The Choice is Yours

the cognitive and neural mechanisms underlying the beneficial effect of autonomy on learning

Zhaoqi Zhang

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Chapter 1

General introduction

I still remember my childhood experience of learning traditional Chinese dancing. One day, I told my teacher how much I loved a particular piece and asked if I could perform it at a school event. Although I had learned many equally beautiful dances, this one stayed with me. The difference was not in the steps or the music, but in the fact that I made the choice. That sense of **autonomy**, in other words, self-regulation of one's experience and actions (Ryan & Deci, 2000b, 2006; Ryan & Deci, 2020), leads to stronger and more lasting memory. As Carl Rogers once said, *"The only kind of learning which significantly influences behaviour is self-discovered, self-appropriated learning."* This sentiment illustrates the importance of autonomy in learning and education. Yet, it is surprising that the cognitive and neural mechanisms underlying the beneficial effect of autonomy on learning and memory remain poorly understood.

In the current chapter, I will introduce the benefits of autonomy on learning, along with different ways to satisfy the need for autonomy. Drawing on principles from ecological psychology (Favela, 2023; Gibson, 1983; Sims, 2021), I argue that investigating the interaction effects between autonomy and other modulating factors from micro- to macro-levels would deepen our understanding of how autonomy enhances learning. To begin with, I discuss how the beneficial effect of autonomy on learning is influenced by the information context surrounding a person. Specifically, from the predictive processing perspective (Desantis et al., 2011; Moore & Haggard, 2008), I highlight how uncertainty in the direct perceptual inputs modulates the experience of autonomy. Next, I posit that autonomy is inherently rewarding, like food, money, or other external incentives. Grounded in self-determination theory (SDT), we synthesize how the intrinsic value of autonomy may be modulated by the presence of external rewards, integrating evidence from both behavioural and neuroscientific perspectives. In addition, I discuss the role of macro-level socio-cultural factors that may shape the effect of autonomy during learning. This chapter provides an overview of the key experimental questions that the thesis seeks to answer.

1.1 Autonomy benefits learning and memory

Autonomy, defined as self-regulation of one's experiences and actions, is one of the three basic psychological needs (i.e., autonomy, relatedness, and competence) in self-determination theory (Deci & Ryan, 1985; Deci & Ryan, 1987; Ryan & Deci, 2000b, 2006; Ryan & Deci, 2017). When people experience a sense of autonomy, they tend to be more intrinsically motivated to learn (Deci & Ryan, 1987; Ryan & Deci, 2006; Ryan & Deci, 2020). Educational studies have found that students retain information better after autonomous learning, like exploring an aquarium or a museum, than those who learn through traditional classroom lectures (Falk, 2006). Hence, it is crucial to support autonomy during learning.

1.1.1 Operationalizing autonomy during learning

The need for autonomy could be supported by offering people opportunities to make active choices during learning and memory encoding. Extensive empirical studies have shown that making active choices boosts memory formation (Baldwin et al., 2021; Ding et al., 2021; Fantasia et al., 2020; Kennedy et al., 2024; Lima et al., 2023; Murty et al., 2015; Rotem-Turchinski et al., 2019). In a commonly used paradigm tackling this research question, participants were offered two masked images that they might see. In half of the trials, participants could freely choose which image they wanted to see (i.e., choice condition), while in the other half, it was a forced-choice condition where the image was predetermined for the participants (i.e., no-choice condition), and participants were forced to press the indicated button corresponding to the assigned image. After pressing a button, the corresponding masked image would be revealed, and participants were asked to remember the images as well as possible. It was found that under the active choice condition, participants could remember the images better compared to the forced choice condition (e.g., Murty et al., 2015). Choosing the item appeared to promote greater self-involvement, deeper engagement, and a stronger sense of personal relevance during learning, all of which enhance memory encoding (Baldwin et al., 2021).

Beyond this binary choice paradigm, making decisions in more naturalistic environments also fosters the sense of autonomy. For instance, freely exploring a new city similarly fosters stronger memory encoding for its layout compared to following rigid, prescribed routes. In these cases, exploration itself can be viewed as a continuous series of active choices, fulfilling the need for autonomy. For instance, Voss, et al. (2011b) implemented a free-exploration paradigm, in which participants viewed a 5×5 grid of images obscured by Gaussian noise. An open window revealed the images in this grid one at a time. In some grids, participants could freely control the window's movement, while in other grids, the window followed a fixed trajectory that participants were instructed to track using a joystick. They found that active exploration enhances memory performance compared to when participants were asked to follow a predefined exploration route. This finding has since been replicated by subsequent studies employing similar exploration paradigms (Kaplan et al., 2012; Markant et al., 2014a; Markant, et al., 2016a; Schomaker et al., 2014; Schomaker & Wittmann, 2021; Voss, et al., 2011a; Voss, et al., 2011b).

Together, these findings suggest that autonomy, expressed through either discrete choices or naturalistic exploration, benefits memory encoding. However, despite this growing body of evidence, the cognitive mechanisms through which autonomy facilitates learning and memory remain poorly understood. In the current thesis, two experimental paradigms were employed to address this research topic: one involving discrete, binary choices (e.g., Murty et al., 2015) and the other based on free exploration (e.g., Voss et al., 2011b).

1.1.2 Autonomy and ecological psychology perspective

To understand the effect of autonomy on learning, it is essential to move beyond merely demonstrating its benefits and instead examine the underlying cognitive mechanisms, which remain insufficiently understood. Inspired by ecological psychology (Favela, 2023; Gibson, 1983; Sims, 2021), human behaviours, including motivations in learning, are shaped by the dynamic interplay between predictive processes, external micro-environment, and broader socio-cultural contexts. To start with, integrating with the predictive brain perspective, which hypothesizes that our brain is constantly generating expectations about future events (Clark, 2013). The act of making a choice has been proposed to support the internal active inference about upcoming information, reflecting an interplay between volitional action and uncertainty in the environment (Friston et al., 2013). Moreover, within cognitive evaluation theory, a branch of SDT, intrinsic motivation, like autonomy, could be influenced by external incentives, like rewards (Ryan & Deci, 2017), akin to micro-environmental factors. This is because the perceived locus of causality was moved from purely internal to external when people were rewarded for learning. In other words, people would be dependent on the existence of rewards for learning while losing their internal interest or motivation to gain knowledge. Furthermore, it has been emphasized that human motivation is also shaped by nested socio-environmental influences, from ideological to economic factors (Oishi & Choi, 2017; Oishi & Graham, 2010).

By systematically examining factors across three hierarchical levels (Fig. 1.1), the current thesis investigates the cognitive and neural mechanisms through which autonomy shapes learning and memory. These factors include internal predictions towards upcoming information (predictive processing, **Chapters 2 and 3**), external incentives (monetary rewards, **Chapter 4**), and cultural contexts (**Chapter 5**). Rather than treating these factors as confounds, they are conceptualized as ecologically valid moderators that allow us to reveal how autonomy facilitates memory.

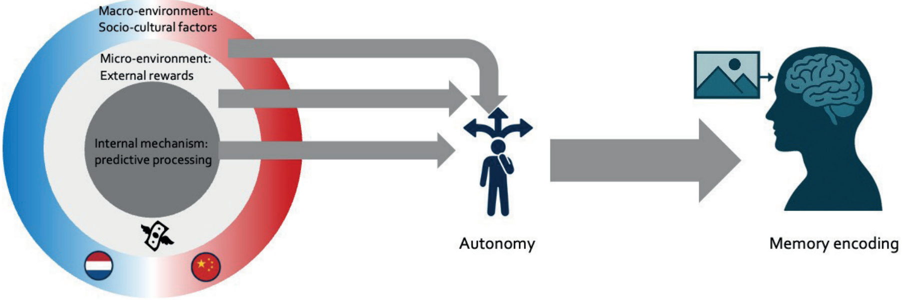

Figure 1.1 Hierarchical structure of the factors that influence the effect of autonomy in memory encoding. From an ecological psychology perspective, the beneficial effect of autonomy in memory encoding is modulated by multiple sources. These sources include: (1) internal mechanisms such as predictive processing of incoming information (grey circle), (2) micro-environmental stimuli like money, grades, or rewards (white circle), and (3) macro-environmental forces such as socio-cultural norms that shape the value placed on different motivational factors (blue and red circle).

1.2 Internal mechanism: Autonomy and predictive processing

To start with, I will introduce how autonomy and predictive processing, which is the most fundamental and internal layer of our framework (Fig. 1.1), interact in the brain to support learning and memory. According to the predictive coding theory of the brain (see Section 1.1.2; Clark, 2013), a prior belief would be generated before making an active choice. Then, when human beings make a voluntary action, like a choice, they build up a causal relationship between this voluntary action and the appearance of a certain outcome following that action (Desantis et al., 2011; Moore & Haggard, 2008). In this sense, choices could shape expectations and the perception of information input. Based on previous studies, two key mechanisms have been proposed to explain how choice interacts with predictive processing during learning. First, individuals are thought to engage in choices and actions to reduce uncertainty in the environment, and the mere act of making a choice may create a feeling of increased predictability. Second, making choices can enhance the attentional alignment, allowing people to better adjust their focus toward the upcoming information.

1.2.1 Autonomy and uncertainty reduction

First, it has been proposed that making choices could cause a sense of control over the outcomes of their choices (agency; Haggard, 2017; Haggard & Chambon, 2012), and that the uncertainty in the environment has been reduced. While this idea has been explored in information seeking, it remains underexamined in the context of memory encoding. For instance, active choices appear to optimize learning by overweighting perceived information, like perceived direction of a motion or the sum of the number shown to them, that is consistent with their choices to reduce the uncertainty in the environment (Talluri et al., 2018). Also, making choices modulates the learning rates in reward learning (Chambon et al., 2020). It showed that learning rates for rewarding outcomes are higher when participants were allowed to make choices compared to when choices were predetermined, suggesting that autonomy promotes a more active update of reward-related information.

Moreover, when people make choices, they predict that the outcome will align with their choices, thereby reducing the prediction error upon receiving information (Peterson et al., 2011). Abir et al. (2024) found that human beings initially chose to seek out uncertainty but later prefer to reduce it. They suggested that individuals initially approach uncertainty to gather sufficient evidence to construct a reliable model of the world, thereby enabling them to reduce uncertainty in the future. More strikingly, Devine et al. (2024) demonstrated that while individuals generally prefer having choices, they abandon this preference when choices no longer provide control over outcomes of the choices. Hence, these studies suggest that the value of choice emerges from its ability to create a reliable link between actions and outcomes. This prompts us to wonder: if this reliable link between choice and the outcome is broken (i.e., under conditions of low predictability), meaning that the choices were only symbolic but conveying no instrumental information, would the effect of active choice on learning diminish?

Taken together, we raise our first research question: How does predictive processing modulate the effect of choice on memory encoding? Previously, Katzman and Hartley (2020) implemented a paradigm to investigate how memory was influenced by choices and the predictability of those choosing behaviours. In their experiment, participants explored “galaxies” where one planet had a higher probability of containing treasure items, or galaxies where both planets had a random probability of finding treasure items. Participants either made a choice or were assigned one planet and were instructed to remember the item they encountered. Results showed that memory for treasure items was better when participants made the choice themselves, but only in galaxies where reward outcomes were not random (Katzman & Hartley, 2020). This suggested that when the outcomes of the choices were predictable, making choices could enhance memory, whereas unpredictability eliminates this benefit of choices on memory, highlighting a close link showing that active choices facilitate predictive processing during learning. Notably, although participants’ choices influenced which planet they visited, the specific information they had to remember (the items) was not directly tied to their choice. To be more specific, participants could only predict the amount of reward associated with the planet they chose, but they could not form a causal link between the planet and the information they needed to remember. Hence, their study offered an initial glimpse into how active choices enhance memory encoding by supporting predictive coding of perceptual information. Building on this, **Chapters 2 and 3** employed a binary choice paradigm, in which choice outcomes were directly tied to the information that participants needed to remember. Also, featuring a clear distinction between consistent and inconsistent outcomes, the binary design allowed a targeted investigation of how predictive mechanisms modulate the difference in memory accuracy of information from visual input between choice and no-choice conditions.

1.2.2 Autonomy and attention modulation

Second, since people more actively predict upcoming information when making choices for what they want to see, it also enables them to coordinate attention in advance, thereby preparing effectively for what they are about to perceive. This is supported by previous findings showing that even if people could only control or choose *when* to adjust their attention to the next object, memory was already boosted (Kennedy et al., 2024; Markant & Gureckis, 2014; Markant, et al., 2016b). This attentional tuning process supports memory encoding and retention before information even appears (Gureckis & Markant, 2012). Meanwhile, this was also indicated from a neuroimaging study suggesting that when autonomy is supported by active exploration, it would engage more attentional control brain regions, including the dorsal lateral prefrontal cortex (DLPFC) and the dorsal anterior cingulate cortex (Dack) (Dubinsky & Hamid, 2024; Voss, et al., 2011a).

In a study conducted by Luo et al. (2022), it was suggested that attention preparation would only happen when the outcome of the choice was predictable. In their experimental setting, participants were more concentrated and exhibited faster reaction times in the subsequent attentional task when they had chosen and could predict the background picture for each trial. However, when participants were unable to predict the consequences of their choices for the background pictures in the same paradigm, the reaction time of the subsequent task was not accelerated by making active choices. Therefore, if choices are not predictive of the outcomes, predictive and/or attentional preparation will lose their merits.

Taken together, these findings offer a compelling explanation that autonomy may enhance attentional tuning before information is perceived, hence, enhance learning and memory. Building on these notions, in **Chapter 4**, we implemented an exploration paradigm in which people were instructed to remember as many objects as possible while their brain activity was recorded with an fMRI (functional magnetic resonance imaging) scanner. By comparing blood oxygenation level dependent (BOLD) signals between free and forced exploration conditions, we aimed to investigate the neural mechanisms underlying learning with autonomy, replicating the involvement of attentional control brain regions as reported by Voss, et al. (2011a).

1.3 Micro-environment: Autonomy and rewards

The next layer of our framework considers the micro-environment, particularly the role of external rewards in modulating the influence of autonomy on learning (Fig. 1.1). From the standpoint of motivation science, it has been argued that the reason why autonomy, like other intrinsic motivators, could support learning is partly because autonomy is rewarding by itself (Leotti & Delgado, 2011). In other words, when people perceive autonomy, they feel satisfied. From self-determination theory, this has been discussed under the situation of how intrinsic motivation and rewards, as extrinsic motivation, work when both of them exist (Ryan & Deci, 2020). In the following section, I will summarize previous findings demonstrating that autonomy is inherently rewarding, as well as how this is reflected in neural mechanisms. I will then outline the existing research gap and provide the rationale for designing a study in this current thesis to further investigate this question.

1.3.1 Converging mechanisms of autonomy and rewards during learning

Autonomy, as one of the key sources of intrinsic motivation (Ryan & Deci, 2000b; Ryan & Deci, 2020), enhances learning because autonomy is rewarding by itself (Leotti & Delgado, 2011). From self-determination theory, choices are internally satisfying and motivate people to continue to learn (Ryan & Deci, 2020). This could be supported by evidence suggesting that inconsequential choices could enhance memory formation (Ding et al., 2021; Murty et al., 2015; Rotem-Turchinski et al., 2019). For instance in Murty et al. (2015), participants were offered two masked images that they might see. In half of the trials, participants could freely choose which image they wanted to see (i.e., choice condition), while in the other half, it was a forced-choice condition where the image was predetermined for the participants (i.e., no-choice condition), and participants were forced to press the indicated button corresponding to the assigned image. After pressing a button, the corresponding masked image would be revealed, and participants were asked to remember the images as much as possible. With this paradigm, although participants could choose between the left and right options, they made their selection without any prior information about the images each option would reveal. Moreover, with a similar design, DuBrow et al. (2019) found that people had a stronger preference towards the stimuli associated with the choice condition compared to the images related to the no-choice condition. More interestingly, it was also demonstrated that making active choices could heighten curiosity towards the outcomes of the lotteries (Verdugo et al., 2023). Taken together, having the opportunity to choose is fulfilling in and of itself and can enhance learning, regardless of the choice outcomes. These findings diverge from previous studies (Section 1.2) suggesting that the memory benefits of choice stem primarily from its role in modulating predictive processing (e.g., Katzman & Hartley, 2020). Extending this distinction, it is possible that choice enhances memory not only by supporting prediction of upcoming information but also by eliciting a more positive or rewarding affective response toward the chosen content (Leotti & Delgado, 2011).

Although few studies have directly compared the neural mechanisms of autonomy to external rewards, research consistently shows that intrinsic and extrinsic motivation in learning engage overlapping brain regions. Given that autonomy is a core source of intrinsic motivation (Ryan & Deci, 2000a; Ryan & Deci, 2020), insights into its neural basis can be drawn by integrating findings from studies on both intrinsic and extrinsic motivational processes. To start with, reward-motivated learning could elicit functional activation and connectivity among a network of distributed regions, including the orbital (OFC) and ventral medial prefrontal cortex (VMPFC) and dopaminergic circuitry, i.e., the ventral tegmental area (VTA), midbrain, and ventral striatum (Adcock et al., 2006; Cohen et al., 2014; Dubinsky & Hamid, 2024; Haber & Knutson, 2010; Schultz, 2015; Sescousse et al., 2013; Shigemune et al., 2014; Wolosin et al., 2012). Importantly, learning with intrinsic motivation also elicits activation and connectivity of the abovementioned brain regions. For instance, curiosity, as a form of intrinsic motivation, is also related to reward-related brain regions (Gruber et al., 2014; Gruber et al., 2019; Kang et al., 2009), and making active choices boosts curiosity (Verdugo et al., 2023). Thus, we argue that making a choice is rewarding because it satisfies a certain need for more information, like satisfying the need for rewards (Litman et al., 2005; Marvin & Shohamy, 2016). However, whether autonomy specifically enhances dopaminergic circuitry remains underexplored, highlighting an important research question for the current thesis.

1.3.2 Undermining intrinsic motivation with extrinsic motivation?

The beneficial effect of autonomy on memory encoding has been found to be modulated by rewards (van Lieshout et al., 2023; Xue et al., 2023). This interaction can be explained according to the “overjustification” hypothesis (Cameron, 2001; Hidi, 2016; Lepper et al., 1973; Murayama et al., 2010). To elaborate, when students were offered external rewards, they would attribute their enjoyment of the learning activity to external rewards instead of to the activity itself. Within self-determination theory, this phenomenon is also known as the undermining effect, in other words, the observation that adding extrinsic motivation where intrinsic motivation is already present might harm this intrinsic motivation (Deci & Koestner, 1999; Hidi, 2016; Houlfort et al., 2002; Kuvaas et al., 2020; Murayama, 2022; Tang & Hall, 2006). This undermining effect is usually observed in settings where intrinsic motivation is measured before and after the introduction of extrinsic rewards. If there is a significant decrease in intrinsic motivation after the removal of extrinsic rewards compared to the baseline, people speak of it as an undermining effect (Deci, 1971; Lepper et al., 1973; Murayama et al., 2010). However, few studies have directly examined the simultaneous effects of autonomy and reward, leaving the interaction between these two motivational factors insufficiently understood.

The undermining effect of external rewards on intrinsic motivation may stem from overlapping neural mechanisms shared by intrinsic and extrinsic motivation, specifically the dopaminergic reward circuitry including the ventral striatum, ventral tegmental area, and substantia nigra (Dubinsky & Hamid, 2024; Gruber et al., 2014; Kang et al., 2009). One possible explanation is that the presence of external rewards already engages the dopaminergic reward circuitry to be activated, limiting the additional activation that intrinsic motivation could elicit for these brain regions. For example, Murayama et al. (2010) demonstrated that participants who received rewards showed higher reward circuitry activation during the task but subsequently exhibited lower intrinsic motivation to perform better once the reward was removed. They argued that the previous presence of external rewards may overshadow the inherent satisfaction of following task engagement, making intrinsic success less salient.

On the other hand, it has also been reported that intrinsic and extrinsic drives benefit memory performance independently (Duan et al., 2020). This may reflect the recruitment of distinct neural mechanisms in parallel, aligning with notions that extrinsic motivation engages reward-related regions, whereas intrinsic motivation additionally evokes attentional control networks such as the DLPFC and dACC (Murty et al., 2015). Altogether, these findings point to conflicting evidence regarding whether or how intrinsic and extrinsic motivational drives interact during learning. Notably, there is a lack of studies that simultaneously manipulated both intrinsic and extrinsic motivational factors in learning while measuring brain activity.

Taken together, we address our next research question: Does reward modulate the beneficial effect of choice on memory, and if so, how? To tackle this research question, we designed a project in **Chapter 4**, in which we implemented the paradigm from Voss, et al. (2011b). Additionally, we added the reward factor parallel with the manipulation of autonomy in their design, in which we could then investigate not only the effect of autonomy and rewards, but also how reward modulates the impact of autonomy on memory encoding and associated brain activity with fMRI scanning during task.

1.4 Macro-environment: socio-cultural factors modulating the effect of autonomy and rewards on learning

There has been an ongoing debate regarding how autonomy is influenced by socio-cultural factors, as well as how external rewards may modulate the motivation underlying autonomy. We propose that much of this debate arises from overgeneralizations in interpreting results without simultaneously considering multiple factors. In the current thesis, we aimed to address this gap by examining autonomy, reward, and socio-cultural influences together within a unified framework. From a social-cognitive perspective (Han, 2017), previous findings have shown contradictory evidence regarding the effect of autonomy on learning and motivation across different cultural groups, suggesting that the role of autonomy may not be universal but context-dependent. In this paragraph, I will specifically discuss how socio-cultural factors shape the effect of autonomy, with a particular focus on how they may influence the interaction between autonomy and reward during learning.

