or inhibiting this choice to initiate (through planning and cognitive flexibility) a different one. Our data also support recent choice models that suggest the crucial role of attentional switching in the balance between exploration and exploitation (Boorman *et al.*, 2009).

A brain system comprising all the regions observed in the present study (FPC, vmPFC, LC-NE system, IPL and IPS, as well as TPJ, FEF and VFC) is involved in the switching between exploitation and exploration. The brain regions and the model discussed here provide support for our second hypothesis. This brain system allows us to integrate the specific roles of brain regions involved in computational, executive, and attentional processes within a single, coherent framework. It provides a precise anatomo-functional characterization of our hypothesis that the medial and lateral areas of the OFC will be involved in ongoing monitoring/evaluation of the reward/punishment value of reinforcers, which may result in a change to current behavior (Kringelbach *et al.*, 2004). Research findings show that the results presented here can be obtained using a computational definition of exploration, rather than a behavioral one (see (Daw *et al.*, 2006)).

### **From stability to change (H3)**

Finally, we examine whether stronger activation of the attentional control brain regions leads to superior decision-making performance (Hypothesis 3). We find significant correlations (see table 4) between activation of each of these regions and total points accumulated in the four-armed bandit task. These results provide support for hypothesis 3 and suggest that stronger activation of the regions associated with behavioral switching to foregone alternatives leads to more efficient decisional switching patterns.

Note that although the LC was related in past research to switching to exploration, its higher activation does not appear to be positively correlated with decision-making performance. This suggests that switching may involve two main neural mechanisms. The first is specifically computational, and involves representation by the FPC of the value of foregone options (Boorman *et al.*, 2009; Koechlin *et al.*, 2003). These are continuously compared with the value of the current choice (represented in the mPFC; (Daw *et al.*, 2006)) by the monitoring performance mechanisms implemented in the anterior cingulate cortex (ACC) (Ridderinkhof *et al.*, 2004). If FPC activity exceeds mPFC activity, this prompts attentional disengagement from the current choice in IPS. This process involves the computational analysis of value, shown by the significant positive correlation between decision-making performance and strength of the activity in the right FPC and IPS, particularly during exploration. The second, more general-purpose mechanism allows attentional disengagement in the IPS when negative feedback from the mPFC changes

the activity of the LC (activity changes from phasic to tonic (Aston-Jones *et al.*, 2005)). This mechanism may be a basic prerequisite of attentional disengagement, with no computational role, which would seem to be confirmed by the lack of significant correlations between strength of activity in the LC and decision-making performance.

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Insert Table 4 about here  
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To check the robustness of our argument that higher attentional control leads to superior decision-making performance, we investigated whether the total numbers of exploration/exploitation choices, or the total number of switches between these two choices, were correlated with superior decision-making performance. We proposed that what matters for decision-making performance is neither the amount of exploration (i.e. number of exploration choices) nor the relative numbers of exploitation and exploitation choices, but rather how one switches between the two. We tested our argument further by controlling for whether the total number of explorative or exploitative choices affected decision-making performance.

We found a negative correlation between number of exploration choices and decision-making performance. In other words, participants who engaged less in exploration generally achieved superior decision-making performance (see table 5). We also tested for whether the number of switches from exploration to exploitation, and vice versa, was correlated with decision-making performance, and found no significant correlation. These findings support our argument that the higher the attention, the higher the payoff.

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Insert Table 5 about here  
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## **Discussion and Conclusions**

This study contributes to the ambidexterity debate by revealing the cognitive processes behind exploration and exploitation, and the superior decision-making performance derived from switching between exploitation and exploration. The literature provides various solutions to the exploration-exploitation trade-off, and there is consensus that key decision-makers must be able to reconcile exploration and exploitation (Gibson *et al.*, 2004; Lubatkin *et al.*, 2006; O'Reilly *et al.*, 2011). To advance knowledge in this area, we focused on how expert decision-makers deal with the ambidexterity problem, and have shed light on the neural processes involved.

From a neuroscientific viewpoint, the paper puts forward a coherent functional framework that includes the brain regions that constitute the microfoundations for superior decision-making performance, and in which the LC-NE system and the FPC play a pivotal role. These brain areas appear to control

individuals' awareness of the broader environmental conditions, and the ability to adapt their behavior to changing environmental circumstances (Aston-Jones *et al.*, 2005; Cohen *et al.*, 2007).

On this basis, we make several contributions. First, we identify the neural correlates of exploitation and exploration decision-making by expert managers, and their underlying cognitive processes. Exploitation relies on brain regions associated mainly with anticipation of rewards; exploration depends on regions associated mainly with attentional control. In line with Gupta *et al.* (2006), we find that, at the individual level, exploration and exploitation are separate behaviors involving different cognitive processes. The neurological findings on the activation of different brain regions are evidence of the separation between two important constructs in the innovation literature (Willingham and Dunn, 2003). We show that superior decision-making performance relies on the ability to sequence exploitation and exploration appropriately, and to recognize when to switch to exploration.

Second, from a learning theory perspective, our results show that both bottom-up and top-down learning are involved in explorative and exploitative decisions. The striatal habituation mechanisms associated with learning by doing (Aston-Jones *et al.*, 2005) that we identify during exploitative choices are associated with bottom-up learning processes, while the attention control mechanisms are associated with top-down learning processes. A related contribution is on the complementarity between experiential and deliberate learning (Zollo and Winter, 2002); future studies could evaluate the relative effectiveness of each.

Thirdly, our findings relate to the role of emotion in decision-making. We found that exploration has an emotional cost because it involves abandoning less uncertain gains for more uncertain but potentially larger rewards. March (1991, p. 81) points out that the returns from exploration are 'uncertain, distant, and often negative.' This implies not only an economic trade-off, but also the resolution of conflicting feelings, since the outcomes might be negative.

Finally, we contribute to the attention-based view in the firm literature. Many definitions of organizational control stress the role of cognitive processes, especially attention. Ocasio suggests that attention 'is not a unitary concept but a variety of interrelated mechanisms and processes that at the level of the human brain operate in diverse ways.' (2011, p. 1286). Our findings could contribute to theories at the intersection of control and attention through our focus on attentional control as the cognitive mechanism that experienced decision-makers use to switch to alternative options (Ocasio and Wohlgezogen, 2008). Attention control guides cognition, particularly when there is no predetermined means to achieve goals. Researchers have emphasized the importance of this type of attention in novel situations with conflicting alternatives (Fernandez-Duque, Baird, and Posner, 2000; Ocasio, 2011). In line with these theories, we find a positive correlation between the strength of attentional control and decision-making performance.

## **Managerial implications**

Our findings suggest new ways to develop simple but robust baseline models using very precise techniques such as fMRI, and ultimately to develop training tools targeted precisely at specific cognitive processes.

We know that neurological processes deteriorate with age. This is important, since leaders tend to be older. Can they still innovate, and look beyond what they already know? The cognitive processes associated with attentional control can be learnt and improved, as demonstrated by the ‘cognitive remediation’ procedures used to treat certain psychiatric disorders. These might be adapted to train healthy individuals (Tchanturia *et al.*, 2005).

Also, our framework shows that sustained high performance depends not on individual specialization, but on the ability to shift between exploitation and exploration, which in turn depends on stronger activation of the brain regions responsible for attentional and cognitive control. Research shows that attentional and cognitive capacities are impaired by stress and sleep deprivation, often prevalent in organizational decision-making settings (Baumeister *et al.*, 1998; Vohs *et al.*, 2008). Also, repeated use depletes cognitive control in the short term, so subjects are more likely to make shortsighted decisions if they have recently made several decisions requiring the use of cognitive control.

Neurological methods enable the construction of a more complete map of these processes, showing how they are connected, revealing the core ‘circuitry’ underpinning managers’ ability to shift their learning strategies. Our implications are about training, not selection and hiring. The plasticity of the systems we have identified open up avenues to develop precise, and customized, training tools for managers.

## **Limitations and future research**

Our work has several limitations that correspond to promising areas for future research.

In our definition of exploration, the alternatives are known, but their outcomes are uncertain. This line of work should be extended such that both alternatives and outcomes are unknown. We speculate that attention control regions will be used to identify promising new options, and that emotion might play a larger role.

We chose the simplest operationalization of exploration and exploitation. Future studies could restrict the definition of exploitation to participants persisting with the same slot choice for N trials. Also, exploration and exploitation could be framed according to different reinforcement learning models. For example, in ongoing related work by the authors, exploration occurs only if the participant chooses a slot machine with a lower expected value than the previous one. This definition emphasizes the ‘computational’ element in human decision-making.