1.4.1 Autonomy and socio-cultural factors

On the one hand, there is sufficient evidence suggesting that the beneficial effect of autonomy for learning is universal across Eastern and Western cultures (Chirkov et al., 2003; Chirkov, 2009; Chirkov et al., 2010; Helwig, 2006; Nalipay et al., 2020; Ryan & Deci, 2006; Vansteenkiste et al., 2006; Vansteenkiste et al., 2020; Vansteenkiste et al., 2005; Wichmann, 2011; Yu et al., 2016). Although it is more intuitive to think that autonomy is a Western philosophical concept rooted in individualism and self-development (Christman, 2003), Eastern Confucian culture has also emphasized the importance of personal choices (i.e., autonomy) in learning, conceptualized as “self-cultivation” (Helwig, 2006; Ryan & Deci, 2017; Zusho, 2005). In Chinese culture, Taoism especially emphasizes the sense of autonomy and freedom in personal behaviours (Wenzel, 2003). This was also in line with the Basic Psychological Needs Theory in self-determination theory, suggesting that autonomy is an instinctive psychological need, and it is not influenced by social contexts (Ryan & Deci, 2017; Vansteenkiste et al., 2020).

On the other hand, some studies have suggested that having autonomy is more valuable for students from Western cultures than for students from Eastern cultures (Iyengar & Lepper, 1999; Markus & Kitayama, 2003; Sastry & Ross, 1998). This could be explained by potential differences in the origins of intrinsic motivation to learn between Eastern and Western cultures (Liu et al., 2020b). They elaborated that for European students, intrinsic motivation usually comes from their own interest in learning (i.e., autonomy). However, for Eastern students who were deeply influenced by Confucian philosophy, their intrinsic learning motivation comes from the internalization of the importance of learning. In other words, they derived a strong personal belief that learning is important for their future development, social status, and career success, despite their lack of interest in the learning content. These differences in values might also shift learning styles and preferences. For example, Chinese students embrace teacher-led instructions, aligning with cultural norms of respect for guidance, whereas American students often view the same approach as constraining and prefer a more self-dependent learning style (Zhou et al., 2012).

However, most existing studies have focused on workplace settings or survey-based educational research approaches to investigate the influence of socio-cultural factors in learning motivation. In the current thesis, we aim to investigate autonomy as a motivator during learning within a controlled but naturalistic learning environment for students across different cultural backgrounds. By doing so, we aim to generate insights with direct relevance for educational practice, highlighting how fostering autonomy can support more effective and culturally responsive learning and memory encoding behaviours in real-world educational settings. In **Chapter 5**, we implemented the same exploration paradigm as **Chapter 4**, in which we compared factors of autonomy on learning in both Dutch and Chinese cultural groups, aiming to investigate socio-cultural differences in the beneficial effect of autonomy on memory encoding.

1.4.2 Overgeneralization of autonomy and rewards: socio-cultural factors

Moreover, findings regarding how rewards influence the beneficial effect of autonomy on learning remained inconsistent. Although an undermining effect of rewards on autonomy has been proposed (van Lieshout et al., 2023; Xue et al., 2023), there is also contradicting evidence that intrinsic motivation in learning is not influenced by extrinsic motivation (Duan et al., 2020). The differing results in these studies may stem from an overgeneralization of the circumstances (Eisenberg, 2002). It was proposed that the Eastern population might be more intrinsically motivated to work with external regulation from other people, whereas the Western population might be less intrinsically motivated to work with outside control (Eisenberg, 2002). Hence, we propose that the variability in inconsistent findings of the interaction effect between autonomy and reward on learning may be due to the lack of consideration for additional moderating factors, such as cultural contexts or achievement levels (Han, 2017). Since the sources of intrinsic motivation differ across cultural backgrounds, responses to extrinsic motivation from students with Eastern or Western cultural backgrounds may also diverge. For instance, survey studies have found that students from Eastern cultures often internalize the value of education as a pathway to future development, which may lead them to perceive extrinsic rewards, like achievement, rewards, or excellence in certain skills, as supportive. In contrast, Western students who are typically driven by personal interest may experience extrinsic motivation as controlling (Liu et al., 2020b). However, little research has explored how cultural factors shape the interaction between extrinsic and intrinsic motivation in learning contexts. Therefore, **Chapter 5** of this thesis aims to address this gap by investigating how cultural background influences the relationship between autonomy and rewards during learning.

1.5 Thesis outline

The current thesis presents four projects designed to investigate the cognitive and neural mechanisms underlying the beneficial effect of autonomy on learning. The four projects were developed across three levels of analysis: the predictive processing of the brain, external motivational influences, and socio-cultural factors. In **Chapters 2 and 3**, autonomy was manipulated in a binary choice paradigm, providing a straightforward manipulation of internal predictive processing dynamics associated with the choices. In **Chapters 4 and 5**, autonomy was manipulated through an exploration paradigm, in which participants were either given the opportunity to actively control their exploration route in their learning or were required to follow predetermined paths. **Chapter 4** examined how extrinsic rewards influence the autonomy effect on learning, while **Chapter 5** explored how cultural contexts modulate the beneficial effect of autonomy on learning.

In **Chapter 2**, we investigated how the predictability of choice outcomes modulated the beneficial effect of choice on memory encoding by employing a binary choice task (Murty et al., 2015; Zhang et al., 2024). We manipulated choice and the predictability of the choice outcomes in the following way. In half of the blocks, participants could choose which object they wanted to see, while in other blocks, the choices were made for them. Meanwhile, in half of the choice and no choice blocks, they would always see the selected object, while in other blocks, they had a 50% chance to see the selected object. Their memory accuracy was tested using a recognition task. This design allowed us to examine how active choices enhance memory encoding by engaging stronger predictive processing towards upcoming information.

In **Chapter 3**, based on the findings from **Chapter 2**, we implemented a stronger control over the choice outcomes by holding predictability constant throughout memory encoding and manipulating only the surprise of the choice outcomes on each trial in the encoding task. Participants were required to learn associations between colours and categories. Then, in the memory encoding phase, participants were asked to choose between two category options on each trial or simply press a button following the predetermined choice made for them. In half of the trials, participants saw an image belonging to the category they chose or assigned for them, while in the other half of the trials, they saw an image belonging to a different category from the one they chose or assigned for them. We hypothesized that memory accuracy would benefit from active choices when participants saw a consistent category to their choice, while it remained unknown how active choices would modulate memory accuracy when the prediction of the choice outcome was violated by surprising information.

In **Chapter 4**, we investigated how the beneficial effect of autonomy on learning was influenced by monetary rewards. We adapted a well-controlled explorative learning paradigm from Voss and colleagues for use in the fMRI scanner (Voss, et al., 2011b). In this paradigm, participants were presented with a 5 x 5 grid consisting of object images obscured by visual noise except for a (circular) searchlight window. These objects could be revealed by moving the searchlight window around the screen. Autonomy was manipulated as follows: In the autonomous condition, participants were given volitional control over the temporal and spatial trajectory of the searchlight window using a joystick. In the non-autonomous condition, participants were instructed to follow (mimic with the joystick) an exploration trajectory shown on screen. Importantly, we adapted this paradigm by introducing a reward manipulation orthogonal to the autonomy manipulation. This was done by offering participants a monetary reward for their memory performance for objects from selected autonomous and non-autonomous grids, and not for other grids. Participants' recognition and spatial memory performance were assessed in a separate memory task. As such, this design allowed us to investigate the effects of autonomy, reward, and their interaction on memory accuracy as well as brain activity during learning.

In **Chapter 5**, we implemented the same paradigm and design as in **Chapter 4**, for which we collected behavioural data in both Nijmegen, the Netherlands, and Beijing, China. We compared the influence of reward on autonomy from different cultural groups of interest. **Chapter 5** provided a socio-cultural perspective of the motivations in learning.

Chapter 6 provides a summary of the main findings of the current thesis, discussing the most relevant findings of this thesis and future directions.

In the current thesis, by investigating these various factors, including internal predictive processing, external reward, and overall socio-cultural environment, we aim to unravel the cognitive and neural mechanisms of the beneficial effect of active choice on learning.

Chapter 2

Predictability modulates the beneficial effect of choice in memory encoding

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Abstract

When people are offered the opportunity to choose, they tend to learn better. However, the cognitive mechanisms of the beneficial effect of choice on learning and memory encoding have been rarely investigated. On one hand, self-determination theory has proposed that choices themselves might be rewarding, even when their consequences are not predictable. On the other hand, from a predictive coding perspective, choices facilitate learning because they enhance the prediction of upcoming information. To delve deeper into these two interpretations, we conducted 2 experiments using a memory encoding task in which we independently manipulated choice and predictability. In half of the blocks, participants could choose which object they wanted to see (choice), while in other blocks, the choices were made for them (no choice). Meanwhile, in half of the choice and no choice blocks, they would always see the selected object (high predictability), while in other blocks, they had 50% chance to see the selected object (low predictability). The memory accuracy was tested by a recognition task. In both experiments, we found that the facilitatory effect of choice on memory accuracy existed under both high and low predictability. However, this effect was smaller under low predictability. These findings provided evidence for both interpretations: choices enhance learning because they are rewarding by themselves while, at the same time, facilitating prediction processes. This study has important implications for education, urging teachers to offer choices to students and to satisfy students' needs in classroom settings.

2.1 Introduction

The world around us offers an enormous number of possibilities to satisfy our needs. For example, when we learn to play the piano, we must decide which music style to start with. The fact that you can choose might make you happy in and of itself: simply having the opportunity to choose which style to play might delight you. However, choices also lead to different consequences. Thus, perhaps the choice itself is not rewarding, but the fact that you can predict the outcome of the choice (the music) is. The current study aims to investigate how choices affect our learning and memory encoding under different predictabilities.

Learning and memory formation can be promoted when people can make their own choices. According to the self-determination theory (SDT), autonomy (i.e. the freedom to choose), is defined as a key motivational drive for learning. People are more likely to continue to learn when their need for autonomy is satisfied (Ryan & Deci, 2020). Indeed, a multitude of studies have demonstrated that the freedom to choose boosts memory encoding (e.g., Ding et al., 2021; Lima et al., 2023; Murty et al., 2015; Rotem-Turchinski et al., 2019). For example, Murty et al. (2015) found higher memory accuracy in a condition in which participants could choose which picture they would like to see (choice condition), compared with a condition in which the choice was made by the computer (no-choice condition). Similar beneficial effects of choice on learning performance have been found when choice was manipulated as having volitional control over the spatial learning trajectory over a map of objects (van Lieshout et al., 2023; Voss et al., 2011b), or as choosing the time of viewing object pictures (Markant et al., 2014a). Therefore, the beneficial effect of active choices on learning is consistent and stable. Nevertheless, little is known about its cognitive mechanisms.

Multiple cognitive processes could drive these choice-related memory benefits. First, it might be the case that having a choice is rewarding in and of itself. According to Ryan and Deci (2020), choices are internally satisfying and motivate people to continue to learn. For example, DuBrow et al. (2019) found that people naturally preferred symbols associated with the choice condition compared with the no-choice condition. These symbols were not linked with the pictures that they were asked to remember. Also, a positive correlation was found between the magnitude of the choice-induced preference over the symbols and the memory accuracy of the pictures shown after the selection of the symbols across participants. These findings suggested that inconsequential choices could enhance memory formation (Ding et al., 2021; Murty et al., 2015; Rotem-Turchinski et al., 2019) likely by inducing a more pleasant emotional response (DuBrow et al., 2019). Taken together, having the opportunity to choose is fulfilling in and of itself and can enhance learning, regardless of the choice outcomes.

However, we build up a causal relationship between a voluntary action and the appearance of a certain outcome following that action (Desantis et al., 2011; Moore & Haggard, 2008). Therefore, another line of reasoning suggests that the beneficial effects of choice on learning are due to enhanced predictability of the choice outcomes. According to the predictive coding and free energy principle framework (Friston et al., 2013), active choices help to predict what you are going to perceive (i.e. choices help you to build a prior belief of the upcoming perceptual information). More specifically, when people make choices, they predict that the outcome will be in line with their choice. These consequential choices reduce the prediction error over time (Peterson et al., 2011). On the contrary, if the choices do not predict the outcome, the prediction error cannot be reduced, and learning is not enhanced. Hence, only choices that are associated with smaller prediction errors will improve learning (Peterson et al., 2011). For instance, some studies have suggested that the beneficial effects of choice on learning disappear when the choice is not predictive of the outcome (Chambon et al., 2020; Katzman & Hartley, 2020; Schneider et al., 2018).

By means of two experiments, we aim to investigate the cognitive mechanisms of the beneficial effects of choice on learning. Specifically, we aim to unravel whether the beneficial effect of choice on learning stems from the inherent reward from choice itself (i.e., independent from the choice outcome) or if it relies on the correct prediction of the outcome of the choice (i.e., dependent on the choice outcome). To address this inquiry, we designed a learning experiment in which we independently manipulated 2 factors: (1) the presence of a choice itself (yes or no), and (2) the predictability of the choice outcome (high or low). In each trial, participants were presented with two object names. These names corresponded to actual object images that participants had to remember. Participants could sometimes choose which of these two objects they wanted to learn (choice condition), and sometimes the choice was made for them (no-choice condition). After the selection, participants saw one of the object images. In high predictability blocks, this object image always corresponded to the object name that they chose or that was chosen for them. In other words: participants could predict which of the object images they would see. In low predictability blocks, participants could not accurately predict which of the two object images would be revealed to them. This was the case because participants would see the selected object in half of the trials but would see the not selected object in the other half of the trials. Afterwards, participants' learning performance was evaluated by a separate recognition memory test.

Given the two explanations regarding the source of the choice effect outlined above, we raise two possible hypotheses. If the choice effect on learning purely comes from the inherent reward caused by making a choice, the beneficial effect of choice on memory accuracy would be present in both high and low predictability scenarios (e.g., Murty et al., 2015). Alternatively, if the positive effect of choice on learning solely comes from the effective prediction of choice outcomes, the beneficial effect of choice on memory accuracy would be present in high predictability scenarios, but not when participants could not predict the upcoming picture (e.g., Katzman & Hartley, 2020). These experiments will help us to further understand the beneficial effects of choice on learning performance and to better utilize choices in industrial and educational contexts.

2.2 Experiment 1

2.2.1 Methods

2.2.1.1 Preregistration & data and code availability

Experiment 1 and its analyses were preregistered on the Open Science Framework (https://doi.org/10.17605/OSF.IO/TNQRE). All data and code used for stimulus presentation and analyses of both experiments are freely available on the Donders Repository (https://data.ru.nl/login/reviewer-2730442050/2T3HWWOJY7CNIAESJ76XPFLZVHG7Q23GSSFLCMY).

2.2.1.2 Participants

To determine the sample size of our experiments, we conducted a power analysis with MorePower (Campbell & Thompson, 2012). The power analysis suggested that we need at least 52 participants to detect a large effect size (*partial eta*^{2} = 0.14) with 80% power for the interaction between choice and predictability conditions using a 2 x 2 repeated measures ANOVA.

We recruited a total of 58 participants in total, of which 55 participants (age = 22.7 ± 3.7 (M ± SD), 37 females, 17 males, 1 non-binary) were included for the final analysis. One participant (57 years old) was excluded because his age was more than 3 standard deviations removed from the average age of the participant sample. Another participant was excluded because of a procedural mistake by the experimenter, and one participant was excluded for unavoidable disruption during the learning task. Participants all reported their English fluency as “very good” and had normal or corrected-to-normal vision.

The experiment was approved by the Ethics Committee of the Faculty of Social Sciences (ECSW) at Radboud University, Nijmegen, under the general ethics approval for standard studies conducted at the Donders Centre for Cognition (ECSW.2018.115). Prior to participation, all participants gave written informed consent according to the Declaration of Helsinki and confirmed that they were all over 18 years old.

2.2.1.3 Procedure

To test the effect of choice on memory accuracy under different predictabilities, we designed a task consisting of a memory encoding phase and a memory test phase. The experiment was performed using Presentation® software Version 23.0 (Neurobehavioral Systems, Inc., 2023).

For the memory encoding phase of the experiment, 448 pictures of unique objects were selected from a database for visual stimuli (Brady et al., 2008). Before object presentation, the names of the objects were presented on the screen. These object names were taken from the original database. All the names were checked and, when necessary, corrected by 2 native English speakers. For each participant, the 448 objects were randomly combined into 224 pairs. During the memory encoding phase, only one object of each pair was made visible to the participants, and the participants were instructed to remember these 224 objects as well as possible. During the memory test phase, participants were tested on 448 objects, consisting of the 224 objects they had seen and the 224 objects they had not seen during the memory encoding phase. Participants were asked to indicate whether they had seen the object during the memory encoding phase or not.

During the memory encoding phase, the factors “choice” and “predictability” were manipulated as follows. For the choice manipulation, participants either choose among 2 object name cues representing the object they wanted to see (choice condition), or this choice was made for them (no-choice condition). Next, for the predictability manipulation, they either always saw the object corresponding to the selected name (high predictability condition), or they had a 50% chance to see the object corresponding to the selected name and a 50% chance to see the other object (low predictability condition). In the low predictability condition, participants were not explicitly told that the chance of seeing the selected object was 50%. Instead, they were told that “you might have a chance to see the object that you select”. Hence, the whole experiment was a 2 (choice vs no-choice) x 2 (high predictability vs low predictability) within-group design.

More specifically, in every trial of the memory encoding phase (Fig 2.1A), participants first saw a fixation cross in the centre of the screen with presentation time jittered between 500 and 1500 ms (uniformly distributed). Next, 2 object names were presented left and right to the fixation cross together with a red up-arrow on the screen for a maximum of 5000 ms. In the choice condition, participants would see the red up arrow pointing at the fixation cross, indicating that they could select one of the objects that they wanted to see by pressing the button on the left or right. In the no-choice condition, the red up-arrow would already point at one of the object names, and the participants were instructed to press the button on that corresponding side. As soon as the participants pressed the button, only the selected object name would stay on the screen for another 1500 ms. Next, a white screen was presented (1000 ms), followed by one of the object pictures presented in the middle of the screen with its name above it (1000 ms). In the high predictability condition, participants always saw the object picture that they selected or that was selected for them. In the low predictability condition, participants had a 50% chance to see the object picture that they selected or that was selected for them, and a 50% chance to see the object picture corresponding to the other object name. In other words: There was low predictability regarding whether they would or would not see the object that was selected before. The trial ended with a white screen (700 ms).

During the memory encoding phase, the four conditions (Fig. 2.1B) were presented separately in 4 blocks. The order of the conditions was fully randomized and counterbalanced across participants. Each block contained 56 pairs of objects, which were randomly paired and assigned to one of the conditions beforehand for each participant separately. Participants were instructed to remember the pictures that were made visible as well as possible in all conditions.

After the 4 blocks of the memory encoding phase, participants performed a recognition memory test (Fig. 2.1C). Every trial of the memory test started with a fixation cross presented in the middle of the screen (700 ms), followed by a white screen with a jittered duration between 500 and 1000 ms (uniformly distributed). Then, an object picture was presented on the screen until a button was pressed. Participants were asked to press a button to indicate whether they had seen the object during the memory encoding phase or not. From left to right, there were four buttons corresponding to “Definitely not seen”, “Probably not seen”, “Probably seen”, and “Definitely seen”. After pressing a button, a white screen would be presented

(700 ms) after which the next trial would start. Participants were instructed to perform as accurately as possible.

Before the experiment started, participants underwent a practice session. The practice session consisted of all 4 learning conditions, which were presented in the same order as the formal learning blocks. There were 4 trials for each condition and each condition was presented in a different block. Before each block, participants were asked to read the instructions on the screen and summarize them to the experimenter. This was done to ensure that they understood each condition. During the practice session, we showed participants that, if they failed to press a button within 5000 ms after the object names were presented, a "Too late!" message would be presented on the screen together with one of the object names (1500 ms). In the choice condition, this object name would be randomly selected for them, while for the no-choice condition, the object name corresponding to the correct selection would stay on the screen. If participants pressed the wrong button in the no-choice condition, they would see the message "Wrong button!" together with the name corresponding to the selection they should have made. In other words, making a wrong response did not affect the selection made for them. There was also a short practice of the memory test, consisting of 4 trials. In these trials, objects that they saw during the practice learning block were presented. It should be noted that the objects used during the practice session were not included in the actual experiment.

Participants spent between 75 and 90 minutes in the lab and were paid 15 euros or an equivalent amount of course credits.

2.2.1.4 Data preprocessing

We prepared data with Python 3.11 (Van Rossum, 2023). Only the objects that were seen by participants were considered for analysis. If a seen object was rated as "probably seen" or "definitely seen" during the memory test phase, this memory trial was coded as 1 (accurate). While if a seen object was rated as "probably not seen" or "definitely not seen", this memory trial was coded as 0 (inaccurate). Therefore, for each participant, there were at most 224 memory trials considered for the final analysis. These objects were categorized according to their learning conditions. Objects in the learning trials during which participants did not press a button within the maximum object name viewing time (5000 ms) or pressed the wrong button in no-choice learning blocks were excluded (12 out of 12320 trials in total, 12308 trials left for analysis).

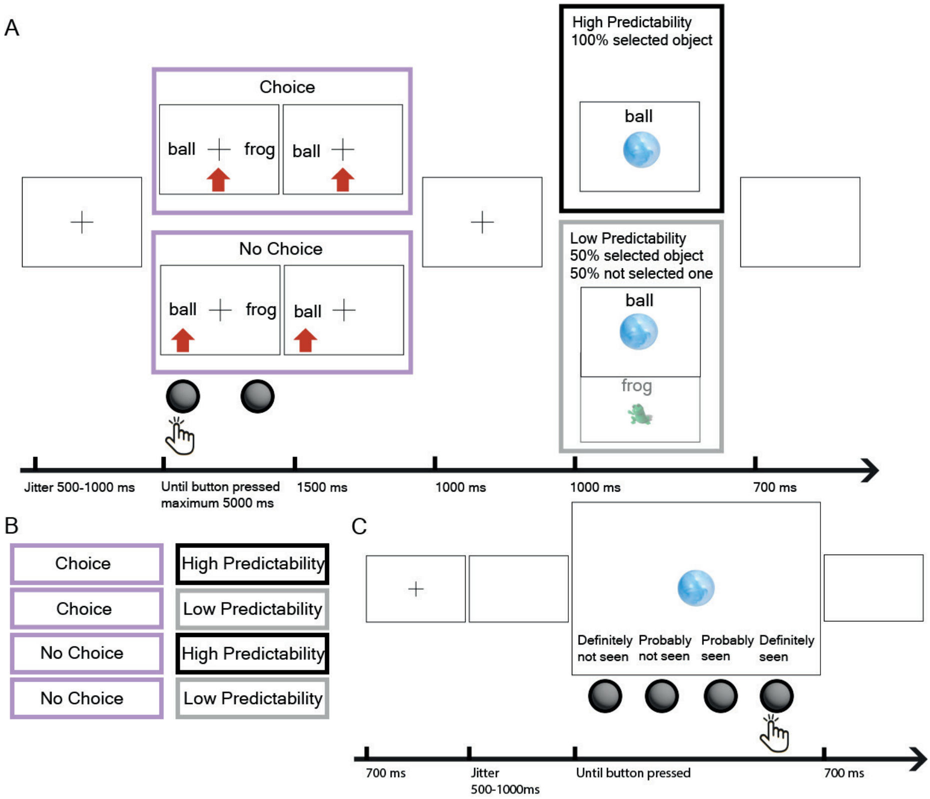


Figure 2.1. Procedure for Experiment 1. **A.** In the memory encoding phase, each trial started with a fixation cross. Then, in choice conditions, participants would see the red arrow appear in the middle of the screen along with 2 names of the objects on the left and right side of the screen. They were instructed to choose one of the names by pressing one of the buttons. In no-choice conditions, participants would see a red arrow on one side of the screen, indicating that they had to press the corresponding button. After this, only the selected name stayed on the screen together with the fixation cross. After the selection stage, in the high predictability conditions (black box), participants would always see the object that they selected or that was selected for them. In the low predictability conditions (grey box), participants were told that they might have a chance to see the selected object. In practice, this meant that the selected object was presented in 50% of the trials, whereas the not-selected object was presented in the other 50% of the trials. **B.** Overview of the conditions. The choice or no-choice condition was paired with the high predictability or low predictability condition. Hence, we had four conditions that would be presented in 4 separate blocks. The order of the blocks was randomized across participants. **C.** During the memory test phase, participants saw a fixation cross followed by an object in each trial. They can press one of the four buttons to indicate whether they have seen the object or not. The possible responses were as follows: “Definitely not seen”, “Probably not seen”, “Probably seen”, and “Definitely seen”. After pressing the button, the object will disappear, and they will see a blank screen. Then the next trial will start.

Furthermore, we also coded how confident participants were that they had seen the object during the memory encoding phase (confident: 1; not confident: 0). Objects that participants indicated to have “definitely seen” or “definitely not seen” in the memory test phase were coded as “confident”, and objects indicated as “probably seen” or “probably not seen” were coded as “not confident”. In the end, out of the 12308 trials included in the analyses, there were 9676 trials that participants were confident about during the memory test phase and 2632 trials that participants were not confident about. The high portion of confident trials suggested an absence of guessing and a high-quality memory (Meliss et al., 2022).

2.2.1.5 Data analysis

For the primary analyses, we only considered the confident trials (the 9676 trials participants indicated as “definitely seen” or “definitely not seen” in the memory test phase). This was done because when participants responded that the object was “probably seen” or “probably not seen” during the memory test, it might reflect a guess instead of being a signature of actual learning and remembering. This decision was based on a meta-analysis suggesting that intrinsic motivation (e.g., choices, curiosity, or interest) would improve the actual learning performance instead of guesses during the memory test (Cerasoli et al., 2014). In accordance with this argument, it has been suggested that intrinsic motivation could boost learning only for the knowledge that participants were confident about (Galli et al., 2018; Gruber et al., 2014; Meliss et al., 2022; Murphy et al., 2021). Consequently, although we preregistered to include all valid trials for analyses, we decided to perform our analyses on the confident trials alone. The results including only the confident trials are reported in the main text, whereas the results of the preregistered analyses including all trials can be found in the supplement (see Supplementary Material 1). It should be noted that both analyses yielded similar results.

The data were modelled with linear mixed effect modelling (LME) using the *glmer* function of the lme4 package in R (Bates et al., 2015). The main model included accuracy as a binomial dependent variable. The independent variables were choice (yes/no) and predictability (high/low), for which we both created sum-to-zero contrasts. The main model included the main effects of “choice (yes/no)” and “predictability (high/low)”, as well as the interaction effect between “choice (yes/no)” and “predictability (high/low)” as fixed effects. The main model included a full random effects structure (Barr, 2013; Barr et al., 2013) meaning that a random intercept and random slopes for all effects were included per participant. We fitted the model with 10,000 iterations (5000 warm-ups) and diagnosed the model with DHARMa (Hartig, 2020).

If the interaction effect between “choice (yes/no)” and “predictability (high/low)” was significant in the main model, we would perform follow-up analyses to investigate the choice effect (memory accuracy (choice) – memory accuracy (no-choice)) under different predictabilities. To this end, we modelled the data of the high predictability and low predictability conditions separately. We compared the memory test accuracy between choice and no-choice conditions with the *emmeans* function in R (Lenth, 2022). In this way, we were able to detect differences in the choice effect under different predictabilities. On the other hand, with the same procedure as above, we also compared predictability effects (memory accuracy (high predictability) – memory accuracy (low predictability)) under choice or no-choice conditions separately.

Furthermore, to delve deeper into the attenuated choice effect under low predictability, we conducted secondary analyses by separating the trials in the low predictability conditions into "selected" or "not selected" objects. The "selected" objects were the ones consistent with the name that participants pressed the button on (i.e., selected "ball" and saw the picture "ball"), and the "not selected" objects were the ones under the other name that participants did not press the button on (i.e., selected "ball" but saw the picture "frog"). The details and results of these secondary analyses are described in Supplementary Material 2.

2.2.2 Results

For the primary analysis (Fig. 2.2A & 2.2B), we found a main effect of choice ($\beta = 0.29$, $z = 2.28$, $p < 0.001$) on memory accuracy. This indicated that when people could choose, their memory accuracy was higher (M = 84.3%, SD = 12.6%) than in no-choice conditions (M = 76.6%, SD = 16.2%). In contrast, there was no significant main effect of predictability ($\beta = -0.08$, $z = -0.71$, $p = 0.21$), indicating that there was no difference in memory accuracy under high predictability (M = 81.4%, SD = 13.3%) or low predictability (M = 79.7%, SD = 14.6%).

However, we also found a significant interaction effect of choice and predictability on memory accuracy ($\beta = 0.42$, $z = 2.33$, $p = 0.02$). This means that, under the high predictability conditions, memory accuracy was significantly higher in the choice condition (M = 86.3%, SD = 12.5%) than in the no-choice condition (M = 75.6%, SD = 17.4%; $\beta = 0.71$, $z = 5.28$, $p < 0.001$). The same was true for the low predictability conditions. The memory accuracy was higher in the choice condition (M = 81.9%, SD = 14.8%) than in the no-choice condition (M = 77.21%, SD = 17.19%; $\beta = 0.29$, $z = 2.28$, $p = 0.02$). However, the difference in memory accuracy between choice and no choice conditions under high predictability was larger than this difference under low predictability (Fig. 2.2A). Additionally, there was a difference in memory accuracy between high and low predictability conditions when people could choose ($\beta = 0.34$, $z = 2.58$, $p = 0.01$), but not when people could not choose ($\beta = -0.08$, $z = -0.71$, $p = 0.48$).

To summarize, we found an effect of choice on memory accuracy for both the high as well as the low predictability condition. However, this effect appeared to be stronger for the high predictability condition compared with the low predictability condition (Fig. 2.2A).

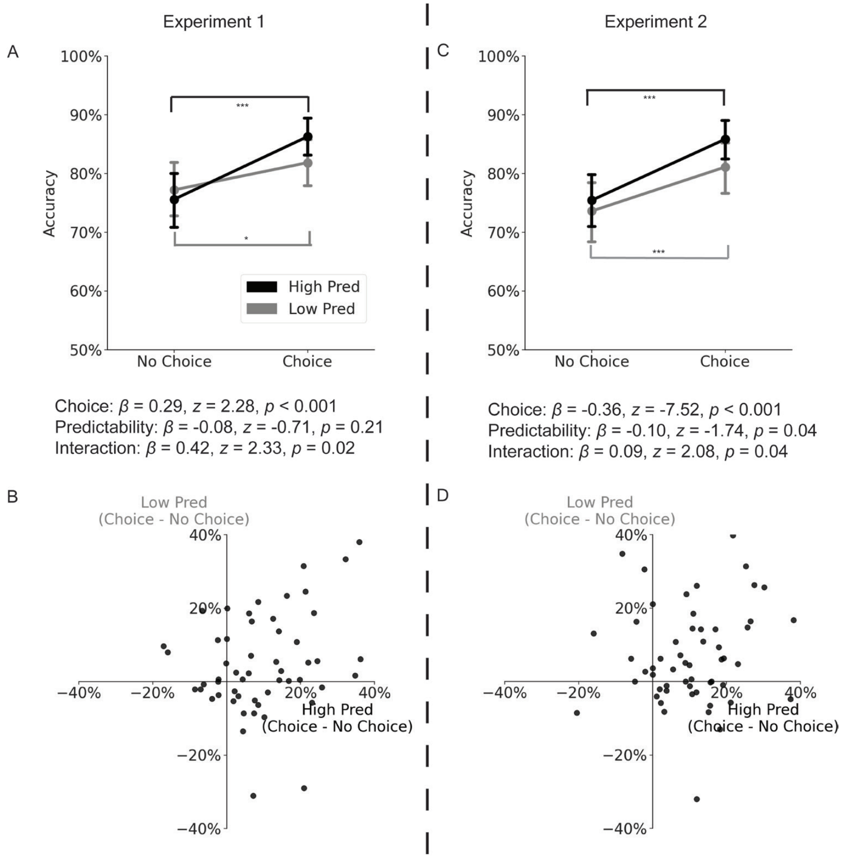


Figure 2.2 Results for Experiment 1 & 2. **A.** For Experiment 1, we found the effect of choice on memory accuracy was significant under different predictabilities, albeit larger for the high predictability than the low predictability conditions. The black colour represents the high predictability (High Pred) condition and the grey colour represents the low predictability (Low Pred) condition. The black or grey coloured lines represent the simple effect comparison (choice – no-choice) under different predictabilities. Asterisks next to the lines indicate the significance of the effects (***, p<0.001; *, p<0.05). **B.** Individual variability in the effect of choice for high predictability conditions (x-axis) compared with low predictability conditions (y-axis). Each dot represents one participant. For high predictability, most participants showed a positive choice effect (positive x-values). For low predictability, the choice effect appeared to be less strong (indicated by a more even distribution of positive and negative y-values). This reflects the reported interaction between choice and predictability on memory accuracy. **C.** As in Experiment 2, the effect of choice on memory accuracy was also larger for the high predictability than the low predictability condition. The results pattern was similar to that in Experiment 1. All other conventions are the same as Panel A. **D.** For Experiment 2, the individual variability in the effect of choice under different predictabilities is similar to that reported for Experiment 1 (Panel B).

2.2.3 Discussion: Experiment 1

In the first experiment, we found a significant main effect of choice on memory accuracy. Participants showed better memory for objects when they had the opportunity to choose than when they could not choose. More interestingly, we found a noteworthy significant interaction effect on memory accuracy between the manipulated factors of choice and predictability. The improvement in memory accuracy attributed to the choice effect was somewhat diminished, but still statistically significant under low predictability conditions.

These findings provide evidence that supports both interpretations of the choice effect. On one hand, the existence of the choice effect under both high and low predictability suggested that choices were rewarding by themselves regardless of the consequences (Murty et al., 2015). On the other hand, the interaction effect between choice and predictability, indicating that the choice effect diminished under low predictability conditions, suggested that choices aided in learning because they enabled individuals to predict the outcomes associated with their choices (Katzman & Hartley, 2020).

However, these findings left open questions behind. In the current setup, within the low predictability conditions, half of the objects that participants saw were not the ones they selected, thus creating an inconsistency between the outcome and predictions associated with their choices. This inconsistency might cause a worse memory of the objects (Frankenstein et al., 2020). Secondary analyses were carried out to ascertain whether the presence of these not selected objects was the sole cause for the dampening of the choice effect (see Supplementary Material 2). We separated the objects under low predictability into "selected" and "not selected". It was revealed that the choice effect on memory accuracy for both selected and non-selected objects in the low predictability condition was significant and comparable, albeit noticeably attenuated compared to the high predictability condition. In other words, this reduction in the choice effect was not limited to not selected objects; it also applied to selected objects.

In summary, based on the findings of Experiment 1, we can conclude that the choice effect on memory was attenuated when participants could not predict the outcome of choices, regardless of whether the outcome was consistent with their choices or not. Thus, the choice effect seems to be related to both the satisfaction of having a choice and the (sensorimotor) consequences that the choice was associated with.

2.3 Experiment 2

Nonetheless, a conspicuous distinction existed between the choice and no-choice conditions. Making a choice is time-consuming (Supplementary Material 3). As a consequence, participants viewed the object names (object name viewing time) longer in the choice than in the no-choice condition, and this effect of choice on object name viewing time was larger under high than low predictability (Supplementary Material 3, Fig. S2.3). Experiment 2 is designed to investigate this fact in more detail since these differences in viewing times might explain the reported effects of choice and predictability on memory accuracy.

To rule out this possibility, we conducted Experiment 2. To this end, we adjusted the paradigm such that (1) the amount of time that the object names were shown to the participants was controlled and kept constant between conditions and (2) ensured that participants always read both object names before seeing the objects themselves. The latter was done by separately presenting each object name for a fixed amount of time before participants were asked to make their choice.

If the reported effects of choice and predictability on memory accuracy are annihilated when controlling for object name viewing time, it might be the case that these object names function similarly to cues that facilitate memory (e.g., Thomson & Tulving, 1970). Consequently, longer exposure to these cues might result in better memory of the affiliated pictures. However, if we find similar effects on memory accuracy as reported for Experiment 1, the main effect of choice on memory accuracy and the interaction between choice and predictability on memory accuracy is likely not driven by object name viewing time.

2.3.1 Methods

2.3.1.1 Participants

For Experiment 2, we recruited 56 participants (average age = 22.27 ± 2.42, 42 females, and 14 males) with the same criteria as Experiment 1.

2.3.1.2 Procedure

In Experiment 2, a similar paradigm was used as in Experiment 1. We made a few adaptations to control for differences in object name viewing time between conditions.

Instead of the choice screen shown right after the jittered fixation cross, participants would first see one object name at a time. For example, the object names “ball” and “frog” were each presented for 1000 ms (one after the other), separated by a 500 ms fixation cross (Fig. 2.3). Following the second object name, another 500 ms fixation cross was presented. Next, the choice screen with the object names and the red up-arrow is presented for a fixed duration of 2000 ms, during which participants had to press a button. In this way, we ensured that both object names were visible for a fixed amount of time (instead of disappearing after the button press, as was the case in Experiment 1). The rest of the trial remained the same as for Experiment 1.

The memory test phase was the same as in Experiment 1. For Experiment 2, participants spent between 100 and 110 minutes in the lab and were paid 20 Euros for participation or an equivalent amount of course credits.

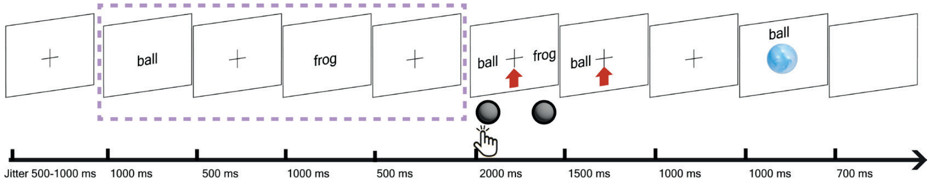


Figure 2.3 Procedure for Experiment 2 (Choice/High-predictability trial as an example). The paradigm from Experiment 1 is adapted to control the amount of time that participants viewed the names corresponding to the objects. After the jittered fixation, participants would view the names of the objects one at a time for 1000 ms, followed by 500 ms fixation. Since both object names were shown in the middle of the screen one by one, we ensured that participants would perceive and process both object names (see purple frame). Afterwards, participants were presented with both object names again and were asked to respond by pressing one of the buttons (2000 ms). Crucially, both object names were on the screen for the full 2000 ms. The rest of the experiment remained the same as Experiment 1.

2.3.1.3 Data analysis

The data were preprocessed in the same way as for Experiment 1. Over data from all the participants, we eliminated 136 (out of 12,544) trials because of wrong or too-late responses. Out of the total 12,408 valid trials, there were 10,142 trials for which participants were confident (responded with “definitely seen” or “definitely not seen”), reflecting high-quality memory in the current experiment (Meliss et al., 2022). As to Experiment 1, we also omitted the unconfident trials (responded with “probably seen” or “probably not seen”) and conducted a main 2 (choice or no-choice) × 2 (high predictability or low predictability) LME analysis on memory accuracy. As for Experiment 1, the results including all trials are reported in the supplement (Supplementary Material 1).

The same secondary analyses as mentioned for Experiment 1 were conducted on the data of Experiment 2. Also, these results can be found in the supplement (Supplementary Material 2).

2.3.2 Results

By means of Experiment 2, we have replicated the main findings of Experiment 1 (Fig 2.2C & 2.2D). First, we found a main effect of choice ($\beta = 0.36$, $z = 7.52$, $p < 0.001$) on memory accuracy. This indicated that when people could choose, their memory accuracy was higher (M = 83.7%, SD = 13.9%) than in no-choice conditions (M = 74.8%, SD = 16.3%). Second, there was also a significant main effect of predictability ($\beta = 0.10$, $z = 1.74$, $p = 0.04$). It indicated that people remembered objects better under high predictability (M = 80.8%, SD = 14.0%) than under low predictability (M = 77.7%, SD = 16.9%). Last but not least, as in Experiment 1, there was also a significant interaction effect of choice and predictability on memory accuracy ($\beta = 0.09$, $z = 2.08$, $p = 0.04$).

Also, follow-up analyses with *emmeans* yielded similar results as found in Experiment 1. When people could predict the outcome of their choices well (high predictability), we found that the accuracy in the choice condition (M = 85.9%, SD = 13.3%) was significantly higher than in the no-choice condition (M = 75.5%, SD = 16.9%; $\beta = 0.89$, $z = 6.99$, $p < 0.001$). When people could not predict the outcome of their choices well (low predictability), we found that the accuracy under the choice condition (M = 81.1%, SD = 16.6%) was also significantly higher than the no-choice condition (M = 73.6%, SD = 20.0%; $\beta = 0.53$, $z = 4.17$, $p < 0.001$). Under the choice condition, people remembered objects better when there was high predictability compared with low predictability ($\beta = 0.37$, $z = 2.82$, $p = 0.005$), but this difference was not present in the no-choice condition ($\beta = 0.02$, $z = 0.12$, $p = 0.91$).

To conclude, in Experiment 2, we found an effect of choice in both the high as well as low predictability conditions. As in Experiment 1, this effect appeared to be stronger for the high predictability condition compared with the low predictability condition (Fig. 2.2C).

2.3.3 Discussion: Experiment 2

In Experiment 2, we employed a similar paradigm as in Experiment 1. However, in each trial, the object names were presented one at a time before the choice screen. Also, the object name viewing time remained the same for 2000 ms across all trials (Fig. 2.3). We replicated the main results on memory accuracy from Experiment 1. That is, the beneficial effect of choice on memory accuracy always stayed statistically significant under both high and low predictabilities. At the same time, the choice effect on memory was notably diminished under low predictability.

In conclusion, in Experiment 2, the main results were replicated, suggesting that choice would always help with memory, even when participants could not predict. At the same time, this choice effect on memory was attenuated when the choice outcome predictability was low. Interestingly, in Experiment 2, the choice effect on memory accuracy got smaller for not selected objects, but not for selected objects under low predictability. This was different from Experiment 1 (see Supplement Material 2).

2.4 Discussion

In a set of 2 experiments, we aimed to gain a better understanding of the beneficial effect of choice on memory. For this purpose, we designed a well-controlled experimental paradigm to test the choice effect on memory accuracy under different predictabilities. On one hand, if the choice effect on accuracy stayed would be the same for high and low predictabilities, we would conclude that choices are rewarding by themselves regardless of the outcome (Ding et al., 2021; DuBrow et al., 2019; Murty et al., 2015; Rotem-Turchinski et al., 2019). On the other hand, if the choice effect is solely present under high predictability, it would suggest that choices are beneficial for learning because they facilitate predictive processing (Cockburn et al., 2014; Desantis et al., 2011; Gureckis & Markant, 2012; Katzman & Hartley, 2020; Luo et al., 2022; Markant et al., 2014a; Meng & Ma, 2015; Moore & Haggard, 2008; Schneider et al., 2018; Sharot & Sunstein, 2020; Voss et al., 2011b). Based on our results, we found evidence for both explanations. We found a facilitatory effect of choice on memory accuracy for both high and low predictability conditions. Yet, the choice effect on memory accuracy was markedly smaller under low predictability than under high predictability. These results together support both hypotheses we raised. In essence, choices are internally rewarding by themselves, but they also enhance memory by fostering predictive processing.

2.4.1 The rewarding nature of choices

In both experiments, it also was found that participants remembered objects better when they could choose than when they could not choose. This main effect of choice on memory accuracy maintained statistical significance throughout both high and low predictabilities, even for the objects that were not selected in low predictability conditions (Fig. S2.2). This finding substantiates the hypothesis that choices (partially) facilitate learning due to the intrinsic reward associated with the opportunity to choose.

According to the self-determination theory (SDT), choices enhance the feeling of autonomy, one of the three fundamental needs in intrinsic motivation for learning (Ryan & Deci, 2020). Autonomy is defined as the feeling of ownership and freedom of one's actions. One of the core arguments in SDT for education is that students would feel more engaged and self-related during learning when their need for autonomy is satisfied. Students would even show higher emotional arousal during learning when their need for autonomy is supported (Streb et al., 2015). Even when the subsequent outcome did not align with the choices that participants made, having the opportunity to choose by itself already contributed to the facilitation of learning. This is in line with previous studies indicating that even inconsequential choices boost memory formation (Ding et al., 2021; Murty et al., 2015; Rotem-Turchinski et al., 2019). In conclusion, the inherent satisfying and rewarding feelings that choices bring for people can already enhance learning processes and performances.