There are other individual-level factors that might affect ambidexterity. For example, personality traits might shape individual abilities and preferences. Further research could focus on the factors present

from birth or early life (temperament) vs. personality traits acquired through experience (character). This could be measured using a biologically and neurobiologically grounded personality scale (Cloninger, 1994).

The gap between individual behavior and organizational ambidexterity also needs further investigation. For example, escalation of commitment drives many macro-level crises, but avoiding such perverse dynamics is problematic (McNamara, Moon, and Bromiley, 2002).

Adding neuroscientific theories and methods to strategy research might add 'detail to our accounts of human behavior' (Becker, Cropanzano, and Sanfey, 2011, p. 950) by encouraging new research directions, and by resolving the conceptual disagreements in organizational research (Volk *et al.*, 2012). However, while the neuroscientific theories and methods in this study make an important contribution, they do not allow us to see the 'bigger picture' of the interactions involved in individual action. We believe that other methods could suggest what mechanisms to search for using neuroscientific techniques. For example, ethnographical studies and in-depth case studies might uncover the processes involved in strategic problem-solving (Kaplan, 2008; Tripsas *et al.*, 2000). Despite its limitations, we believe neuroscience can illuminate similar organizational theories that might rely on the same individual mechanisms. For example, our findings could help identify the individual-level origins of mental models (Porac and Thomas, 1990; Porac, Thomas, and Baden-Fuller, 2011), frames (Kaplan, 2008), and schemas (Rerup and Feldman, 2011; Walsh, 1995).

Another research direction might be to examine how executives formulate and implement strategic visions. Several studies have found that leaders who can 'see' trends and develop strategies to suit are most likely to succeed; however, the roots of these abilities are unclear (Larwood *et al.*, 1995). The results of our study, particularly on the cognitive origins of exploration and the negative emotions present during exploration, contribute to the literature.

More generally, our work responds to recent calls for the study of rationality to be more 'process-focused' (Levinthal, 2011; Levinthal *et al.*, 1993). The processes we identify relate to both expected utility (central to the 'economic' view) and the ability to frame a problem in one of many possible ways, central to Levinthal's (2011) discussion of the behavioral view. While we do not claim to reconcile these views, our paper helps to highlight the boundary conditions between them.

Neuroscientists have suggested that human decision-making processes should be studied as a complex system of interconnected elements. Much of the discussion so far has focused on cognition as a cold and rational process: calculative, attention-related, and reward-oriented. However, there is growing recognition of the role of *emotions* in decision-making, and our unexpected findings on emotion during exploration support this (Hodgkinson and Healey, 2011). More analysis is needed of how multiple cognitive systems interact to govern behavior.

We are far from completely understanding how exploitation and exploration decisions are formed in managers' brains, and from providing a solid micro-foundation to organizational ambidexterity. However, we hope this paper makes a small but significant contribution by grounding a classic strategic dilemma in a firmer understanding of human cognition.

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## Tables and figures

**Table 1. Brain regions' acronyms and full names**

<b>Acronym</b>	<b>Full name</b>
Ac	anterior commissure
Acb	nucleus accumbens
ACC	anterior cingulate cortex
Amg	amygdala
AnG	angular gyrus
BG	basal ganglia
Cb	cerebellum
dAAC	dorsal anterior cingulate cortex
DLPFC	dorsolateral prefrontal cortex
DS	dorsal striatum
FEF	frontal eye fields
FPC	frontopolar cortex
Hip	hippocampus or hippocampal formation
IFG	inferior frontal gyrus
Ins	insula
IPL	inferior parietal lobule
IPS	intraparietal sulcus
LC	locus coeruleus
LC-NE	locus coeruleus-norepinephrine
MFG	middle frontal gyrus
MTG	middle temporal gyrus
mPFC	medial prefrontal cortex
OFC	orbitofrontal cortex
pao	parietal operculum
PL	parietal cortex
PoG	postcentral gyrus
poCC	posterior cingulate cortex
pre-SMA	pre-supplementary motor area
Sub	subiculum
SFG	superior frontal gyrus
SMA	supplementary motor area
SN	substantia nigra
SOG	superior occipital gyrus
SPL	superior parietal lobule
STG	superior temporal gyrus
Str	striatum
Th	thalamus
tmp	temporal pole
TPJ	temporo-parietal junction
VFC	ventral frontoinsula cortex
vmPFC	ventro medial pre frontal cortex
VS	caudate nucleus
VTA	ventral tegmental area