2.4.2 Choices enhance memory encoding by facilitating prediction of outcomes

In both experiments, we found that the choice effect on memory accuracy was attenuated under low predictability compared with high predictability. This implies that part of the advantage that choices bring for learning is due to the more active prediction that choices elicit.

To start with, the act of choosing transforms the information process from passive perceiving to active predicting. Our brains are not old-fashioned computers that can only take passive inputs and produce responses. On the contrary, our brains are active inference agents that constantly predict upcoming events in the surrounding environments (Friston, 2010; Friston et al., 2016; Friston et al., 2013). Choices could enhance active inference, leading to a facilitation of reducing prediction error between predicted states and perceived information (Friston et al., 2013). This would explain that when participants could not accurately predict the outcome of their choices, their prediction was violated. Under this circumstance, the sense of agency (i.e., autonomy, the feeling of control when having the chance to choose) would also be attenuated (Friston et al., 2013). The loss of sense of agency also results in a feeling of losing control over the situation. Such uncontrollability would cause frustration and learned helplessness, leading to impaired motivation and learning performance (Mineka & Hendersen, 1985; Seligman, 1972). Furthermore, some studies also posit that choices would lead to a distortion of the information value after it was perceived.

When people are choosing, they might feel that information is more valuable than when they could not choose (Meng & Ma, 2015; Sharot & Sunstein, 2020; Dubrow et al., 2019; Izuma et al., 2013). For example, it was found that people would have a higher expectation of success in a cognitive task that they chose, proven by both behavioural and electrophysiological evidence (Meng & Ma, 2015). As a result, the choice effect on memory accuracy became smaller under low predictability.

Since people would more actively predict upcoming information when they could choose, they could also coordinate their attention beforehand. This was supported by previous findings showing that even if people could only control *when* to adjust their attention to the next object, memory would already be boosted (Markant et al., 2014a). This attentional tuning process supports memory encoding and retention before information even appears (Gureckis & Markant, 2012). In a study conducted by Luo et al. (2022), it was suggested that attention preparation would only happen when the outcome of the choice was predictable. In their experimental setting, participants were more concentrated and exhibited faster reaction times in the subsequent attentional task when they had chosen and could predict the background picture for each trial. However, when participants were unable to predict the consequences of their choices for the background pictures in the same paradigm, the reaction time of the subsequent task was not accelerated by making active choices. Therefore, if choices are not predictive of the outcomes, predictive and/or attentional preparation will lose their merits.

These findings can be translated to the experiments described here. If our participants chose “ball” by themselves, they might have already adjusted their attention to the state of seeing a ball picture later. However, if the “ball” was chosen for them, this prior prediction and attention tuning might be less active (Fig. 2.1).

In summary, in the current experiment, we found that the choice facilitatory effect on memory diminished under low predictability. This finding supported the hypothesis that choice improves learning by enhancing prediction over the consequences. Two potential explanations for this attenuation of the choice effect emerge. On one hand, choices brought a more active prediction of future information so that people would coordinate their attention in advance. On the other hand, choices evoked a sense of lower prediction error between the choice and the perceived information.

Taken together, our results support both hypotheses raised in the introduction. Firstly, choices contribute to learning with its inherent value and rewards. This was supported by the presence of choice effect on memory accuracy under all circumstances. Secondly, choices aid learning by enhancing the prediction of subsequent outcomes. This was evidenced by the attenuation of choice effect on memory under low predictability.

2.4.3 Consistency between choice and outcome can partially explain the choice effect on memory encoding

However, when we dissected the condition of low predictability into selected and not selected objects, we found different patterns of results in the two experiments (Supplementary Material 2, Fig. S2.2 C&D). To be more specific, the choice effect on memory accuracy diminished under low predictability for both selected and not selected objects in Experiment 1. In contrast, in Experiment 2, the choice effect on memory accuracy did not diminish for selected objects under low predictability.

This discrepancy may be attributed to the fact that in Experiment 2, participants were guaranteed to view both object names for a fixed amount of time. This might elicit predictions regarding both objects in the low predictability conditions, causing confusion and perhaps even false memory. This is consistent with the mechanism of proactive interference and divided attention since more encoded cues might cause a higher cognitive load (Jacoby et al., 2010; Kane & Engle, 2000). Hence, memory accuracy for selected objects in the low predictability condition might be reduced when participants had no choice. In contrast, when participants were choosing objects by themselves, even under low predictability, they might have constructed a stronger anticipation of the selected object (Meng & Ma, 2015). As a consequence, memory under choice but low predictability condition might not be confused by these multiple predictions. Therefore, the choice effect on memory accuracy for selected objects under low predictability was larger in Experiment 2 compared with Experiment 1. Based on this result, we could demonstrate that when the upcoming information fits the prediction, the choice effect would not be attenuated. These findings provided more evidence to the prediction explanation of choice facilitatory effect on learning and memory.

2.4.4 Preference was not the only reason for the choice effect on memory encoding

Additionally, there might be a possibility that the choice effect on memory accuracy is driven by participants' preferences. When participants had the opportunity to choose, they would most likely choose the objects that they preferred (Verdugo et al., 2023). This was not the case in the no-choice conditions: participants would be allocated to one of the objects randomly and there was no opportunity to follow their preferences. Hence, the beneficial effect of choice on memory might also be caused by participants' higher preference for chosen compared with not chosen objects. However, our results mostly rule out this possibility, since we found that choices also improved learning when we solely focused on objects that were not the ones that they selected and thereby preferred (Supplementary Material, Fig. S2.2D). If preference were the driving factor behind the observed effect of choice on memory accuracy, we would expect that the choice effect on memory accuracy would disappear for the not-selected objects under low predictability. However, we found that choices enhanced memory accuracy for all conditions.

2.4.5 Future directions

Although the current study elucidated that the beneficial effect of choice on memory is modulated by the predictability of choice outcomes, there is still more to be investigated under this topic. For example, Luo et al. (2022) found that the facilitatory effect of choices on attention allocation (measured by reaction time in an attentional task) completely disappeared when the participants had inaccurate predictions over the outcome of the choices. On the contrary, in the current study, the choice effect on memory remained significant but was smaller under low predictability. Yet, it is hard to get a better understanding of these partially conflicting findings with only behavioural measures. Therefore, neuroimaging studies are required to delve deeper into the mechanisms of how choices facilitate learning by modulating predictions. It would be intriguing to implement fMRI scanning along with the same paradigm in the future. For instance, based on our findings, it might be the case that having a choice is both rewarding in itself, while at the same time helping us to better predict future outcomes (i.e. by adjusting our attention to upcoming information). Considering both perspectives, we hypothesize that the connectivity between the prefrontal cortex and striatum would be stronger in choice than no-choice condition (Leotti et al., 2010; Murty et al., 2015), and this choice effect on brain connectivity would be attenuated by low predictability.

2.4.6 Limitations

Based on the findings presented in this chapter, we investigated how predictability modulates the beneficial effect of choice on memory. Our results suggest that one reason choices enhance memory is their consequential link to predictable outcomes. However, in the previous experiment, the predictability manipulation introduced confounds: in the low predictability condition, participants experienced both increased entropy and greater surprise of the information context (details see Chapter 3.1). For example, when participants expected to see a "frog" but instead saw a "ball," they encountered both an unpredictable context and a prediction error. This design makes it unclear whether the reduced choice effect was driven by unpredictability or by surprise itself. Therefore, in the next experiment, we aim to disentangle these factors by keeping predictability constant and manipulating surprise directly.

2.5 Conclusion

In conclusion, the current study showed that choices can help people to learn better under both high and low predictabilities of the choice outcomes. However, the choice facilitatory effect on memory was diminished when the outcomes of the choices could not be accurately predicted. Our findings demonstrate that an opportunity to choose will help with learning and memory since choices have satisfactory and rewarding values by themselves. At the same time, the predictability of upcoming information also modulates the facilitatory effect of choice on learning. This indicates that the choice effect on learning is partially dependent on prediction processes. These results can easily be adapted to educational situations. As an illustration, in the context of learning to play the piano, instructors may inquire about students' musical preferences and tailor educational plans accordingly. This personalized approach, rooted in individual choices, holds the potential to enhance the likelihood of success in learning and education.

2.6 Author note

The project is funded by the Chinese Scholarship Council (CSC) and an interdisciplinary research fund provided by the Radboud Teaching and Learning Centre. All data and code used for stimulus presentation and analyses of both experiments are freely available on the Donders Repository (https://data.ru.nl/login/reviewer-2730442050/2T3HWWOJY7CNIAESJ76XPFLZVHG7Q23GSSFLCMY). The authors thank Parker Winkel, Marketa Mickova, and Samantha Hamm for their help with data collection for Experiment 2. We also thank Josh Ring and Randi Goertz for their help with coding, checking the object names and data analysis.

2.7 Supplement

2.7.1 Supplement 1: Primary analysis with all trials

Following the preregistration, we conducted the same primary analysis as reported in the main text on all trials instead of only the confident trials. We did so for both Experiment 1 and Experiment 2.

2.7.1.1 Results

As reported in the main text, we found an interaction between choice and predictability on memory accuracy in Experiment 1 and 2 when only confident trials were included. We also found this interaction when including all trials in Experiment 1, but the interaction effect did not reach significance in Experiment 2 (see Table S2.1, Figure S2.1).

A possible explanation for not finding this effect in Experiment 2 is that the effect of choice was attenuated when also considering trials that participants were not confident about. This is in line with previous work suggesting that intrinsic motivators (e.g., choice or curiosity) boost our learning, but only for information that participants were confident about (Galli et al., 2018; Gruber et al., 2014; Meliss et al., 2022; Murphy et al., 2021).

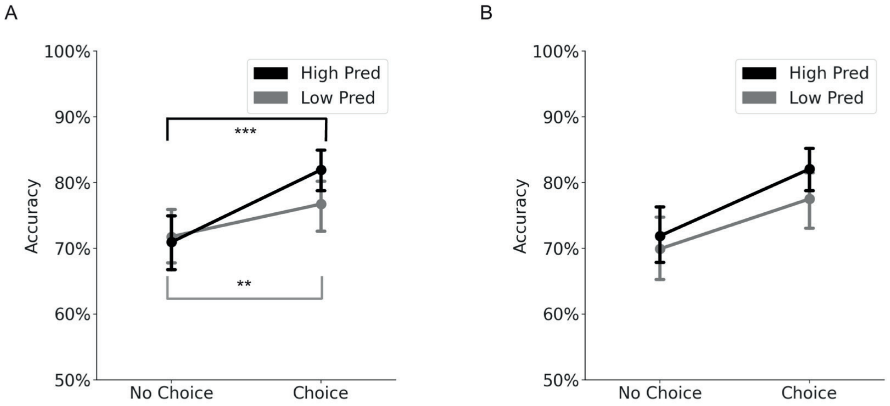
Table S2.1 Linear Mixed Effect Model from Primary Analyses

	Experiment1	**Experiment2**
Memory accuracy: all trials		
Choice	$\beta = 0.23, z = 6.10, p < 0.001$	$\beta = 0.29, z = 7.38, p < 0.001$
Predictability	$\beta = 0.06, z = 1.84, p = 0.16$	$\beta = 0.06, z = 1.79, p = 0.06$
Choice × Predictability	$\beta = 0.09, z = 2.47, p = 0.01$	$\beta = 0.06, z = 1.57, p = 0.12$
Follow-up t-tests:		
Choice – No choice (High Pred)	$\beta = 0.64, z = 6.04, p < 0.001$	-
Choice – No choice (Low Pred)	$\beta = 0.29, z = 2.81, p = 0.005$	-
High Pred - Low Pred (Choice)	$\beta = 0.31, z = 2.81, p = 0.005$	-
High Pred - Low Pred (No Choice)	$\beta = -0.05, z = -0.52, p = 0.606$	-
Memory accuracy: confident trials (as also reported in the main text)		
Choice	$\beta = 0.29, z = 2.28, p < 0.001$	$\beta = 0.36, z = 7.52, p < 0.001$
Predictability	$\beta = -0.08, z = -0.71, p = 0.21$	$\beta = 0.10, z = 1.74, p = 0.04$
Choice × Predictability	$\beta = 0.42, z = 2.33, p = 0.02$	$\beta = 0.09, z = 2.08, p = 0.04$
Follow-up t-tests:		
Choice – No choice (High Pred)	$\beta = 0.71, z = 5.28, p < 0.001$	$\beta = 0.89, z = 6.99, p < 0.001$
Choice – No choice (Low Pred)	$\beta = 0.29, z = 2.28, p = 0.02$	$\beta = 0.53, z = 4.17, p < 0.001$
High Pred - Low Pred (Choice)	$\beta = 0.34, z = 2.58, p = 0.01$	$\beta = 0.37, z = 2.82, p = 0.005$
High Pred - Low Pred (No Choice)	$\beta = -0.08, z = -0.71, p = 0.48$	$\beta = 0.02, z = 0.12, p = 0.91$

Note: Memory accuracy ~ choice × predictability + (1 + choice × predictability|subject)

Table S2.2 Descriptive statistics for memory accuracy based on primary analysis

		Experiment 1 M ± SD	Experiment 2 M ± SD
Accuracy: all trials			
Choice main effect	Choice	79.3 % ± 11.9%	79.9% ± 13.6%
	No choice	71.4% ± 14.3%	70.9% ± 15.4%
Predictability main effect	High pred	76.4% ± 11.8%	77.0% ± 13.5%
	Low pred	74.7% ± 13.8%	73.8% ± 15.9%
Follow-up comparison	*Choice (High pred)*	*81.9% ± 11.6%*	-
	Choice (Low pred)	*76.7% ± 14.8%*	-
	No choice (High pred)	*70.9% ±15.2%*	-
	No choice (Low pred)	*71.8% ± 15.6%*	-
Accuracy: confident trials (main text)			
Choice main effect	Choice	84.3% ± 12.6%	83.7% ± 13.9%
	No choice	76.6% ± 16.2%	74.8% ± 16.3%
Predictability main effect	High pred	81.4% ± 13.3%	80.8% ± 14.0%
	Low pred	79.7% ± 14.6%	77.7% ± 16.9%
Follow-up comparison	*Choice (High pred)*	*86.3% ± 12.5%*	*85.9% ± 13.3%*
	Choice (Low pred)	*81.9% ± 14.8%*	*75.5% ± 16.9%*
	No choice (High pred)	*75.6% ± 17.4%*	*81.1% ± 16.6%*
	No choice (Low pred)	*77.21% ± 17.19%*	*73.6% ± 20.0%*



Choice: $\beta = 0.23$, $z = 6.10$, $p < 0.001$
Predictability: $\beta = 0.06$, $z = 1.84$, $p = 0.16$
Interaction: $\beta = 0.09$, $z = 2.47$, $p = 0.01$

Choice: $\beta = 0.29$, $z = 7.38$, $p < 0.001$
Predictability: $\beta = 0.06$, $z = 1.79$, $p = 0.06$
Interaction: $\beta = 0.06$, $z = 1.57$, $p = 0.12$

Figure S2.1. Main results including all trials. **A.** Experiment 1. Even including all trials in Experiment 1, we still found the significant main effect of choice and interaction between choice and predictability on memory accuracy. Participants remember objects better when they could choose than when they could not choose.

Meanwhile, the choice effect was stronger under high than low predictability. These results are the same as the results including only the confident trials, as reported in the main text. **B.** Experiment 2. When we controlled for object viewing time in Experiment 2, the interaction between choice and predictability was not found in memory accuracy including all trials. However, there was still a main effect of choice on memory accuracy. This is perhaps unsurprising, given that non-confident guesses likely reflect random guesses instead of actual learning, hereby indicating a low quality of memory. As suggested by previous studies (Cerasoli et al., 2014; Meliss et al., 2022), low quality memory might be less boosted by intrinsic motivators (i.e. choices).

2.7.2 Supplement 2: Secondary analyses

For both experiments, we conducted additional analyses to get a better understanding of why the choice-related memory benefits are less strong for low predictability compared with high predictability. Specifically, we looked at (1) whether the choice effect in low predictability conditions was still diminished after omitting the not selected objects from the analyses and (2) whether the choice effect on memory accuracy differed between selected and not selected objects under low predictability.

2.7.2.1 Inconsistency between selection and perceived information attenuates the choice effect on memory

It should be noted that, in low predictability conditions, participants only saw the object picture corresponding to the selected object name in 50% of all trials. In the other 50% of the trials, participants were presented with the object picture that was not selected. In the latter case, there was inconsistency between the selection they made (selected object name) and the visual information (object picture) they perceived. On the contrary, in the high predictability conditions, all objects that participants saw were selected. Therefore, there is a possibility that the reduction of choice effect on memory accuracy under low predictability merely resulted from the inconsistency in the not selected trials. Two secondary analyses were implemented to investigate this assumption.

First, we conducted the same analysis as described for the primary analysis on selected trials only, with memory accuracy as the dependent variable. These are all trials from the high predictability conditions and half of the trials (trials in which the selected object names were consistent with the presented objects) from the low predictability conditions. The model included the main effects of “choice (yes/no)” and “predictability (high/low)”, as well as the interaction effect between “choice (yes/no)” and “predictability (high/low)” as fixed effects, as well as a full random effects structure per participant (Barr, 2013; Barr et al., 2013). If the inconsistency between the selected name and object picture could explain part of the interaction effect between choice and predictability in the primary analysis, then omitting the not selected trials would lead to insignificance of this interaction effect. Otherwise, the results should remain the same as the primary analysis before.

Second, we compared the choice effect for selected and not selected objects under low predictability to validate whether the choice effect only existed for selected objects. The model included the main effects of "choice (yes/no)" and "selection (yes/no)", as well as the interaction effect between "choice (yes/no)" and "selection (yes/no)" as fixed effects, as well as a full random effects structure per participant (Barr, 2013; Barr et al., 2013). If the inconsistency between the selected name and object picture could diminish the choice effect, we would find that the choice effect for memory accuracy would not exist for not selected objects under low predictability.

2.7.2.2 Results

First, the same 2×2 analysis of choice and predictability effects was conducted as the primary analysis after omitting the not selected objects from low predictability conditions. In Experiment 1, we found the same main choice effect and interaction effect between choice and predictability (Fig. S2.2A, Table S2.3) as the primary analysis including both selected and not selected objects. However, in Experiment 2, the main choice effect was still significant, but the interaction effect was not significant anymore after omitting the not selected objects (Fig. S2.2C, Table S2.3). In other words, in Experiment 2, with the selected objects only, participants showed the same choice effect between high and low predictability.

Second, we separated the objects under low predictability into selected and not selected objects. We conducted a 2×2 analysis between choice conditions (choice or no-choice) and selection conditions (selected or not selected). In Experiment 1, we found the main effects of choice and selection (Fig. S2.2B, Table S2.3). This suggested that the decline of choice effect under low predictability in Experiment 1 happened for both selected and not selected objects.

However, in Experiment 2, we found the main effect of choice and the interaction between choice and selection. This suggested that after controlling object name viewing time in Experiment 2, the choice effect got smaller only when they saw a not selected object under low predictability (Fig. S2.2D, Table S2.3). It is also worth mentioning that the choice facilitatory effect remained significant for not selected objects.

2.7.2.3 Summary

In summary, these results indicated that inconsistency between the selected object name and object picture could explain part of the reduction of choice effect under low predictability. However, even if participants did not see the object they selected, they still remembered objects better when they could choose than when they could not choose. By conducting these secondary analyses, we found that the choice effect on memory under low predictability declined for both selected and not selected objects in Experiment 1. In contrast, the choice effect on memory only declined for not selected objects under low predictability in Experiment 2.

In Experiment 1, when people could control how much time they spent viewing the object names, under the low predictability condition, both selected and not selected objects had a smaller choice effect than under the high predictability condition. However, when the object name viewing time could not be controlled by the participants (Experiment 2), the choice effect for selected objects under low predictability remained the same as high predictability. The choice effect on memory did not reduce for the selected objects under low predictability, but it was diminished for not selected objects. It is worth noting that for both experiments, choice always notably enhanced memory accuracy for objects under high predictability, selected and not selected objects under low predictability.