**Table 2. Neural correlates of exploitation.** The table columns indicate, from left to right, the critical data concerning the regions that were more strongly activated by exploitation than exploration, namely: their size (K) based on the most common measure in neuroimaging studies, i.e. number of voxels of size 2 x 2 x 2 mm<sup>3</sup>; their hemispheric side (H), i.e. left (L) or right (R); the localization coordinates on a normalized brain map (i.e. Brodmann areas) in terms of x (left to right), y (back to front) and z (bottom to top) coordinates; the level of activation of their local-maxima (i.e. voxel T-score). Significant values appear in bold text. The last column shows the p-value associated with each cluster of voxels. This represents a whole activated brain region. A cluster p-value depends both on the number of voxels (K) and on the t-scores of the single voxels that belong to that cluster. For this reason, only one p-value per cluster is shown. All the reported voxels and clusters survive a statistical threshold of  $p < 0.05$  corrected for multiple comparisons.

K	H	Anatomical region (BA)	x	y	z	Voxel T-score	Cluster p-value
2462	L	Medial orbital gyrus (MOrg)	-4	54	-4	<b>10.07</b>	<b>0.00001</b>
	L	Rectus gyrus (part of vmPFC)	0	48	-20	<b>6.89</b>	
	L	Superior medial gyrus (SmG)	-8	58	22	<b>7.94</b>	
	R	Superior medial gyrus (SmG)	8	56	20	<b>7.06</b>	
	L	Superior frontal gyrus (SFG)	-20	28	44	<b>6.83</b>	
	L	Anterior cingulate cortex (ACC)	0	36	0	<b>6.10</b>	
131	L	IFG pars orbitalis	-36	34	-12	<b>7.92</b>	<b>0.00001</b>
85	L	Inferior Frontal Gyrus (IFG)	-50	28	8	<b>6.58</b>	<b>0.00001</b>
74	R	Supplementary motor area (SMA)	8	-20	54	<b>5.70</b>	<b>0.00001</b>
26	L	Middle cingulate cortex	-6	-20	48	<b>5.23</b>	<b>0.001</b>
27	L	Paracentral lobule	-4	-22	60	<b>5.26</b>	<b>0.001</b>
195	R	Rolandic operculum	56	0	6	<b>6.01</b>	<b>0.00001</b>
	R	Superior temporal gyrus (STG)	60	-2	-10	<b>5.18</b>	
	R	Temporal pole (tmp)	58	4	-8	<b>5.20</b>	
12	R	Parietal operculum (pao)	40	-28	24	<b>5.26</b>	<b>0.004</b>
11	L	Postcentral gyrus (PoG)	-54	-4	16	<b>5.27</b>	<b>0.005</b>
230	L	Precuneus (Pcu)	-20	-50	12	<b>6.57</b>	<b>0.00001</b>
	L	Posterior cingulate cortex (poCC)	-6	-48	30	<b>6.53</b>	
418	L	Superior temporal gyrus (STG)	-56	-6	-10	<b>6.32</b>	<b>0.00001</b>
	L	Middle temporal gyrus (MTG)	-58	-4	-20	<b>7.12</b>	
77	L	Middle temporal gyrus (MTG)	-58	-40	0	<b>6.11</b>	<b>0.00001</b>
12	L	Angular gyrus (AnG)	-46	-58	26	<b>5.39</b>	<b>0.004</b>
	L	Middle temporal gyrus (MTG)	-48	-56	22	<b>5.28</b>	
301	L	Hippocampus (Hip)	-22	-16	-16	<b>8.39</b>	<b>0.00001</b>
216	R	Hippocampus (Hip)	24	-16	-16	<b>8.03</b>	<b>0.00001</b>

**Table 3. Neural correlates of exploration:** The columns indicate, from left to right, critical data concerning the regions that were more strongly activated by exploitation than exploration, namely: their size (K) based on the most common measure in neuroimaging studies, i.e. number of voxels of size 2 x 2 x 2 mm<sup>3</sup>; their hemispheric side (H), i.e. left (L) or right (R); the localization coordinates on a normalized brain map (i.e. Brodmann areas) in terms of x (left to right), y (back to front) and z (bottom to top) coordinates; the level of activation of their local-maxima (i.e. voxel T-score). Significant values appear in bold text. The last column shows the p-value associated with each cluster of voxels. This represents a whole activated brain region. A cluster p-value depends both on the number of voxels (K) and on the t-scores of the single voxels that belong to that cluster. For this reason, only one p-value per cluster is shown. All the reported voxels and clusters survive a statistical threshold of  $p < 0.05$  corrected for multiple comparisons.

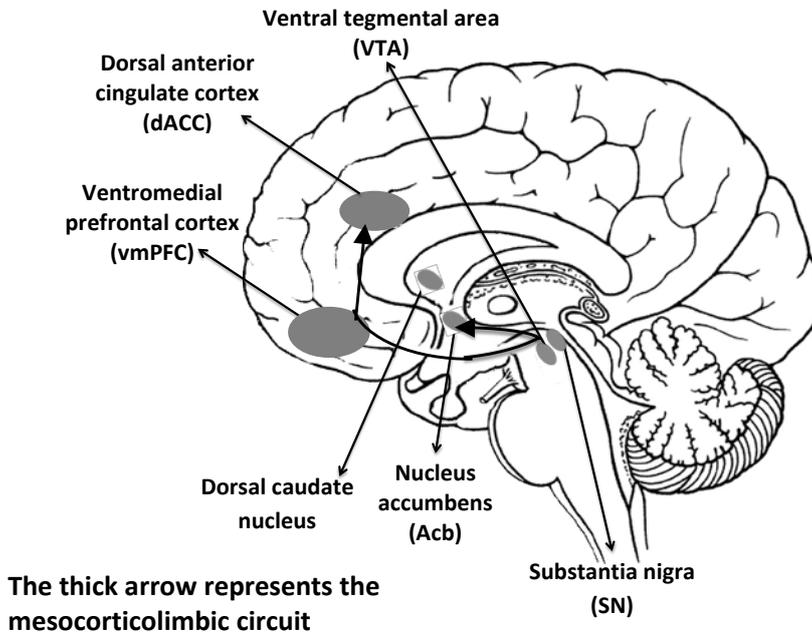
K	H	Anatomical region (BA)	x	y	z	Voxel T-score	Cluster p-value
965	L	Superior frontal gyrus (SFG)	-24	-4	52	<b>12.97</b>	<b>0.00001</b>
361	L	Precentral gyrus (PrG)	-48	4	34	<b>8.51</b>	<b>0.00001</b>
759	L	Middle frontal gyrus (MFG)	-42	28	30	<b>8.36</b>	<b>0.00001</b>
3828	R	Superior frontal gyrus (SFG)	24	-4	54	<b>14.59</b>	<b>0.00001</b>
	R	Middle frontal gyrus (MFG)	36	40	30	<b>9.02</b>	
	R	IFG pars opercularis	46	10	36	<b>6.40</b>	
	R	IFG pars triangularis	44	30	28	<b>8.69</b>	
355	L	Insula (Ins)	-34	16	2	<b>7.55</b>	<b>0.00001</b>
229	R	Insula (Ins)	36	22	-2	<b>7.18</b>	<b>0.00001</b>
407	L	SMA	-4	10	50	<b>7.72</b>	<b>0.00001</b>
	R	SMA	2	10	52	<b>7.27</b>	
	L	Superior medial gyrus	-4	24	38	<b>5.48</b>	
	R	Middle cingulate cortex	8	24	38	<b>6.77</b>	
9365	L	Superior parietal lobule (SPL)	-16	-68	56	<b>17.50</b>	<b>0.00001</b>
	L	Superior parietal lobule (SPL)	-26	-56	46	<b>15.77</b>	
	R	Superior parietal lobule (SPL)	20	-66	56	<b>16.82</b>	
	L	Inferior parietal lobule (IPL)	-38	-36	40	<b>13.30</b>	
	R	Inferior parietal lobule (IPL)	36	-42	44	<b>14.73</b>	
	R	Precuneus (Pcu)	12	-68	58	<b>16.12</b>	
	R	Superior occipital gyrus (SOG)	22	-66	44	<b>14.24</b>	
21	L	Locus coeruleus (LC)	-4	-32	-14	<b>5.38</b>	<b>0.001</b>
16	L	Locus coeruleus (LC)	-8	-32	-26	<b>5.71</b>	<b>0.003</b>
151	R	Cerebellum (Cb)	34	-36	-32	<b>7.59</b>	<b>0.00001</b>
	R	Cerebellum (Cb)	22	-40	-26	<b>5.67</b>	
25	R	Cerebellum (Cb)	12	-32	-26	<b>5.47</b>	<b>0.001</b>
7	L	Thalamus (Th)	-12	-16	10	<b>5.07</b>	<b>0.009</b>
6	R	Thalamus (Th)	16	-22	12	<b>5.13</b>	<b>0.011</b>