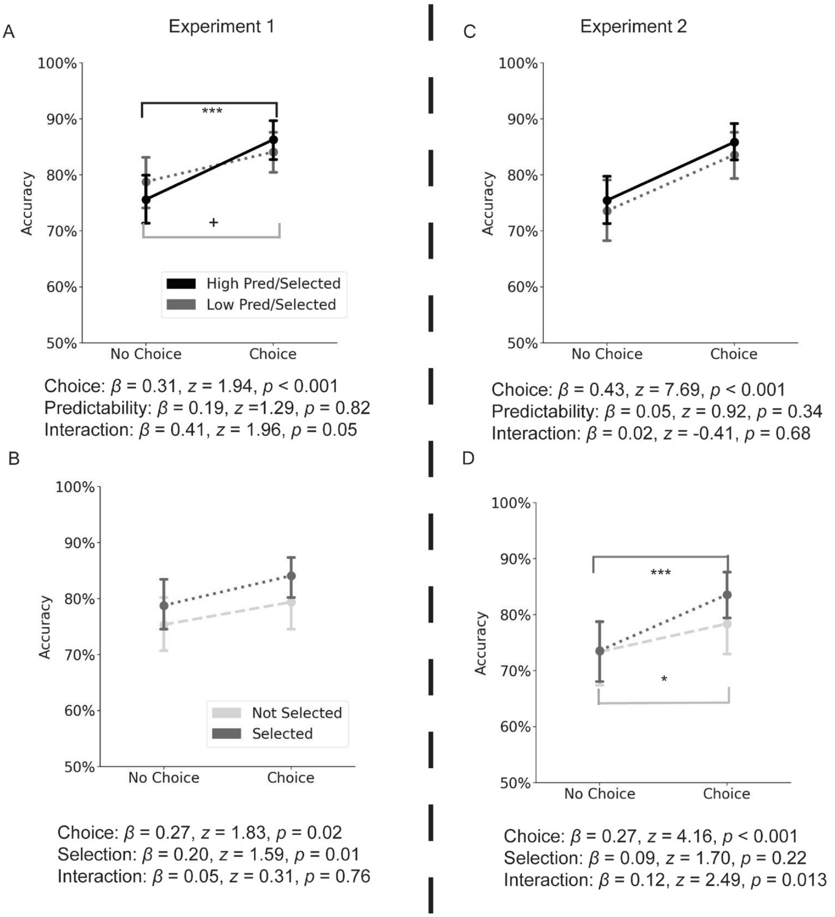
Table S2.3 Linear Mixed Effect Model from Secondary Analyses

	Experiment 1	**Experiment 2**
Accuracy: primary analysis after omitting not selected objects		
Choice	$\beta = 0.31, z = 1.94, p < 0.001$	$\beta = 0.43, z = 7.69, p < 0.001$
Predictability	$\beta = 0.19, z = 1.29, p = 0.82$	$\beta = 0.05, z = 0.92, p = 0.34$
Choice × Predictability	$\beta = 0.41, z = 1.96, p = 0.05$	$\beta = 0.02, z = 0.41, p = 0.68$
Follow-up t-tests:		
Choice – No choice (High Pred)	$\beta = 0.72, z = 5.36, p < 0.001$	-
Choice – No choice (Low Pred)	$\beta = 0.31, z = 1.94, p = 0.05$	-
High Pred - Low Pred (Choice)	$\beta = 0.22, z = 1.54, p = 0.12$	-
High Pred - Low Pred (No Choice)	$\beta = -0.19, z = -1.29, p = 0.20$	-
Accuracy: comparing selected and not selected objects for low predictability		
Choice	$\beta = 0.27, z = 1.83, p = 0.02$	$\beta = 0.27, z = 4.16, p < 0.001$
Selection	$\beta = 0.20, z = 1.59, p = 0.01$	$\beta = 0.09, z = 1.70, p = 0.22$
Choice × Selection	$\beta = 0.05, z = 0.31, p = 0.76$	$\beta = 0.12, z = 2.49, p = 0.013$
Follow-up t-tests:		
Choice – No choice (Selected)	-	$\beta = 0.79, z = 4.59, p < 0.001$
Choice – No choice (Not selected)	-	$\beta = 0.31, z = 2.05, p = 0.04$
Selected - Not selected (Choice)	-	$\beta = 0.41, z = 2.69, p = 0.01$
Selected - Not selected (No Choice)	-	$\beta = -0.06, z = -0.50, p = 0.62$

Note:
Omitting not selected objects:
Memory accuracy ~ choice × predictability + (1 + choice × predictability|subject)
Selected or not selected objects for low predictability conditions:
Memory accuracy ~ choice × selection + (1 + choice × selection|subject)

Table S2.4 Descriptive statistics for memory accuracy based on secondary analysis

		Experiment 1 M ± SD	**Experiment 2 M ± SD**
Accuracy: omitting not selected objects			
Choice main effect	Choice	85.7% ± 11.9%	85.3% ± 13.3%
	No choice	76.9% ± 16.0%	75.0% ± 16.0%
Predictability main effect	High pred	81.4% ± 13.4%)	80.8% ± 14.1%
	Low pred	81.6% ± 13.8%	79.1% ± 15.9%
Follow-up comparison	*Choice (High pred)*	*86.3% ± 12.6%*	-
	Choice (Low pred)	*84.1% ± 13.8%*	-
	No choice (High pred)	*75.6% ± 17.5%*	-
	No choice (Low pred)	*78.8% ± 17.4%*	-
Accuracy: selected or not selected objects for low predictability conditions			
Choice main effect	Choice	81.9% ± 14.9%	81.1% ± 16.7%
	No choice	77.2% ± 17.3%	73.6% ± 20.1%
selection main effect	Selected	81.6% ± 13.8%	79.1% ±15.9%
	Not selected	77.6% ± 16.9%	76.2% ± 19.2%
Follow-up comparison	*Choice (Selected)*	-	*83.6% ± 16.2%*
	Choice (Not selected)	-	*78.4% ± 19.5%*
	No choice (Selected)	-	*73.6% ± 20.5%*
	No choice (Not selected)	-	*73.4% ± 22.0%*



Choice: $\beta = 0.31$, $z = 1.94$, $p < 0.001$
Predictability: $\beta = 0.19$, $z = 1.29$, $p = 0.82$
Interaction: $\beta = 0.41$, $z = 1.96$, $p = 0.05$

Choice: $\beta = 0.43$, $z = 7.69$, $p < 0.001$
Predictability: $\beta = 0.05$, $z = 0.92$, $p = 0.34$
Interaction: $\beta = 0.02$, $z = -0.41$, $p = 0.68$

Choice: $\beta = 0.27$, $z = 1.83$, $p = 0.02$
Selection: $\beta = 0.20$, $z = 1.59$, $p = 0.01$
Interaction: $\beta = 0.05$, $z = 0.31$, $p = 0.76$

Choice: $\beta = 0.27$, $z = 4.16$, $p < 0.001$
Selection: $\beta = 0.09$, $z = 1.70$, $p = 0.22$
Interaction: $\beta = 0.12$, $z = 2.49$, $p = 0.013$

Figure S2.2. Secondary analyses results.A & B, Experiment 1. **A.** In this panel, we only included the trials in which objects were selected and seen, and the same effects as the primary analysis in Fig 5.2A were found, namely the main effect of choice and the interaction effect between choice and predictability on memory accuracy. This indicated that the choice effect was larger under high predictability than under low predictability. **B.** Only objects in the low predictability condition were considered, and they were categorized as either selected or not selected. We compared the choice effect on memory accuracy for selected and not selected objects. It was found that in the low predictability conditions, the selected or not selected objects showed similar choice effects. Taken together, in Experiment 1, the reason for the choice effect reduction under low predictability was that the choice effect was smaller for both selected and not selected objects. C & D, Experiment 2. **C.** In this panel, akin to Panel A (Experiment 1), we exclusively considered the objects that were selected and conducted the same analysis. In contrast to Experiment 1, we only found a main effect of choice on memory accuracy. This indicated that the choice effect on memory accuracy remained the same between the high and low predictability after omitting objects that were not selected. **D.** In this panel, we analysed the choice effect for selected or not selected objects under the low predictability conditions, the same as Panel B (Experiment 1). We found that the choice effect and interaction effect between choice and selection conditions were significant. In other words, when object name viewing time was controlled, choice had a more pronounced impact on selected objects compared to non-selected objects, which differs from the findings of Experiment 1. It is worth mentioning that the choice effect remained significantly positive even for the not selected objects. To summarize, in Experiment 2, the decline of the choice effect from high to low predictability (Fig. 2.2C, the slope for the dark grey line was bigger than the light line) was caused mainly by the not selected objects.

2.7.3 Supplement 3: object name viewing time

In Experiment 1, we found that participants remembered objects better in choice than in no-choice conditions. Meanwhile, this choice effect on memory accuracy was attenuated when participants could not predict the outcome of their choices well. However, in Experiment 1, the object names would disappear once participants pressed a button (Fig. 1A). Hence, participants could control not only the content (which picture they would like to see) but also the object name viewing time (the amount of time that each pair of words was presented on the screen). In the current setup, object names potentially functioned as cues for the pictures that participants needed to remember, which could facilitate memory encoding and formation (Crouse & Idstein, 1972; Neumann & Strack, 2000; Thomson & Tulving, 1970). In other words, the longer participants could view the object names, the better they would remember the objects that the names are attributed.

To summarize, if we find similar effects of choice and predictability on object name viewing time as for memory accuracy, it might be the case that (part of) the findings of memory accuracy can be explained by the object name (cue) viewing time differences.

2.7.3.1 Methods

For this analysis, we used the object name viewing time in Experiment 1 as a dependent variable. We conducted the same analysis as the primary analysis (2 × 2 LME model including choice and predictability main effect and the interaction effect) described in the main text (Barr, 2013; Barr et al., 2013). In accordance with the primary analysis on memory accuracy, this analysis on object name viewing time also only included confident trials. Before conducting inferential statistical analysis on object name viewing time, we log transferred the raw viewing time to gain a normally distributed dependent variable.

2.7.3.2 Results and conclusion

Similar to the results on memory accuracy (Fig. 2.2A), we found the main effect of choice and the interaction effect between choice and predictability on object name viewing time (Table S2.5 & S2.6, Fig. S2.3). Therefore, according to these results, we designed Experiment 2 to control the object name viewing time to control the strength of the cues, isolate the influence of the cues, and validate our findings.

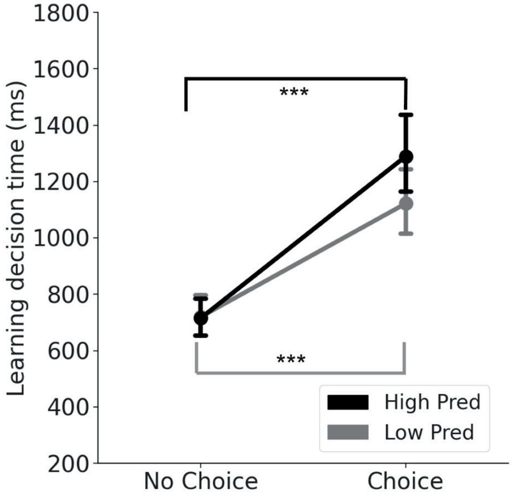
Table S2.5 Linear mixed effect model for object name viewing time, Experiment 1

Object name viewing time: confident trials	
Choice	$\beta = 0.43$, $t = 9.90$, $p < 0.001$
Predictability	$\beta = 0.02$, $t = 0.75$, $p = 0.08$
Choice × Predictability	$\beta = 0.13$, $t = 3.14$, $p = 0.003$
Follow-up t-tests:	
Choice – No choice (High Pred)	$\beta = 0.56$, $t = 12.00$, $p < 0.001$
Choice – No choice (Low Pred)	$\beta = 0.43$, $t = 9.90$, $p < 0.001$
High Pred - Low Pred (Choice)	$\beta = 0.15$, $t = 3.58$, $p < 0.001$
High Pred - Low Pred (No Choice)	$\beta = 0.02$, $t = 0.75$, $p = 0.46$

Note: Object name viewing time ~ choice × predictability + (1 + choice × predictability|subject)

Table S2.6 Descriptive statistics for object name viewing time, Experiment 1

Object name viewing time: confident trials (M ± SD)		
Choice main effect	Choice	1211ms ± 442ms
	No choice	717ms ± 244ms
Predictability main effect	High pred	1020ms ± 353ms
	Low pred	927ms ± 318ms
Follow-up comparison	*Choice (High pred)*	*1295ms ± 510ms*
	Choice (Low pred)	*1122ms ± 428ms*
	No choice (High pred)	*717ms ± 251ms*
	No choice (Low pred)	*717ms ± 264ms*



Choice: $\beta = 0.31$, $z = 1.94$, $p < 0.001$
Predictability: $\beta = 0.19$, $z = 1.29$, $p = 0.82$
Interaction: $\beta = 0.41$, $z = 1.96$, $p = 0.05$

Figure S2.3. The same analysis as the primary analysis (Fig. 2A) was conducted but with object name viewing time as the dependent variable. There was a main effect of choice and no main effect of predictability on object name viewing time. Also, the interaction between choice and predictability on object name viewing time was found. These results were similar to the results found on memory accuracy depicted in the main text (Fig.2). These suggested that participants would view the object names longer when they have a choice than no choice, and the choice effect is bigger under high predictability than low predictability. In the current paradigm, object names can be seen as cues facilitating memory of the pictures. Since longer exposure to cues might result in better memory (e.g., Crouse & Idstein, 1972), the object name viewing time should be controlled. We designed Experiment 2 based on this finding.

Chapter 3

Surprise reduces the beneficial effect of choice on memory

Abstract

When people are offered the opportunity to choose, their memory is enhanced. For example, people would be able to remember the map of a new city better if they explore by themselves instead of following Google Maps. However, the cognitive mechanisms of the beneficial effect of choice on learning have rarely been investigated. From a predictive coding perspective, choices facilitate learning because the act of choosing modulates the prediction of upcoming information. When the outcome of a choice mismatches with the prediction, it creates a surprise. This surprise, in turn, may affect how well the chosen information is remembered. To investigate this, we conducted a memory experiment, independently manipulating choice and surprise. First, in a training phase, participants learned associations between colours and object categories by viewing exemplar images cued by coloured circles. For instance, a red circle represents the object category “mammals”. Thereafter, participants completed a memory encoding task in which they were instructed to remember as many images of objects as possible. On each trial, before the object images were shown, participants either chose (choice condition) or were assigned a category (no-choice condition) of objects to view. Categories of objects were cued by the presence of the associated coloured circle belonging to each category. In half of the choice and no-choice trials, the object shown would match the selected colour (low surprise condition), while in the other half of trials, the colour and the object shown would be incongruent with the learned association (high surprise condition). The memory accuracy was tested by a recognition task after the memory encoding phase. We found that choice enhances memory only when choice outcomes are unsurprising based on the participants’ choices. Our finding provides insights into the cognitive mechanism of the beneficial effect of autonomy, empowered by active choices, in memory encoding.

3.1 Introduction

People tend to remember information better when they are given the opportunity to make choices, compared to when they have no choice (e.g., Ding et al., 2021; Lima et al., 2023; Murty et al., 2015; Rotem-Turchinski et al., 2019; Zhang et al., 2024). For example, we may be more likely to remember a route taken when we are driving rather than sitting in the passenger's seat. When we are driving the car, we are making a voluntary choice of where to go. Our brain builds up a causal relationship between a voluntary choice and the appearance of a certain outcome following that choice (Desantis et al., 2011; Moore & Haggard, 2008; Numan, 2021; Sharot & Sunstein, 2020).

In a previous study, we manipulated the predictability of choice outcomes and tested whether predictability interacted with the effect of choice on subsequent recognition memory (see Chapter 2; Zhang et al., 2024). Specifically, predictability refers to how well information can be anticipated before the sensory input is presented (Bubic et al., 2010). We demonstrated that when the context was more predictable, the act of choosing could improve memory encoding more than when the context was unpredictable (see Chapter 2; Zhang et al., 2024). This finding indicated that making active choices could enhance learning by facilitating stronger predictions prior to the information perceived, in line with active inference theory and predictive coding perspectives (Friston et al., 2013). However, it remains unclear which element of predictive processing contributes to the facilitative effect of choice on memory.

In the previous experiment, we offered participants two names of the objects that they might see (see Chapter 2; Zhang et al., 2024). Sometimes, participants could choose between these two objects freely, while sometimes, the choice was made for them. Meanwhile, within the high predictability condition, the selected object was always presented, allowing participants to generate a single strong prediction with no surprise at the outcome. In contrast, within the low predictability condition, the presented object could be either the selected or the unselected object, leading participants to generate two ambiguous predictions and experience surprise when either image was shown. This design inadvertently confounded two core components of information contexts: entropy (Procedure, Equation 1) and surprise (Procedure, Equation 2; Modirshanechi et al., 2022; Shannon, 1948). Specifically, the low-predictability condition simultaneously induced high entropy and high surprise, whereas the high-predictability condition was associated with no entropy and the absence of surprise.

As a result, although we found that choices enhanced learning more under the high predictability condition compared to the low predictability condition, it remains an open question whether entropy or surprise in information contexts modulated the effect of choices on memory encoding. To address this, the present study aimed to disentangle these two closely related but distinct elements of predictive processing by isolating the effects of surprise while holding entropy constant, thereby providing a more precise understanding of how active choices and predictive processing interactively shape recognition memory. Previous studies have investigated either the (beneficial) effect of choice or the effect of surprise on memory encoding independently. However, to our knowledge, there have not been any studies that have manipulated both choice and surprise within the same experimental design. Although it is commonly agreed upon that making active choices enhances memory encoding (Baldwin et al., 2021; Cheng et al., 2023; Ding et al., 2021; Ding et al., 2024; DuBrow et al., 2019; Katzman & Hartley, 2020; Kennedy et al., 2024; Lima et al., 2023; e.g., Murty et al., 2015; Rotem-Turchinski et al., 2019; Zhang et al., 2024), it is not fully clear how surprise influences memory encoding.

Although some studies have found that surprising information tends to be better remembered than non-surprising information (Axmacher et al., 2010; Ben-Yakov et al., 2022; Foster & Keane, 2019), a substantial body of studies has suggested that memory retrieval is more accurate when information conforms to, rather than violates, prior expectations (Frank et al., 2022; Frank et al., 2018; Sinclair & Barense, 2018; Sinclair et al., 2021). Specifically, Frank et al. (2022) asked participants to learn associations between cues and objects, then tested memory by presenting objects following either expected or unexpected cues. They found that memory accuracy was higher when objects followed expected cues. This suggests that expectation alignment highlighted the temporal contingency of the context, enhancing the salience or integration of subsequent information. Bein et al. (2023) similarly argued that congruent events benefit from stronger contextual reactivation of memory-related brain regions at retrieval. In contrast, surprising or incongruent events may disrupt the integration of information into the established schema (Sinclair & Barense, 2018; Sinclair et al., 2021). Supporting this notion, Sinclair and Barense (2018) showed that memory of videos containing surprising information was more vulnerable to being intruded by intervening videos, leading to more false memory and impaired recall.

Hence, due to the mixed findings regarding the impact of surprise on memory, a critical gap emerged in understanding how active choices interface with surprising information during memory encoding. If active choices enhance the prediction of upcoming information to facilitate memory formation, then mnemonic benefit from active choices should be strongest when the incoming information aligns with those predictions. Towards this aim, we designed a memory encoding task in which we independently manipulated two factors: (1) the presence of choice (yes or no) and (2) the surprise of the choice outcome (yes or no). Participants first learned the correspondence between colours and object categories, in which there were seven colours (*red, orange, yellow, green, cyan, blue, purple*) and seven categories (*insects, mammals, musical instruments, furniture, clothing, food, vehicles*) in a behavioural training task (Fig. 3.1A). In the memory encoding task, we ensured that the degree of predictability of the choice outcomes was stable while only the surprise elicited by choice outcomes was manipulated, adapted from Chapter 2 (Zhang et al., 2024; Fig. 3.1B). Similar to the previous experiment, in the memory encoding task, in each trial, participants were offered two colours corresponding to two object categories. Depending on the choice condition, participants either freely chose one of the two object categories that they would like to see (by selecting one of the two colours; choice condition), or they were instructed to select one of the object categories by means of an arrow pointing towards one of the two colours (no-choice condition) (see Fig. 3.1C). After selecting one of the two colours, an image that either matched the selected category (low surprise condition) or belonged to a different category (high surprise condition). Participants were instructed to remember the images as much as possible. Memory performance was later assessed through a separate recognition memory test (Fig. 3.1D). Based on the results from Chapter 2, we hypothesized that the beneficial effect of choice on memory accuracy would be reduced under the high surprise condition as compared with the low surprise condition.

To preview, the results showed that making active choices only enhanced memory encoding for images that were consistent with expectations, in other words, the low surprise images. These results further elucidate how choice and predictive processing, particularly surprise, jointly influence memory encoding. Our results supported the hypothesis, indicating that active choices could facilitate memory encoding when the perceived information after making a choice was consistent with the prediction of the choice outcome.

3.2 Methods

3.2.1 Participants

In the current behavioural experiment, 44 participants were recruited, of whom 36 provided valid data (age 22.61 years ± 3.00, 25 female, 10 male, and one non-binary). One participant was excluded due to a procedural mistake. Two participants were excluded due to low response rates in the memory test (less than 200 out of 336 trials). Five participants were removed from the analysis since their accuracy in the memory test was lower than 55%(chance level performance being 50%).

All participants gave written informed consent according to the Declaration of Helsinki prior to participation. The experiment was approved by the local ethics committee (CMO Arnhem-Nijmegen, The Netherlands) under a general ethics approval protocol (“Imaging Human Cognition”, CMO 2014/288) and was conducted in compliance with these guidelines. Participants were told that they would get 37.5 euros as standard participation compensation.

3.2.2 Materials

The real-life images used in the current experiment were selected from the Things database (Hebart et al., 2019), a large-scale, high-quality image set designed for research on object recognition. The images from this database were all well-labelled and categorized. The experiment contained three sessions, namely a behavioural training session (Fig. 3.1A) during which they learned a correspondence between seven colours and seven categories (Fig. 3.1B), a memory encoding task (Fig. 3.1C), and a memory test (Fig. 3.1D). A total of seven categories were selected: *insects, musical instruments, food, vehicles, clothing, mammals, and furniture* (Fig. 3.1B). For each category, we chose eight objects for the training phase and 8 different objects for the learning and memory test. 6 images were chosen for each object, resulting in 336 images for the behavioural training session as well as 336 images for the learning and memory test. Note that “object” here refers to the type of object within its object category, not the individual images themselves. For example, there were eight different insect-objects shown during the behavioural training, and each of these eight insect-objects consisted of six exemplar images. During the encoding phase, participants were exposed to all objects. Each participant saw only three exemplars for each object, while the remaining three exemplars served as fillers for the memory test. Thus, each participant viewed 168 pictures during learning, with the other 168 pictures designated as fillers in the memory test.