**Table 4. Activation of switching brain regions and decision-making performance:** Correlation between the intensity of the activation in the brain regions in charge of switching to explore and decision-making performance (measured as total number of points accumulated over the 300 trials of the four-armed bandit task).

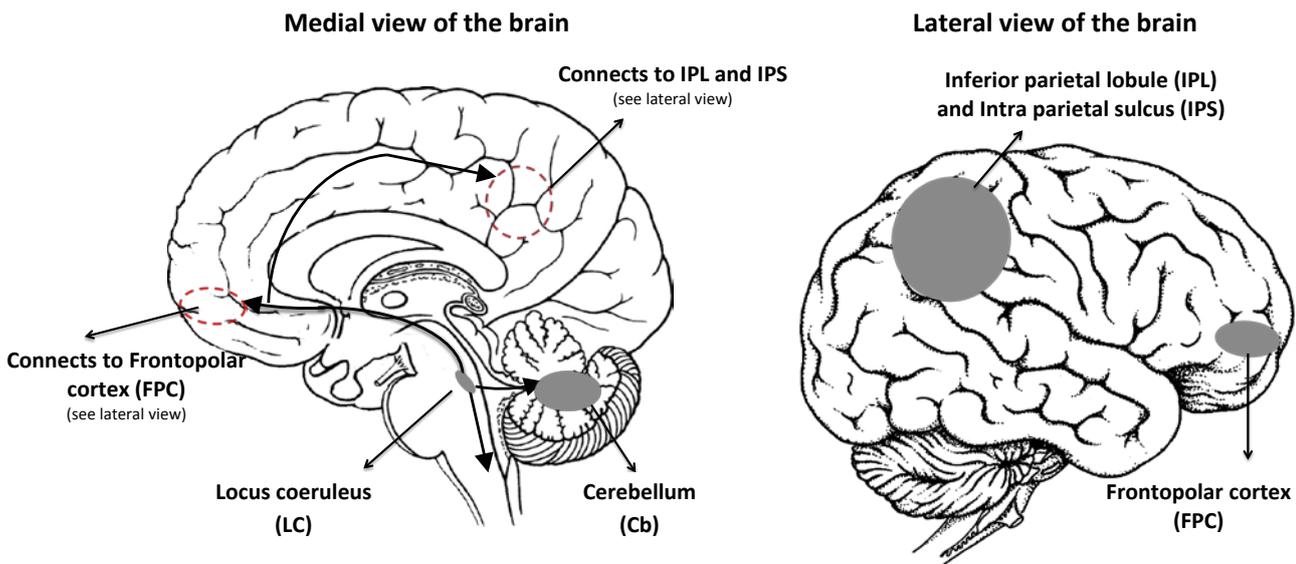
<b>Brain activation and performance</b>	<b>Correlation</b>	<b>p-value</b>
left fronto polar cortex (l FPC)	0.243	0.05
right fronto polar cortex (r FPC)	0.262	0.04
left Intraparietal sulcus (l IPS)	0.173	0.18
right Intraparietal sulcus (r IPS)	0.388	0.00
Locus coeruleus (LC)	0.169	0.19
right middle frontal gyrus (MFG)	0.347	0.01
ventro medial prefrontal cortex (vmPFC)	0.228	0.07

**Table 5. Extent of exploration and exploitation and decision-making performance:** The rows show the significance levels for the numbers of exploitation choices, exploration choices, switches from exploration to exploitation, and switches from exploitation to exploration, correlated with decision-making performance. Decision-making performance is measured as the total number of points accumulated over the 300-trials of the 4-armed bandit task.

<b>Type of behavior correlated with decision-making performance:</b>	<b>Correlation</b>	<b>p-value</b>
Number of exploitative choices	0.774	0.000
Number of explorative choices	-0.736	0.000
Number of switches from exploration to exploitation	-0.216	0.125
Number of switches from exploitation to exploration	-0.238	0.090



**Figure 1. Graphical representation of the medial view of the brain, with the location of the main brain regions involved in exploitation (H1).**

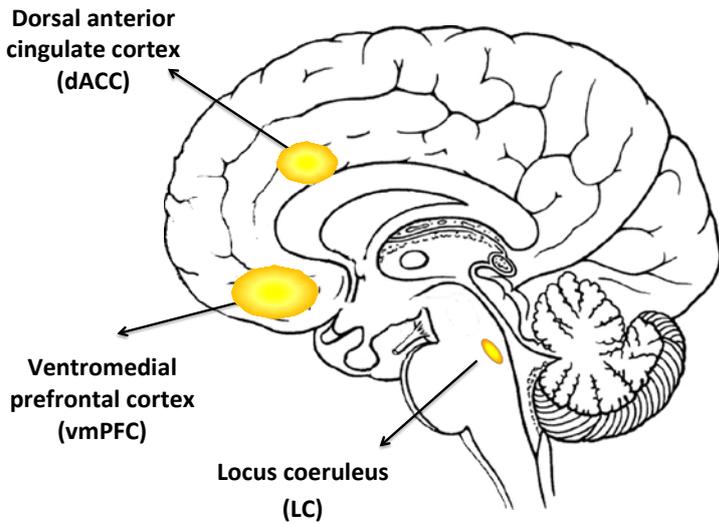


**Figure**

The thick arrow represents the attention control circuit

**2. Graphical representation of the medial (left) and lateral (right) views of the brain, with the location of the main brain regions involved in exploration (H2).**

Medial view of the brain



Lateral view of the brain

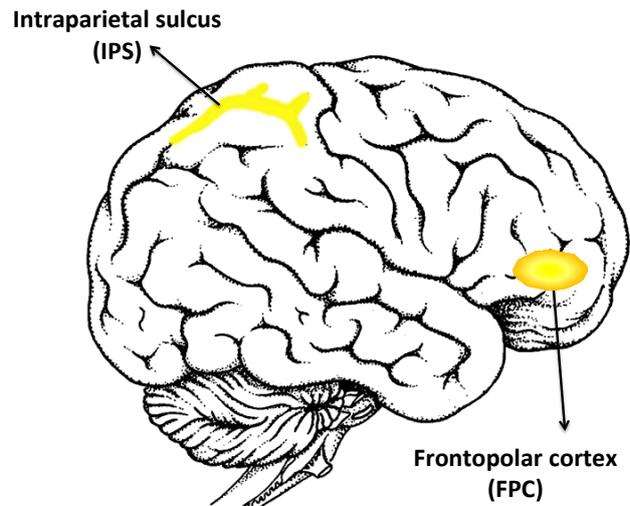


Figure 3. Graphical representation of the medial (left) and lateral (right) views of the brain, with highlighted the main brain regions involved in switching to exploration (H3).