3.2.3 Procedure

Before the formal experiment started, participants signed an informed consent form upon their arrival. Thereafter, they were asked to read the instructions of the whole experiment printed on paper and explain the procedure verbally to the experimenters. This was done so that the experimenters could confirm that participants understood the task. Participants first completed a behavioural training session, followed by a practice round of the memory encoding task and memory test, including eight trials with cartoon images generated by an image generator (https://openai.com/index/dall-e-3/). Noticeably, in the current memory encoding task, we designed it on the basis of the paradigm from Chapter 2. In Chapter 2, on top of manipulating the choice factor, we manipulated predictability which changed both entropy (Equation 1) and surprise (Equation 2) of the information context to cause differences, while in the current experiment, we designed it meticulously, changing only surprise (Equation 2) but maintain the entropy (Equation 1) to be constant. Participants were informed that they did not need to remember these cartoon images. Data from the practice round were not used for analyses. Once it was confirmed that participants understood both tasks, they proceeded to the formal learning and memory test phases. The tasks were programmed with MATLAB 2019a (Mathworks, 2019) and Psychtoolbox 3.0.19 (Brainard & Vision, 1997; Kleiner et al., 2007, http://psychtoolbox.org/).

$$Entropy(X) = -\sum_i P(X_i) \log P(X_i) \qquad \text{Equation 1}$$

$$Surprise(X_i) = -\log P(X_i) \qquad \text{Equation 2}$$

3.2.3.1 Training

Upon arriving at the lab, participants first conducted a training session (Fig. 3.1A). The goal of this session was to ensure participants explicitly learned the associations between colours and categories (Fig. 3.1B). In each trial, a colour dot appeared at the centre of the screen for 500 ms, followed by an image from one of the object categories presented for 2000 ms. Participants were instructed to indicate whether the colour and object category matched during the image presentation using a button box. The button under the index finger corresponded to the left option, while the button under the middle finger corresponded to the right option. To counterbalance response mapping, odd-numbered participants used the left button for “Match” and the right for “No Match,” whereas even-numbered participants used the left button for “No Match” and the right for “Match.” After each response, feedback (“correct” or “error”) was shown for 500 ms to facilitate learning of the colour-category associations. Then, a blank screen with a jittered inter-stimulus interval (ISI) jitter from 500 ms to 1000 ms was presented. Participants would gradually obtain the correct pairings between each colour and its corresponding category. Each block consisted of 28 trials, including four exemplar images from each of the seven categories. After completing a block, participants received feedback on their overall accuracy and were instructed to improve their performance as much as possible.

Participants completed a minimum of six blocks, and training continued until they achieved an accuracy above 85% in a single block, with a maximum of 12 blocks allowed. All participants included in the final analysis reached this accuracy criterion within 12 blocks, indicating that they all explicitly learned the pairing matrix of colours and categories. For example, in the current case (Fig. 3.1B), participants learned specific colour-category associations: red for insects, orange for musical instruments, yellow for food, green for vehicles, blue for mammals, and purple for furniture. The pairings between colours and categories were randomized and counterbalanced across participants to control for potential colour-category biases.

3.2.3.2 Memory encoding task

Once the associations were learned, the same colour-category mapping was implemented during this learning task. We orthogonally manipulated two experimental conditions for encoding, choice/no-choice and high surprise/low surprise (Fig. 3.1B & 3.1C). During this task, in each trial, participants were asked either to choose between two colours (indicating the associated object categories) or to press a button following the choice made for them between two colours. Thereafter, participants saw an image, which they were instructed to try to remember as accurately as possible.

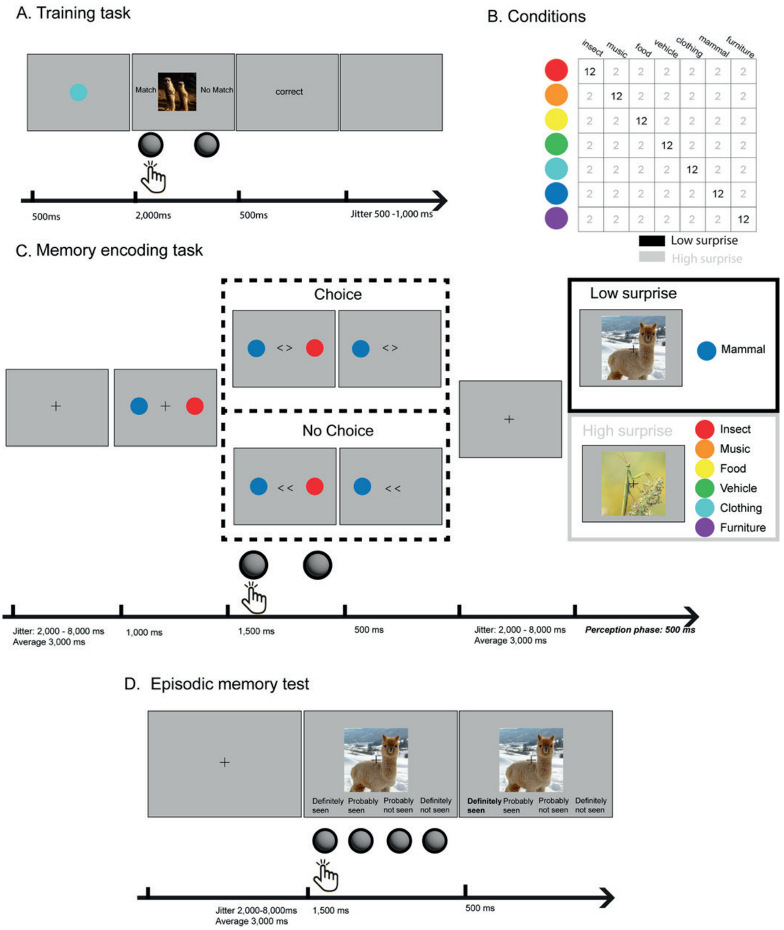
Choice manipulation - In the learning task (Fig. 3.1C), each trial began with a fixation cross shown for 2000–8000 ms with an average of 3000 ms (jittered), followed by two coloured dots presented on the left and right sides of the cross for 1000 ms. Next, the cross transformed into double arrows—either the arrows were pointing left and right (<>), indicating a choice trial, or the arrows were both pointing to one predetermined side (<< or >>), indicating a no-choice trial. In choice trials, participants could select which colour (and thus category) they wanted to see. In no-choice trials, the selection was made for them, and they had to press the button following the direction of the arrow (the colour presented on the left or right). After 1500 ms, the selected or assigned colour was displayed alone for 500 ms, followed by another jittered fixation cross (2000–8000 ms, with a mean of 3000 ms).

In the choice condition, if participants failed to make a choice within 1500ms, a selection was made for them, and they would also see “Too late!” during the confirmation of the selected colour. If participants pressed the wrong button under the no-choice condition, the message “Wrong button!” appeared, and the correct colour selection would still be enforced. Also, if participants failed to make a response under the no-choice condition, the message “Too late!” appeared with the correct colour selection automatically made for them.

Surprise manipulation – Following the fixation cross, an image was presented that, in 50% of the trials, matched the selected category (low surprise), and in the other 50%, led to a different category (high surprise), as defined by the participant-specific design matrix (Fig. 3.1B). The design matrix used to generate this manipulation featured colour-category mappings along the diagonal (low surprise) and mismatched pairings off the diagonal (high surprise). For example, a participant might learn that red corresponds to insects, orange to musical instruments, yellow to food, green to vehicles, blue to mammals, and purple to furniture. Then, if blue was selected or assigned, a mammal image would appear in the low surprise condition, while an image from any other category (excluding mammals) would be shown in the surprise condition. This intentional violation of learned pairings in 50% of the trials allowed us to obtain the same number of encoding trials under surprise and low surprise conditions. For a more specific example, the mammal category included eight objects of *alpaca, cat, dog, horse, otter, panda, piglet, and seal*, with three images per object perceived by each participant during the learning task. Two objects from each category were randomly assigned to each of the four experimental conditions: choice/low surprise, choice/high surprise, no-choice/low surprise, and no-choice/high surprise. Thus, if *alpaca* and *cat* were assigned to the choice/low surprise condition, selecting the corresponding colour (e.g., blue) would reliably lead to one of these two mammals. If *dog* and *horse* were assigned to the choice/surprise condition, choosing a different colour could unexpectedly result in one of these two images being shown. This structure of high and low surprise assignment was applied to both choice and no-choice conditions. This resulted in six images from each category for each experimental condition, leading to a total of 168 images presented to each participant. Each image was shown twice under the same experimental condition to ensure sufficient exposure for memory encoding.

3.2.3.3 Memory test

After participants finished the learning task, participants would immediately complete a memory test. In this memory test (Fig. 3.1D), each trial started with a jittered fixation cross presented for 2000 ms to 8000 ms, with a mean of 3000 ms. Then, an image was displayed on the screen for 1500 ms, together with four Likert-scale options under the image, namely “Definitely seen”, “Probably seen”, “Probably not seen”, and “Definitely not seen”, arranged from left to the right. Participants were instructed to indicate whether they had seen this picture or not during the learning task with four buttons under their index, middle, ring, and little fingers corresponding to the four options from the left to the right. If a response was made in time during the presentation of the image, the selected option would become bold, appearing on the screen for 500 ms to confirm the response.



	insect	music	food	vehicle	clothing	mammal	furniture
●	12	2	2	2	2	2	2
●	2	12	2	2	2	2	2
●	2	2	12	2	2	2	2
●	2	2	2	12	2	2	2
●	2	2	2	2	12	2	2
●	2	2	2	2	2	12	2
●	2	2	2	2	2	2	12

Figure 3.1. Procedure **A.** Training procedure. Participants first learned the correspondence between seven colours and seven categories, with each colour matching one category. On each trial, they saw a colour dot followed by a picture and guessed if the colour matched the category of the picture. Feedback ("correct" or "error") was provided based on their response. Each block had 28 trials, and participants aimed for 85% accuracy to end training. Training included up to 12 blocks but stopped early if the accuracy threshold was met after six blocks. **B.** Design matrix for conditions. This design matrix shows an exemplar of correspondence between colours and categories that participants might learn during the training process in panel A. This correspondence will be the knowledge that participants use in the memory encoding phase when they are selecting the categories that they wanted to see. In both CHOICE and NO-CHOICE conditions, participants saw pictures paired with colours and categories. During encoding, pictures followed colour dots, but only 50% matched the learned category from training (LOW SURPRISE), while 50% did not match the learned category from training (HIGH SURPRISE). For example, if blue corresponded to mammals, there was a 50% chance of seeing a mammal and a 50% chance of seeing another category. While the matching category had the highest chance, trial numbers for high and low surprise conditions were balanced. **C.** In the memory encoding phase, each trial began with a fixation cross and two colour-dots. In choice conditions, the fixation cross turned into arrows, prompting participants to choose a category by pressing a button. In no-choice conditions, arrows indicated the preselected category, requiring participants to press the corresponding button. In LOW SURPRISE trials (black box), the image matched the selected category according to the correspondence

between colours and categories (panel B) that they learned in the training phase (panel A), while in SURPRISE trials (grey box), the image could belong to any other 6 categories but not the matching one with the colour that they selected. LOW SURPRISE and HIGH SURPRISE trials each occurred in 50% of the trials. **D.** During the memory test phase, participants saw a fixation cross followed by an object in each trial. They pressed one of the four buttons to indicate whether they had seen the object or not. The possible responses were as follows: "Definitely not seen", "Probably not seen", "Probably seen", and "Definitely seen". After 2000ms, the object will disappear, and they will see a blank screen. Then the next trial will start.

3.2.4 Data preprocessing

Data were prepared with Python 3.6 (Van Rossum et al., 2009). First, each image was rated with a memorability score from the THINGS database, which was log-transformed and used as the factor of image memorability in the analysis (Kramer et al., 2023). Additionally, we binned the images based on their log-transformed memorability scores, using intervals of 0.1 ranging from -0.6 to 0. Each bin grouped images with similar levels of inherent memorability, allowing us to visualize how the effects of choice and surprise on memory accuracy varied across different levels of image memorability. Then, only the objects that were seen by participants were included in the final analysis. Images from trials with no responses during either the learning or memory phases, and all filler images were excluded. Finally, the Likert-based responses were transformed into a dependent variable reflecting weighted accuracy inspired by confidence accuracy quotient (https://en.wikipedia.org/wiki/Confidence_weighting; Ebel, 1965; Lundeberg et al., 1994), which incorporated both recognition accuracy and confidence level, providing a more nuanced measure of memory performance. If a seen image was rated as "definitely seen" during the memory phase, this image was coded as 2 (confident/accurate), while a "probably seen" response was coded as 1 (unconfident/accurate). If a seen image was rated as "probably not seen", it was coded as -1 (unconfident/inaccurate), while a "definitely not seen" response was coded as -2 (confident/inaccurate).

3.2.5 Statistical Model Constructions

Data were modelled with Bayesian regression modelling (*brms*) using the *brm* function of the *brms* package in R (Bürkner, 2017) with weighted memory accuracy as a continuous dependent variable. The independent variables were image memorability (Kramer et al., 2023), factors of choice (choice/no-choice), and surprise (high-surprise/low-surprise), for which we all created sum-to-zero contrasts. We fitted the models with 10,000 iterations (5000 warm-ups), with four chains. Model 1 included only factors of choice and surprise and the interaction effect between factors of choice and surprise. The model included random intercepts and random slopes for choice and surprise, as well as the interaction effect between choice and surprise effects grouped by participant (Barr, 2013; Barr et al., 2013).

$$Weighted\ memory\ accuracy \sim choice \times surprise + (1 + choice \times surprise\ |sub)$$

Model 2 included the main effects of image memorability, choice, and surprise, along with the two-way interaction effect between two of these independent variables, and the three-way interaction between factors of memorability, choice, and surprise as fixed effects. The model also included random intercepts and random slopes for choice and surprise, as well as the interaction effect between choice and surprise effects grouped by participant (Barr, 2013; Barr et al., 2013).

$$\begin{gathered} Weighted\ memory\ accuracy \sim choice \times surprise \times memorability \\ + (1 + choice \times surprise\ |sub) \end{gathered}$$

Given our primary interest in the effects of choice and surprise on memory accuracy, if a significant interaction effect was found between factors of choice and surprise in the models, we would prompt follow-up analyses to examine the surprise effect respectively within the choice and no-choice conditions. Specifically, we compared the weighted memory accuracy between high and low surprise conditions separately under choice and no-choice conditions with the *emmeans* toolbox in R (Lenth, 2022). In parallel, with the same procedure as above, we also compared the weighted memory accuracy between choice and no-choice conditions under the high or low surprise condition separately.

In Model 3, as an exploratory analysis, we aimed to investigate whether participants' subjective preference for object categories would account for more variance in memory accuracy. We applied a straightforward probability-based approach to compute the subjective value of each category for each participant as a measurement for preference, using data from the active choice condition in the learning task. Participants were instructed that they would be choosing which colour they wanted to see based on the pairings between colours and categories. The design matrix was structured to ensure equal exposure to each category so the number of times a colour was chosen would be equal. Hence, the number of times a colour was selected could not be used as a direct measurement of preference. However, the frequency with which participants avoided each colour provides meaningful variation. In every choice trial, participants were presented with two colour options and instructed to select one, implicitly avoiding the other. Importantly, the avoided colour from each trial remained in the pool and reappeared in future trials, ensuring that all colours would eventually be chosen the same number of times. As a result, the frequency of avoidance reflects relative "dislike" for that category for each participant. We calculated the total number of times that each colour, each representing a specific category, appeared on either the left or right side across trials in the choice condition. We also counted how many times each colour was avoided, that is, not selected when presented. Then, we calculated the probability of avoidance of each colour using these values.

$$probability_{avoid} = time_{avoid}/times_{appear}$$

Afterward, we ranked the avoidance probabilities across the seven categories for each participant. Categories with lower avoidance probabilities suggested a higher preference, which were assigned with higher rank. Conversely, categories that were avoided more frequently received lower ranks. This yielded a personalized ranking from 1 to 7 for each participant, reflecting their valuation of the categories. A smaller rank number indicated a more preferred category. In an exploratory model (Model 3), we extended Model 2 by including the category value rank as an additional control factor to account for subjective category preference.

$$Weighted\ memory\ accuracy \sim choice \times surprise \times memorability + category\ value\_rank + (1 + choice \times surprise\ |sub)$$

3.2.6 Model comparison

We compared the three models using the *loo* function from the *looic* toolbox to evaluate the predictive performance of each statistical model (Pareto Smoothed Importance Sampling Leave One Out, PSIS-LOO, Vehtari et al., 2017). Expected log predictive density (*ELPD*) and the effective number of parameters (*p_loo*) were calculated for each model. To assess relative model performance, we calculated the difference in ELPD (*ΔELPD*) between each model and the best-performing model, along with the corresponding standard error (*SE*) of these differences, using the *loo_compare* function. In this comparison, the function automatically designates the best-performing model with the highest *ELPD* as the baseline. As a general rule of thumb, a *ΔELPD/SE* greater than two is considered to reflect a substantial difference in model comparison (https://en.wikipedia.org/wiki/68–95–99.7_rule).

3.3 Results

3.3.1 Model comparison

Importantly, we aimed to understand which combination of the factors best explained variability in weighted memory accuracy, particularly whether choice, surprise, memorability, and category value rank contributed to the statistical model. To this end, we compared the three models using the *loo* and *loo_compare* functions from the *looic* toolbox to evaluate their relative predictive performance (Vehtari et al., 2017). Among the three models, Model 2, which included memorability, choice, and surprise, demonstrated the best fit to the data (Table 3.1). This suggested that the most reliable result was the main effect of memorability and the significant interaction between choice and surprise on weighted memory accuracy. Model 1, excluding memorability, performed significantly worse than Model 2 (Table 3.1). Model 3, which included category value rank as an additional predictor, did not explain more variance than Model 2. In the end, we focused on Model 2 as the appropriate model, highlighting the interaction effect between factors of choice and surprise on weighted memory accuracy as the key finding.

Table 3.1 Model comparison

	ELPD	**ΔELPD**	**SE**	**ΔELPD/SE**	***p_loo***
Model1: choice × surprise	-8602.9	-22.4	7.2	-3.1	58.6
Model2: memorability × choice × surprise	**-8580.5**	**-**	**-**		**62.4**
Model3: rank + memorability × choice × surprise	-8581.4	-0.9	0.5	-1.8	63.3

* Bold font indicates significant effects, ΔELPD/SE > 2 indicates a significant difference; Model 2, as the best model among these three models, was recognized as the baseline.

3.3.2 Behavioural statistical models

In Model 2, we added memorability to the model, involving it as another fully structured fixed effect interacting with choice and surprise, with a fully structured random effect of the interaction between choice and surprise per participant (Fig. 3.3). First, we found the main effect of memorability on weighted memory accuracy. In other words, participants were better at remembering the more memorable images. Interestingly, we also found an interaction between factors of choice and surprise on weighted memory accuracy in Model 2 (Fig. 3.3A; Table 3.2).

In the follow-up analysis disentangling this interaction effect, we found that choice improved memory performance only under the low surprise condition (95% CI [-0.250, -0.036]; choice/low-surprise, 1.040 ± 0.660, no-choice/low-surprise, 0.898 ± 0.741). Under the surprise condition, the beneficial effect of choice on weighted memory accuracy was not significant (95% CI [-0.137, 0.072]; choice/high-surprise, 0.860 ± 0.750, no-choice/high-surprise, 0.841 ± 0.719). Additionally, participants remembered images better under the low surprise condition than the high surprise condition only when they made active choices on what they wanted to see (95% CI [0.065, 0.285]). No significant difference in memory accuracy between high surprise and low surprise conditions was found under the no-choice condition (95% CI [-0.047, 0.168]). This was consistent with our previous study investigating predictability and choice effects on memory (Chapter 2), suggesting choice would benefit memory more when the outcome of the choices was predictable compared to unpredictable. When data was visualized by binning objects according to their memorability, a clear and consistent difference between high surprise and low surprise conditions was observed under the choice condition (Fig. 3.3B). However, this difference was less consistent and more variable under the no-choice condition, suggesting a weaker effect of surprise when participants had no choice for upcoming information (Fig. 3.3A).

Table 3.2 BRMS results Model 2

Independent variables: choice, surprise and memorability	Bayesian statistics
Choice	95%CI [-0.179, 0.007]
Surprise	95%CI [-0.051, 0.138]
Memorability	**95%CI [0.866, 1.555]**
Choice × Surprise	**95%CI [-0.192, -0.005]**
Choice × Memorability	95%CI [-0.525, 0.173]
Surprise × Memorability	95%CI [-0.410, 0.276]
Choice × Surprise × Memorability	95%CI [-0.639, 0.059]

* Bold font indicates significant effects

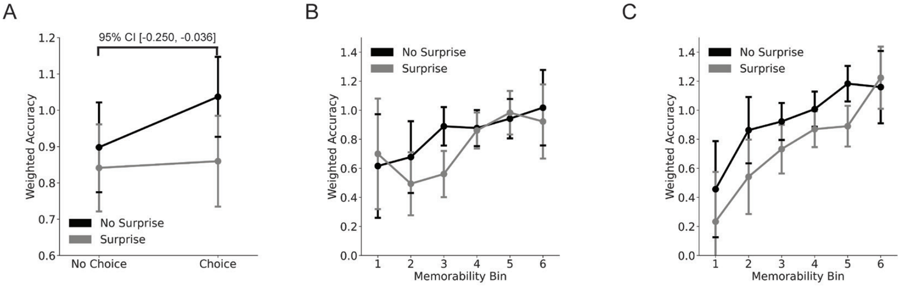


Figure 3.2. Results. **A.** In this panel, we showed the memory accuracy for images seen under all experimental conditions, without separating images into bins according to their memorability. We found the effect of choice on memory accuracy was significant only for the images that were seen under the LOW-SURPRISE condition. The black colour represents the LOW SURPRISE conditions and the grey colour represents the HIGH SURPRISE condition. The black or grey coloured lines represent the simple effect comparison (CHOICE – NO-CHOICE) under different predictabilities. The significant effect of choice under LOW SURPRISE condition was marked by the horizontal black line, with the Bayesian statistical results noted on top. **B.** This figure shows binned log-memorability levels on the x-axis (higher bins indicate more memorable objects) and participant responses on the y-axis. Memory responses were coded from 1 to 4, with higher numbers indicating more accurate and confident responses. The black line represents the LOW-SURPRISE condition, while the grey line represents the SURPRISE condition. The left panel shows NO-CHOICE results, and the right panel shows CHOICE results. Significant main effects of surprise

($p < 0.05$) and memorability ($p < 0.05$) were found: participants remembered objects better under LOW-SURPRISE and recalled more memorable objects more effectively. A significant three-way interaction between factors of memorability, choice, and surprise ($p < 0.05$) revealed that participants remembered LOW-SURPRISE pictures better than HIGH-SURPRISE pictures in the CHOICE condition, but only for highly memorable objects ($p < 0.05$).

3.4 Discussion

The current study aimed to examine how surprise modulated the beneficial effect of choice on memory. To achieve this, we implemented a well-controlled paradigm in which we simultaneously manipulated the freedom of making active choices and the surprise associated with the choice outcomes. Although there were no main effect of choice or surprise factors on memory accuracy, we observed a significant interaction between choice and surprise in the model accounting for memorability, with follow-up analyses revealing that choice enhanced memory performance only in the low surprise condition. This beneficial effect of choice on memory accuracy was eliminated under the high surprise condition, suggesting that unexpected outcomes may disrupt the advantage conferred by active choices. Conversely, surprise impaired memory, but only when participants made an active choice. As expected, we found the main effect of memorability, indicating that more memorable images were recalled with higher accuracy.

Essentially, we extended the findings from Chapter 2 that the act of choice would enhance memory encoding for participants, but only when the information was consistent with their selections (Zhang et al., 2024). Notably, in the current design, participants were only successfully predicting the outcome 50% of the trials, creating a situation in which perceived control over outcomes was low. This suggested that even under conditions of limited control, participants still engaged in an active prediction towards the images, particularly when they were offered the opportunity to choose. This finding aligns with the active inference framework, which suggests that people actively sample information to support their prior beliefs (Friston et al., 2013; Kaanders et al., 2022). Meanwhile, human brains constantly calculate information value and compare it with their expectations (de Lange et al., 2018). When making active choices, this prediction and comparison process was amplified. Some studies have indicated that when people make active choices, they might generate a stronger or even distorted valuation of information following choices (DuBrow et al., 2019; Izuma & Murayama, 2013; Meng & Ma, 2015; Sharot & Sunstein, 2020) to reduce the prediction error (Peterson et al., 2011). In environments with unpredictable choice outcomes, consistent events may stand out due to their temporal consistency, leading to heightened sensory acuity (Sainburg et al., 2025), thus becoming more valuable and salient during memory encoding (Frank et al., 2022).

Meanwhile, we found that memory performance was worse for the surprise condition as compared with the low surprise condition only when participants were making choices freely. Importantly, this is consistent with previous findings indicating that surprise diminishes information encoding (Csink et al., 2021; Frank et al., 2022) but contrasts with other work reporting enhanced visual representation or memory under the high surprise condition compared to the low surprise condition (Filimon et al., 2020; Richter et al., 2018). There are three explanations for this discrepancy in the direction of the surprise effect on memory or visual representation.

First, the detrimental effect of surprise on memory accuracy under the choice condition could be explained by the depth of the violated schema (Bein et al., 2021). In our design, the schema, which is the colour-category pairings, was newly formed. It was argued that when the strength of the activated schema was weak, the violation imposed less cognitive load, making the information easier to process (Schützwohl, 1998). Similarly, de Bruine et al. (2024) suggested that moderate surprise could not boost memory encoding, while consistency and strong surprises both enhanced memory. From a developmental perspective, an infant study also showed no surprise modulation on memory encoding (Csink et al., 2021), since infants also only had a shallow schema towards the world model. Second, this finding can be interpreted within the framework of expected and unexpected uncertainty. In our paradigm, surprise was induced under expected uncertainty. In our design, participants were aware that outcomes could deviate from their choices (Piray & Daw, 2024). In such contexts, there was no model update because of the stochasticity of the information environment, hence, participants could down-weight the perceived information after making the choice, which can impair encoding due to increased cognitive conflict or reduced attentional alignment (Luo et al., 2022; Markant et al., 2014a). Last, the diminishing effect of surprise on memory encoding under the choice condition may also be attributed to the differential influence of surprise on memory processes depending on task demands (Frank & Kafkas, 2021; Kafkas & Montaldi, 2018). It was found that expected information tends to enhance familiarity, whereas unexpected information is more likely to support recollection (Kafkas & Montaldi, 2018). Given that the current task primarily tapped into familiarity-based recognition, the observed memory encoding benefit for expected information is consistent with this notion. In summary, in the current setting, moderate surprise was generated, which diminished memory encoding but only when people were making active choices.

Furthermore, the revelation that the memory impairment for surprising outcomes emerged only under the choice condition may reflect overlapping neural mechanisms between predictive processing and autonomy during memory encoding. Frank et al. (2022) demonstrated that expected objects are better remembered compared to unexpected objects, likely due to co-activation of the hippocampus and SN/VTA when encountering these temporally consistent events. This suggests that prediction-consistent information becomes more salient and better integrated into memory. This co-activation supports memory integration by reinforcing schema-congruent information (Bein et al., 2023). In contrast, prior surprise could disrupt this information integration into an established schema (Sinclair & Barense, 2018; Sinclair et al., 2021). A similar mechanism has been proposed by studies of active choice, where autonomy during learning enhances connectivity between the hippocampus and dopaminergic regions (Dubinsky & Hamid, 2024). Memory encoding with autonomy also induced higher connectivity between dopaminergic circuitry, like the putamen, and the hippocampus (see Chapter 4). Together, these findings suggest that both prediction-consistent outcomes and self-directed choices engage overlapping neural circuits, potentially explaining the interaction effect between choice and surprise on memory encoding.

Interestingly, in the current experiment, the interaction effect between choice and surprise on memory accuracy only emerged when memorability was included as a control variable in the model. This could be because low-level stimulus-specific variances, such as memorability, could obscure higher-level cognitive effects if not accounted for (Kriegeskorte & Kievit, 2013). Specifically, memorability was a strong predictor of memory (Isola et al., 2011) and omitting it from the statistical model perhaps inflated the residual variance, thereby reducing statistical power. As a result, meaningful cognitive effects, for example, the interaction effect between choice and surprise on memory accuracy, may fail to reach significance due to the contribution of uncontrolled stimulus features like memorability. Thus, incorporating memorability in the statistical model allowed a more robust estimation of the effects of interest.

As an exploratory analysis, we found that preference for object categories did not explain more variance in memory accuracy. One possible explanation is that, in the current design, all stimuli were emotionally neutral, resulting in minimal variation in subjective value across categories. By contrast, previous studies using emotionally charged images have shown that when individuals expect emotionally salient content, violations of those expectations elicit stronger contrasts between prediction and perception, thereby subjective values would modulate attentional tuning towards images (Kaskan et al., 2022).

In the current study, surprise was manipulated while predictability was held constant, orthogonal to controlling the factor of choice. As a follow-up of Chapter 2 and the current study, future studies could reverse the current design by manipulating predictability of choice outcomes while keeping surprise constant. For example, participants could choose between two categories, like mammals and food, with one option leading to eight possible images while the other option leading to two possible images. In this way, we could always keep surprise low but manipulate high or low predictability, allowing isolation of the impact of predictability on the beneficial effect of choice on memory encoding. Additionally, while the present study focused on behavioural outcomes, future investigations could incorporate neuroimaging methods to further disentangle how choice and surprise independently and jointly modulate neural processes involved in memory formation (Muttenthaler & Hebart, 2021).

3.5 Conclusion

In conclusion, the current study demonstrated that choice and surprise interactively influence memory encoding. Specifically, choice enhances memory only when choice outcomes are expected based on the participants' choices. The results extend the findings of Chapter 2, leading to important insights into the cognitive mechanism underlying active choices in memory encoding and learning. It is suggested that the benefits of choice on learning depend not only on inherent rewards but also on predictive processing. This has potential implications for educational settings, where providing students with purposeful choices may enhance learning and memory encoding.

3.6 Author note

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Chapter 4

Autonomy modulates the reward circuitry in the brain during memory encoding

Abstract

The freedom to control one's own behaviour, known as autonomy, can enhance learning and memory. As a form of intrinsic motivation, autonomy often coexists with extrinsic motivators such as monetary rewards. However, little is known about how these motivational factors jointly influence memory encoding, particularly at the neural level. To address this, we collected behavioural and functional magnetic resonance imaging (fMRI) data from 47 participants who performed an exploratory learning task. In this task, participants viewed partially obscured images they were later asked to remember. We independently manipulated autonomy, defined as volitional control over exploration, and the existence of monetary rewards. Both autonomy and rewards independently enhanced memory test performance. Critically, only autonomy increased activation in reward-related brain regions, while external rewards had no such neural effect. These findings suggest that autonomy serves as a more effective motivational factor for enhancing memory encoding than monetary rewards. Moreover, exploratory analysis of hippocampal functional connectivity revealed greater engagement of attentional control regions during autonomous learning, whereas passive learning was associated with increased connectivity to lower-level perceptual areas. These findings offer insight into the distinct neural mechanisms of intrinsic and extrinsic motivation, with direct implications for optimizing learning environments in educational contexts.

4.1 Introduction

In our everyday lives, we constantly navigate through environments with an overload of information, such as landmarks on the way to work or a fleeting image of a distinctive car passing by. Our brains must decide which pieces of information to encode and integrate into memory, a process often influenced by motivational factors. Motivation plays a crucial role in shaping what we learn and remember, yet the mechanisms behind this are not fully understood. While intrinsic motivation, such as the sense of autonomy, is known to enhance learning (Ryan & Deci, 2006), it remains unclear how external incentives like monetary rewards interact simultaneously with the beneficial effects of intrinsic motivation on learning. Using fMRI, this study investigates how intrinsic and extrinsic motivational factors affect brain activity during memory encoding, providing new insights into their independent and combined roles.

In cognitive science, a distinction is often made between intrinsic and extrinsic motivational drives to learn. In this distinction, extrinsic motivation can be cognitively described as a drive to acquire rewards from the outside world (Kidd & Hayden, 2015; Szumowska & Kruglanski, 2020), like grades in academic exams or monetary rewards. However, humans are hardly ever driven by a single source of motivation. Intrinsic motivation, for example, can be related to learning driven by curiosity (Cervera et al., 2020; Duan et al., 2020; Loewenstein, 1994; van Lieshout et al., 2018, 2020) or learning with free choices (Murty & Dickerson, 2016). Many would argue that promoting intrinsic motivation is of crucial importance since it supports learning and memory (Deci & Ryan, 1985; Duan et al., 2020; Gruber et al., 2014; Gruber & Ranganath, 2019; Jepma et al., 2012; Kang et al., 2009; Marvin & Shohamy, 2016). In this study, we explicitly focus on autonomy as a drive of intrinsic motivation, which is the feeling one has choices about what to do and how to do it (Ryan & Deci, 2000a). Thus far, multiple studies have indicated that the feeling of having autonomy benefits learning and memory (Ding et al., 2021; DuBrow et al., 2019; Markant et al., 2014a; Murty et al., 2015; Rotem-Turchinski et al., 2019; Voss, et al., 2011a; Voss, et al., 2011b; Voss, et al., 2011c). In these studies, *autonomy* has been operationalized in different ways. Beneficial effects on memory performance have been found when autonomy was defined as simply choosing which button to click (Ding et al., 2021; DuBrow et al., 2019; Murty et al., 2015), as well as having the freedom in exploration (Markant et al., 2014a; Voss, et al., 2011a; Voss, et al., 2011b; Voss, et al., 2011c). In these types of experimental designs, the autonomous condition is compared with an analogous non-autonomous condition in which the choice of the participant is impeded. While the cognitive links between extrinsic and intrinsic motivation have been explored (e.g., Duan et al., 2020; van Lieshout et al., 2023), the neural mechanisms underlying their interaction remain largely understudied.

Synthesizing previous neuroimaging studies focusing on the brain mechanism of autonomy in learning, two core systems consistently emerge: the dopaminergic reward circuitry and the frontal-parietal network, respectively (Dubinsky & Hamid, 2024). On the one hand, dopaminergic reward circuitry, such as the striatum, and the ventral medial prefrontal cortex (vmPFC) were engaged when having the opportunity to choose (e.g., Leotti & Delgado, 2011; Murayama et al., 2015; Murty et al., 2015). These brain regions are also typically triggered by external rewards (e.g., Adcock et al., 2006; Haber & Knutson, 2010) or encode reward prediction errors (Cohen et al., 2014; Di Domenico & Ryan, 2017; Schultz, 2015). It might support the notion that autonomy in learning is intrinsically rewarding (Leotti & Delgado, 2011). On the other hand, the frontal-parietal network, including OFC, ACC, and dorsal lateral prefrontal cortex (dlPFC), related to attentional control, error monitoring, and executive functions, were more active under autonomous learning conditions. This demonstrated that autonomy not only enhances the affective value of learning experiences but also recruits greater cognitive resources toward learning (Kennedy et al., 2024; Luo et al., 2022; Voss et al., 2011b). For instance, Voss et al. (2011b) demonstrated that the functional connectivity between the hippocampus and a broad set of brain regions, including bilateral dorsolateral (dlPFC) and medial prefrontal cortex, left ventrolateral parietal cortex, and left cerebellum, was enhanced when participants had volitional control over exploration compared to deprivation of autonomy. Similarly, Murty et al. (2015) found that both the orbital frontal cortex (OFC) and the anterior cingulate cortex (ACC) showed greater activation during visual information encoding in free-choice versus no-choice conditions. Importantly, they also reported that hippocampal activation was correlated with striatal activation, but only when participants had the freedom to choose learning materials. Together, these findings suggest that autonomy enhances memory encoding by being inherently rewarding and by facilitating attentional engagement during learning.

Although abundant evidence indicates that extrinsic motivators (e.g., monetary rewards) also increase learning and memory performance (Adcock et al., 2006; Elliott et al., 2020; Mason et al., 2017; Murayama & Kuhbandner, 2011), it has been reported that the presence of extrinsic motivation could attenuate the effects of intrinsic motivation on learning (Cameron, 2001; Hidi, 2016; Lepper et al., 1973; Murayama et al., 2010). This interaction can be explained according to the overjustification hypothesis (Lepper et al., 1973): the learner will attribute their enjoyment of the activity to external rewards instead of to the activity itself. Within Self-Determination

Theory, this phenomenon is also known as the undermining effect, in other words, the observation that adding extrinsic motivation where intrinsic motivation is already present might harm this intrinsic motivation (Deci, 1971; Deci & Koestner, 1999; Hidi, 2016; Houlfort et al., 2002; Kuvaas et al., 2020; Lepper et al., 1973; Murayama, 2022; Murayama et al., 2010; Tang & Hall, 2006).

The undermining effect of external rewards on intrinsic motivation may stem from overlapping neural mechanisms shared by intrinsic and extrinsic motivation, specifically the dopaminergic reward circuitry including the ventral striatum, ventral tegmental area, and substantia nigra (Dubinsky & Hamid, 2024; Gruber et al., 2014; Kang et al., 2009). One possible explanation is that the presence of external rewards already engages the dopaminergic reward circuitry to be activated, limiting the additional activation that intrinsic motivation could elicit. For example, Murayama et al. (2010) demonstrated that participants who received rewards showed higher reward circuitry activation during the rewarded task but subsequently exhibited lower intrinsic motivation to perform better once the reward was removed. They argued that the previous presence of external rewards may overshadow the inherent satisfaction of following task engagement, making intrinsic success less salient. On the other hand, it has also been reported that intrinsic and extrinsic motivation benefit memory performance independently (Duan et al., 2020). This may reflect the recruitment of distinct neural mechanisms in parallel, aligning with notions that extrinsic motivation engages reward-related regions, whereas intrinsic motivation additionally evokes attentional control networks such as the dlPFC and ACC (Murty et al., 2015). Altogether, these findings point to conflicting evidence regarding whether or how intrinsic and extrinsic motivational systems interact during learning. Notably, there is a lack of studies that simultaneously manipulated both intrinsic and extrinsic motivational factors during learning while measuring brain activity.

Given the importance of both autonomy and reward on memory performance, we specifically investigate whether autonomy and reward aid memory performance in an additive or interactive fashion. The novelty of our approach primarily lies in our simultaneous and orthogonal manipulation of indicators of intrinsic motivation (i.e., autonomy) and extrinsic rewards (i.e., monetary rewards), rather than sequentially, with the aim of observing their immediate (interactive) effects. By doing so, we provide fresh insights into how these factors interact in affecting memory performance.

To this end, we adapted a well-controlled explorative learning paradigm from Voss et al., (2011b) for use in the fMRI scanner. We chose this paradigm because it provides a well-controlled, but still relatively natural learning environment and because previous results using this paradigm showed robust effects of autonomy on memory performance (Markant et al., 2014a; Voss, et al., 2011a; Voss, et al., 2011b; Voss, et al., 2011c). In this paradigm, participants were presented with a 5 x 5 grid consisting of object images obscured by visual noise except for a (circular) searchlight window. These objects could be unobscured by moving the searchlight window around the screen. Autonomy was manipulated as follows: In the autonomous condition, participants were given volitional control over the temporal and spatial trajectory of the searchlight window using a joystick. In the non-autonomous condition, participants were instructed to follow (mimic with the joystick) an exploration trajectory of a previous participant (i.e., the autonomous trajectories were saved and replayed, so-called 'yoking'). Importantly, we adapted this paradigm by introducing a reward manipulation orthogonal to the autonomy manipulation. This was done by offering participants a monetary reward for their memory performance for objects from selected autonomous and non-autonomous grids and not for other grids. Participants' recognition and spatial memory performance were assessed in a separate memory task. As such, this design allowed us to investigate the effects of autonomy, reward, and their interaction on memory accuracy as well as brain activity during learning.

Previous results have demonstrated that autonomy and reward are strongly related to the dopaminergic reward circuitry, together with regions such as the vmPFC, OFC, dlPFC, and dACC as key components of the frontal-parietal network showing strong signal projection to the reward circuitry (Dubinsky & Hamid, 2024; Haber & Knutson, 2010). In addition, studies have revealed enhanced activation in the hippocampus and parahippocampal gyrus under autonomous compared to non-autonomous conditions (e.g., Murty et al., 2015; Voss et al., 2011b). Building on these findings, the current study focused on a generalized linear modelling (GLM) analysis on preselected voxels within a mask that combined these above-mentioned relevant brain areas. Complementary region-of-interest (ROI) analyses were performed by zooming in on each of the individual structures within dopaminergic reward circuitry, hippocampus, and parahippocampal gyrus. Meanwhile, we expect to find an interaction effect between autonomy and reward in the reward circuitry in the brain. To illustrate, the reward circuitry may be engaged during autonomous learning in the absence of external rewards, but this engagement may diminish when extrinsic rewards are present, as the intrinsic rewarding value of autonomy could be disrupted. Additionally, to extend and optimize the functional connectivity analysis originally conducted by Voss et al. (2011b), we implemented a generalized psychophysiological interaction (gPPI; Studer & Knecht, 2016) analysis over the whole brain with the hippocampus as the seed region as an exploratory analysis. This approach provided insight into how hippocampal functional connectivity across the whole brain was modulated by autonomy and reward conditions at the same time. This could elucidate how the rest of the brain interacts with the memory system during encoding, highlighting information exchange between motivational and memory-related brain regions rather than treating them as separate systems. Understanding whether and how both motivational factors of autonomy and reward interact simultaneously in the brain can help us to support optimal motivation and performance across a range of settings, for example, in education, where both autonomy and extrinsic rewards are commonly used to motivate students.

4.2 Methods

4.2.1 Participants

The current study is conducted based on a collaboration project aiming at conducting cross-cultural comparison of the intrinsic and extrinsic motivation between two groups. We aimed for a final sample size of N = 42 in each cultural group to detect a medium effect size (partial $\eta^2 = 0.09$, alpha level $p<0.05$) with 80% power for the three-way interaction among the two within-group factors (autonomy and reward) and one between-group factor (cultural group) using a 2×2×2 mixed-measures ANOVA (Zhang et al., 2025). In the current chapter, only the data collected in the Netherlands were included.

Fifty-seven healthy individuals participated in the experiment (39 female, 18 male; age: $M = 24.33$, $SD = 5.32$). To implement a yoking design, where each participant observed the searchlight trajectory of the previous participant, the study required N+1 participants. The first participant's searchlight trajectories were presented to the next participant. However, as there was no prior trajectory for the first participant to observe, their data were excluded from the main analysis. Ten participants were excluded based on the motion artefacts. They showed a larger motion artefact than 0.3 mm framewise displacement (FD) over time or had a peak motion artefact of 3mm FD. Therefore, the final sample size was 47 participants (33 female, 14 male; age: $M = 23.98$, $SD = 4.69$). The majority of participants were right-handed (1 left-handed) and all participants used their right hand to control the joystick. All participants had normal or corrected-to-normal vision.

All participants gave written informed consent according to the declaration of Helsinki prior to participation. The experiment was approved by the local ethics committee (CMO Arnhem-Nijmegen, The Netherlands) under a general ethics approval protocol (“Imaging Human Cognition”, CMO 2014/288) and was conducted in compliance with these guidelines.

4.2.2 Stimuli and materials

The stimuli and materials used in this experiment were largely consistent with prior behavioural work (van Lieshout et al., 2023). Similar to the earlier study, participants were presented with a total of 600 images of objects. Those images were selected based on their visibility, recognizability, and lack of lettering from the set “2400 Unique Objects” from the University of California San Diego’s vision and memory lab (Brady et al., 2008). The images were presented in a square grid of 5 x 5 images. Each image was 120 pixels in height and covered by black and white Gaussian noise (SD_{noise} = 3). This was deemed sufficient such that participants could identify the location of the object images, but not their identity (Voss, et al., 2011b; see Fig. 4.1A). The experiment was programmed using PsychoPy version 3 (Peirce & MacAskill, 2018). Participants viewed the images on high-quality 32-inch IPS LCD screens with a resolution of 1920 x 1080 pixels and a 120Hz refresh rate. In the fMRI scanner, the searchlight moved faster compared to in the behavioural lab (van Lieshout et al., 2023) due to the higher refresh rate of the screen, allowing more flexible and responsive control. The screen was positioned behind the participants and visible to them via a mirror mounted on the head coil, allowing them to see the display clearly while lying down in the scanner. During the memory encoding phase, the searchlight window used to uncover the images had a diameter of 180 pixels and was controlled via an HHSC-Tethyx joystick. This joystick is non-magnetic and non-electronic, constructed entirely from plastic, ensuring it does not disrupt the magnetic field or pose safety concerns in an MR environment.