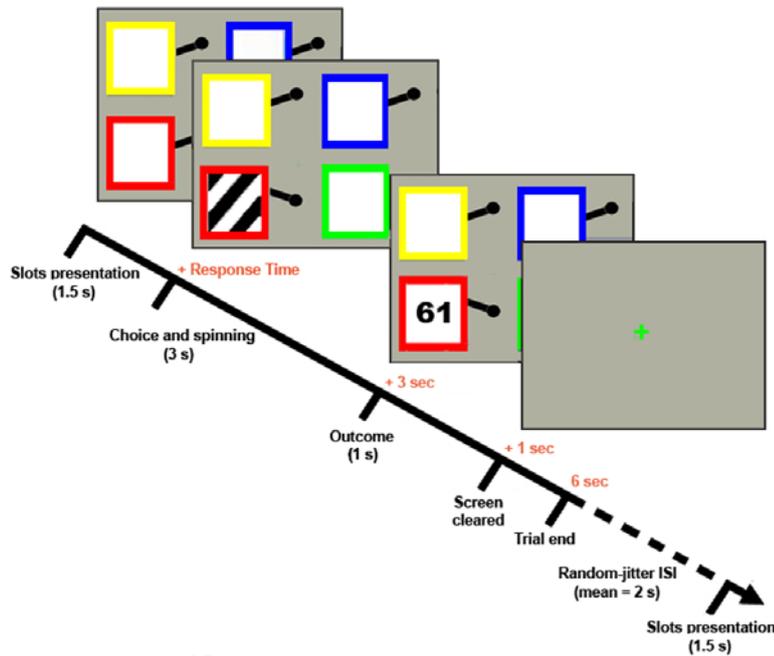
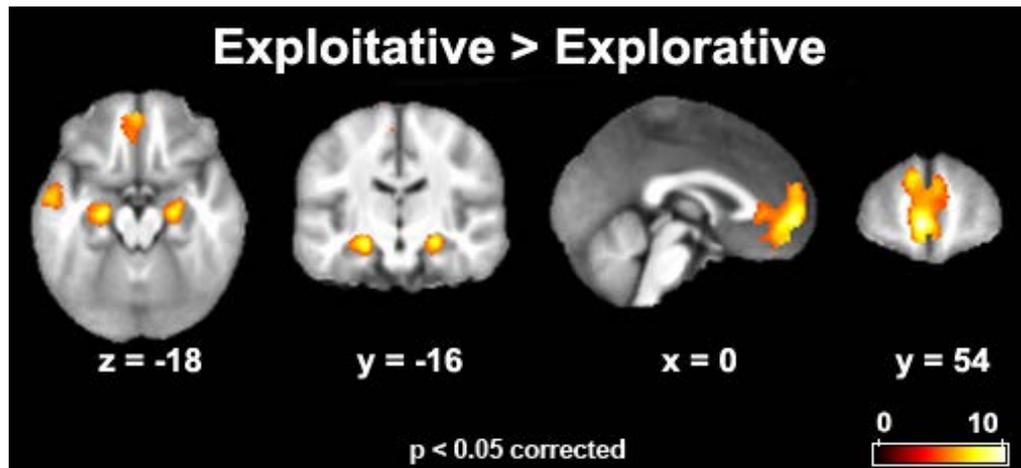
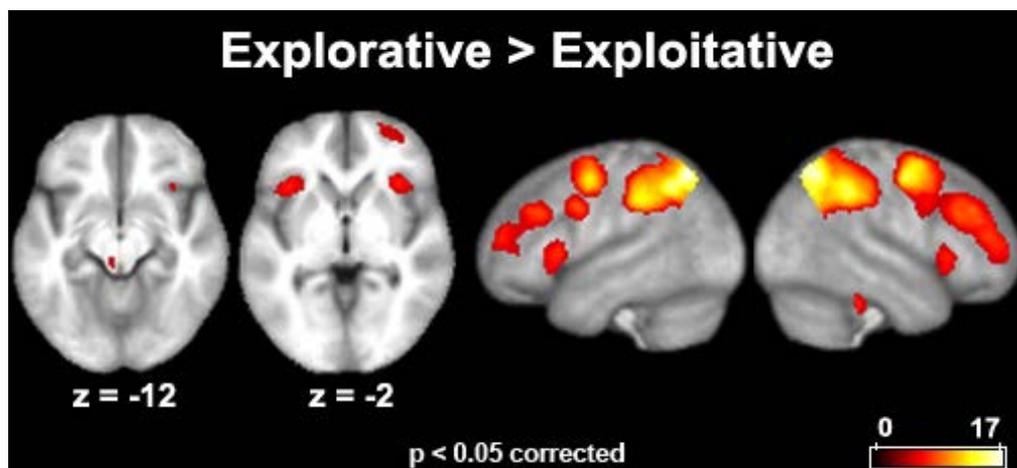


Figure 4. Task presentation and decision-making process



**Figure 5. The neural bases of exploitative choice**

The brain regions that are more strongly activated by exploitation than exploration choices are shown on transverse, coronal and sagittal sections of an average brain obtained from individual subjects' T1-weighted anatomical images. The distance (in mm) of sections from the origin of the stereotaxic space (namely anterior commissure (Ac)) is displayed below each slice. All displayed activations survive a statistical threshold of  $p < 0.05$  corrected for multiple comparisons.



**Figure 6. The neural bases of explorative choice**

The brain regions that are more strongly activated by exploration than exploitation choices are shown on transverse sections and 3D renders of an average brain obtained from individual subjects' T1-weighted anatomical images. The distance (in mm) of sections from the origin of the stereotaxic space (Ac) is displayed below each slice. All displayed activations survive a statistical threshold of  $p < 0.05$  corrected for multiple comparisons.