4.2.3 Procedures

The experiment was divided into two blocks. Each block consists of a memory encoding phase and a memory test phase. There was a break after the first block (i.e., the first memory test phase; Fig. 4.1A). During both memory encoding blocks, participants' brains were non-invasively scanned using functional magnetic resonance imaging (fMRI). Although participants also performed the memory tests inside the scanner, neural activity was not recorded during these phases.

4.2.3.1 Memory encoding phase

The memory encoding phase of the experiment is the same as in previous behavioural work (van Lieshout et al., 2023) and will be repeated here for convenience. Each block of the memory encoding phase consisted of six grids. In each grid, 25 images would be presented on the screen, which could be unobscured from the visual noise using a searchlight window (Fig. 4.1B). We instructed participants to remember as many images as possible.

Autonomy manipulation: The memory encoding phase consisted of an equal amount of autonomous and non-autonomous grids (Fig. 4.1C). In autonomous grids (MOVE grids), participants could use the joystick to control the (temporal and spatial) movement of the searchlight window over the images. In non-autonomous grids (FOLLOW grids), participants were told that the searchlight window moved by itself and were asked to follow the movements with their joystick. In fact, participants were presented with the movements of the previous participant in these non-autonomous grids. In other words, the autonomous (MOVE) grids of the previous participant were shown as non-autonomous (FOLLOW) grids for the current participant. Similarly, the current participant's autonomous grids were recorded and shown as non-autonomous grids to the subsequent participant. This is a commonly used procedure called "yoking", in which stimulus input was identical, but differed in autonomy over the searchlight window (see Voss et al., 2011b). The movements for the non-autonomous grids of the first participant were generated by a seed participant. This seed participant only completed autonomous (MOVE) grids, and we did not use its data for analyses.

Reward manipulation: The participants were instructed that some of the autonomous and non-autonomous grids would be rewarded. Participants could earn a maximum of 5 euros on top of their standard compensation if they correctly recognized images presented during rewarded grids (i.e. 3 cents for each correctly recognized rewarded image).

Each grid started with a pre-grid screen that instructed participants about whether the next grid would be autonomous (MOVE grid) or non-autonomous (FOLLOW grid). In rewarded grids, this instruction was accompanied by a picture of a 5-euro banknote in the middle of the screen and the text ("Be aware: images from this trial are REWARDED!") at the bottom of the screen. During the experiment, terms like "you control the window", "the window moves by itself", and "MOVE and FOLLOW grids" were used. Any use of volitional, voluntary, or autonomous language was avoided to keep participants naïve to the manipulation as much as possible. Participants were not aware that their FOLLOW grids were generated by the previous participants. To ensure that participants paid attention to reward, participants were not told how many grids would be rewarded. The focus was solely on the amount of 5 Euros that they could earn extra during the experiment, and not on the relatively small reward per image.

Within participants, grid types alternated between autonomous and non-autonomous. The starting grid type alternated across participants, with the first participant randomly assigned to begin with an autonomous grid. Rewarded grids were evenly distributed across blocks (three per block) and conditions (three MOVE grids and three FOLLOW grids). Reward was also maintained across yoking: a rewarded MOVE grid for one participant corresponded to a rewarded FOLLOW grid for the subsequent participant. The same applied to unrewarded grids. To achieve this, each block contained two groups of three grids—one group rewarded and the other unrewarded. In one block, there were two rewarded MOVE grids and one rewarded FOLLOW grid, while the other block featured one rewarded MOVE grid and two rewarded FOLLOW grids. Due to the yoking protocol, this alternation was consistent between participants. Within a block, the order of rewarded MOVE grids was randomized among the available MOVE grids. The order of rewarded FOLLOW grids was then determined by the randomization of the yoked MOVE grids from the preceding participant. This approach ensured that while autonomy and reward were independently manipulated, any behavioural differences between reward types were systematically controlled.

Each grid had a total duration of 60 seconds and was interrupted halfway by a 20 second break (i.e., after 30 seconds, following Voss et al., 2011b). By dividing the grid into two segments, we effectively increase the variation in the predicted blood-oxygen-level-dependent (BOLD) signal, which is crucial for ensuring statistical robustness in an fMRI block design (the total variance in BOLD signal introduced by the experimental design determines the detection power). During the break, participants paused before resuming the second half of the grid at the point where they had left off in the first half. Additionally, each grid began with a pre-grid screen lasting 20 seconds, which informed participants whether the upcoming grid was a MOVE or FOLLOW grid and whether it was rewarded or unrewarded. Consequently, each block of the memory encoding phase had a fixed duration of exactly 10 minutes.

4.2.3.2 Memory test phase

After each block of the memory encoding phase, participants completed a memory test to assess their recall of the images presented during the preceding memory encoding phase. As a result, two memory tests were administered in total (one after each memory encoding phase). Both memory tests combined a recognition memory task with a spatial memory task.

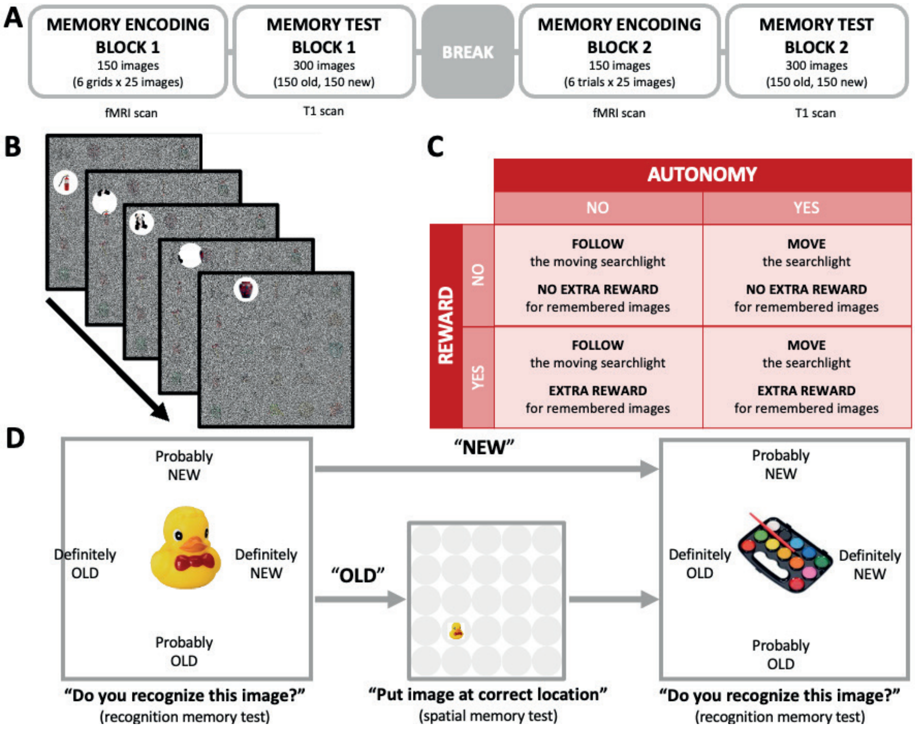

Figure 4.1. Task schematics. **A.** Experimental design and paradigm. The experiment consisted of two blocks that were divided by a break. Each block consisted of a memory encoding phase and a memory test phase. We only conducted fMRI scan during the two memory encoding phases, while during the memory test phases, we did two structural scans (T1). During the memory encoding phase, participants were presented with 6 grids, each containing 25 images presented on a 5 x 5 grid. Participants were instructed to study and remember the images (150 per block) as well as they can. The memory encoding phase was followed by a memory test phase during which participants were presented with 300 images: the 150 images they studied during the memory encoding phase and 150 new images. **B.** Example grid of the memory encoding phase. In each grid, the 25 images were covered by black and white gaussian noise. The images could be uncovered using the searchlight window and participants were instructed to remember as many images as possible. **C.** Overview of the conditions in the memory encoding phase. In autonomous (MOVE) grids, participants could directly control the movement of the searchlight window using a joystick. In non-autonomous (FOLLOW) grids, participants were shown the movements generated by the previous participant and instructed to follow the movements along with their joystick. Each grid was either rewarded, meaning that participants would receive a bonus for correctly remembering the images of that grid, or unrewarded. Before the start of each grid, a screen indicated whether the upcoming grid was an autonomous (MOVE) or non-autonomous (FOLLOW) grid and whether the grid was rewarded or not. **D.** Example grid of the memory test phase. After 6 grids of the memory encoding phase, participants had to perform a memory test. For each image, they had to indicate whether the image was "Definitely OLD", "Probably OLD", "Probably NEW" or "Definitely NEW" by moving the joystick in the corresponding direction (recognition memory test). If participants indicated that they had seen an image before ("Definitely OLD" or "Probably OLD"), they were instructed to place the image on the grid (spatial memory test) before moving on with the next image.

Recognition memory test: During each memory test, participants were exposed to a total of 300 images; 150 of these images were learned during the six grids of the preceding memory encoding phase (i.e., old images) and the other half of the images were not learned before (i.e., new images or 'foils'). We asked participants to indicate whether they had seen each image during the memory encoding phase or not using a 4-point Likert scale (with response options: *definitely old, probably old, probably new or definitely new*). These response options were positioned around the image, and participants could give their response by moving the joystick in the corresponding direction (Fig. 4.1D). If a participant responded to an image with "definitely old" or "probably old," they were asked to report where on the screen they had seen that image during the preceding memory encoding phase (i.e. their spatial memory).

Spatial memory test: To assess participants' spatial memory, we used a modified version of the paradigm used by Markant and colleagues (2014a). If participants indicated that an image was "definitely old" or "probably old" during the recognition memory test, they were presented with another screen consisting of the exploration grid (Fig. 4.1D). The image was initially in the middle, and participants were instructed to move the image to the location on the 5 x 5 grid where they thought they had seen it during the memory encoding phase. The participants could do so using the joystick and confirm their positioning with a button click. We instructed the participants to go for their best guess and to try to be as close as possible to the image's location.

At the end of the experiment, participants were provided with feedback: they were shown their performance in terms of hit rate for both blocks separately (i.e. correct classification of old images) and how well they performed on the rewarded images alone. They also saw how much reward they would receive on top of their standard compensation.

4.2.3.3 Training

Before the start of the experiment, participants underwent a short training session in a behavioural lab to ensure their understanding of the task. After reading the instructions for the experiment, participants verbally explained the purpose of the task back to the experimenter. After ensuring that the participant understood the task, participants performed a short version of the memory encoding phase consisting of four grids (one autonomous unrewarded grid, one non-autonomous unrewarded grid, one autonomous rewarded grid, and one non-autonomous rewarded grid, respectively). Participants were aware that the reward in the memory encoding phase of the training was only exemplary and that their performance during this phase would not actually be rewarded. To assure no memory interference could occur during the main experiment, cartoon images (Rossion & Pourtois, 2004) were used instead of the object images used during the actual experiment. Following these four grids, a short 20-image memory test was conducted to familiarise participants with the general procedure of the memory test phase of the experiment. No data were recorded during training.

The experiment lasted approximately two hours, depending on participants' response times during the memory test. Participants received a standard compensation of 19 Euros and could earn up to an additional 5 Euros based on their performance in the rewarded grids of the memory test. Notably, the standard compensation for this fMRI study was higher than that of the previous behavioural lab study (19 Euros compared to 14 Euros; van Lieshout et al., 2023). However, the bonus of up to 5 Euros remained consistent across both experiments.

4.2.4 fMRI acquisition

The MRI data were collected using a Siemens 3 Tesla (3T) MAGNETOM Prisma scanner and a 32-channel head coil. Each scanning session started with a head-localizer. The AutoAlign head software by Siemens was used, ensuring a similar field of view (FOV) across participants. Fieldmaps were collected before starting the first memory encoding phase (TR = 410 ms, TE1 = 2.20 ms, TE2 = 4.66 ms, voxel size of 2.4 x 2.4 x 2.4 mm, 60 transversal slices, 40° flip angle, interleaved slice acquisition). During both memory encoding phases of the experiment, functional images were acquired using a multiband imaging sequence (TR = 1200 ms, TE = 34.2 ms, voxel size of 2.4 x 2.4 x 2.4 mm, 60 transversal slices, 65° flip angle, multiband acceleration factor of 4, interleaved slice acquisition). Dummy scans were acquired before the start of each BOLD run to reach scanner equilibrium. These volumes were not saved. After each memory encoding phase, anatomical images were acquired using a T1- MPRAGE sequence, using a GRAPPA acceleration factor of 2 (TR = 2300 ms, TE = 3.03 ms, voxel size of 1 x 1 x 1 mm, 192 sagittal slices, 8° flip angle, interleaved slice acquisition), resulting in two anatomical images per participant.

4.2.5 Preprocessing

4.2.5.1 Preprocessing of behavioural data

General data preparation - Data were prepared using Python 3.6 (Van Rossum et al., 2009). All 600 images were classified as either non-autonomous unrewarded, non-autonomous rewarded, autonomous unrewarded, autonomous rewarded, or foil (meaning that they were not presented during the memory encoding phase) for each participant. During the memory encoding phase, images were coded as “seen” if the searchlight window overlapped any pixels with an image's associated grid square (120 x 120 pixels) for at least 200 milliseconds. All episodes were pooled to generate the cumulative time spent on each image. Any image presented during the memory encoding phase that was uncovered for less than 200 milliseconds was reclassified as a foil image, as it was assumed that the image was not studied by the participants or their subsequent yoker (see Markant et al., 2014b). It should be noted that a substantial proportion of all images (99.76%) was coded as "seen" during the memory encoding phase of the experiment and included in the final analyses. In total, 44 out of 14,100 images were coded as "not seen" and reclassified as foils, representing an average of 299.03 images per participant.

Recognition memory weighted accuracy – The measurement for recognition memory was calculated in two different ways, respectively recognition memory weighted accuracy and sensitivity.

Recognition memory weighted accuracy was calculated for all objects. If the Likert response for a "seen" object was rated as "definitely OLD", it was assigned a weighted accuracy of 2; "probably OLD" was assigned 1; "probably NEW" was assigned -1; "definitely NEW" was assigned -2. For the foil objects, the coding for weighted accuracy was reversed: "definitely OLD" was assigned a weighted accuracy of -2; "probably OLD" was assigned -1; "probably NEW" was assigned 1; "definitely NEW" was assigned 2.

Then, we employed signal detection theory to calculate *d'* to measure sensitivity of recognition memory test responses (Hautus et al., 2021). According to signal detection theory, d' represents the discriminability/sensitivity. The higher the *d'* is, the better the participant is at discriminating between old and new objects. To calculate *d'*, we first converted the Likert response from the recognition memory test into binary accuracy codes for each image. If a "seen" image was presented during the memory encoding phase and correctly recognized ("definitely OLD", "probably OLD"), this image was classified as a hit, whereas other unrecognized "seen" images were classified as a miss ("probably NEW", "definitely NEW"). For each grid, the recognition hit rate was calculated by dividing the number of hits per grid by the total number of "seen" images in that grid.

$$Hit\ rate = \frac{Hit\ object\ number\ per\ grid_{Old}}{Object\ number\ per\ grid_{Old}}$$

If a foil image was recognized as "OLD", this image was classified as a false alarm. If a foil image was recognized as "NEW", this image was classified as correct rejection.

The memory encoding phase of the experiment was divided into two runs. In each run, each participant learned six grids with a total of 150 objects, divided into 25 objects per grid, followed by a memory test including these 150 objects intermixed with 150 filler objects (foils). Hence, a false alarm for each run could be calculated.

$$\mathit{False\ alarm} = \frac{\mathit{Hit\ object\ number\ per\ run}_{\mathit{Foil}}}{\mathit{Object\ number\ per\ run}_{\mathit{Foil}}}$$

Eventually, we calculated *d'* for each grid. We implemented *z* transformation for hit rate (Z_H) for each grid and false alarm (Z_{FA}) for the corresponding run for each grid. Then, *d'* for each grid was computed as follows.

$$d(= Z) - Z\%*$$

Spatial memory - The spatial memory hit rate was calculated for the "seen" images that were correctly recognized as "OLD" in the recognition memory test since the spatial memory test was skipped for the "seen" images that were recognized as "NEW". The foil images were also excluded since there were no correct locations for these images during encoding. We coded the spatial memory responses into a binary variable. We counted the spatial memory test trial as "hit" if participants identified the object image's location at the correct location or all 8 locations surrounding that correct location (Fig. 4.2). On the contrary, if they put the object to the rest 16 locations from these nine locations, we counted that trial as a "miss" (general spatial memory score as 0). In this way, we tolerated a range of errors for participants in the spatial memory test.

4.2.5.2 Preprocessing of fMRI data

DICOM images were converted into Niftii files in BIDS format (the brain imaging data structure, https://bids.neuroimaging.io) with BIDscoin (Zwiers et al., 2021). In the BIDSIDS folder for each participant, there were two T1-weighted (T1w) images, one fieldmap estimation, and two functional BOLD runs collected during memory encoding tasks.

We preprocessed fMRI data with fMRIPrep 24.0.0 (Esteban et al., 2019). A field map was estimated from the phase-drift map(s) measure with two consecutive GRE (gradient-recalled echo) acquisitions. The corresponding phase-map(s) were phase-unwrapped with a prelude. An anatomical T1w-reference map was computed after registration of two T1w images (after INU-correction) using mri_robust_template (FreeSurfer 7.3.2, Reuter, Rosas, and Fischl 2010). Brain surfaces were reconstructed using recon-all (FreeSurfer 7.3.2, RRID: SCR_001847, Dale, Fischl, and Sereno

1999), and the brain mask was refined with a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical grey-matter of Mindboggle (RRID: SCR_002438, Klein et al. 2017). Volume-based spatial normalization to the MNI152NLin6Asym standard space with a resolution of 2 x 2 x 2 mm was performed through nonlinear registration with antsRegistration (ANTs 2.5.1), using brain-extracted versions of both T1w reference and the T1w template (Evans et al., 2012, RRID: SCR_002823; TemplateFlow ID: MNI152NLin6Asym). The estimated MNI152Nlin6Asym brain mask was used to conduct brain extraction after preprocessing. The functional data was smoothed using a Gaussian kernel of 5 mm (FWHM).

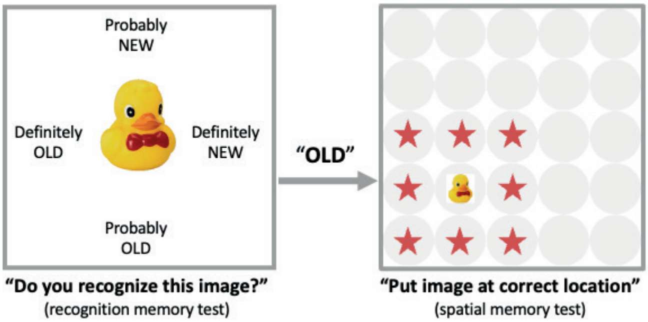

Figure 4.2 General spatial memory score calculation. In the memory test, participants were asked to put the OLD objects back to the locations they saw the object during memory encoding. When computing the general spatial memory score, a margin of error was permitted. Specifically, an object was classified as a "hit" in the spatial memory test if participants positioned it either at the designated location (i.e., where the rubber duck was initially placed) or within any of the eight surrounding locations marked by red stars. If the object is put to the rest 16 locations on the grid (i.e., without any mark), we would count that trial as a "miss" in the spatial memory test. If the correct location of the object is on the corner, only three locations around the corner would be tolerated as "hit" locations. When the correct location of the object is on the border, only five locations around the correct location will be included as "hit" locations.

For each of the two BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. The estimated fieldmap was aligned with rigid registration to the target EPI (echo-planar imaging) reference run. The field coefficients were mapped onto the reference EPI using the transform. The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer), which implements boundary-based registration (Greve and Fischl 2009). Co-registration was configured with six degrees of freedom. Several confounding time series were calculated based on the preprocessed BOLD: framewise displacement (FD), temporal derivatives variance series (DVARS), and three region-wise global signals. FD was computed using two formulations following the absolute sum of relative motions from Power et al. (2014)

and the relative root mean square displacement between affines from Jenkinson et al. (2002). FD and DVARS were calculated for each functional run, using Nipype (following the definitions by Power et al. 2014). We excluded participants who exhibited an average FD larger than 0.3 mm or a peak FD larger than 3 mm.

Three global signals were extracted within the cerebrospinal fluid (CSF), the white matter (WM), and the whole-brain masks (Behzadi et al., 2007). Principal components were estimated after high-pass filtering the preprocessed BOLD time series (using a discrete cosine filter with 128 s cut-off) for the anatomical noise components (aCompCor) within the CSF, WM, and CSF+WM masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, or combined). The remaining components were dropped from consideration. Among the noise confounds, we included the global signal from the whole brain and the first five anatomical noise components to remove physiological noise. Additionally, we included all the cosine regressors as nuisance regressors to conduct highpass filtering for the fMRI data. Then, we preprocessed the data with the same argument with fmriprep 23.0.2 but with ICAroma (Pruim et al., 2015). All the ICA-Aroma components that were recognized as motion were also included in the nuisance regressor file to remove motion artefacts.

4.2.6 Statistical analyses

4.2.6.1 Behavioural data analyses

We conducted statistical analyses on the three dependent variables, recognition memory weighted accuracy, d' calculated from recognition memory accuracy, and the spatial memory hit rate, respectively, using both lme4 (Bates et al., 2015) and brms (Bürkner, 2017) to validate our results across frequentist and Bayesian frameworks R (R core team, 2022). For recognition memory and *d'*—both continuous measures—we employed linear mixed-effects models using the *lmer* function from the lme4 package with a Gaussian family. For spatial memory hit rate, a binary variable, we used generalized linear mixed-effects models via the gamer function with a logistic link function. Corresponding models were also implemented in brms using the same specifications for each dependent variable. The independent variables were the factors autonomy (MOVE, autonomous encoding; FOLLOW, non-autonomous encoding) and reward (REWARD; NO REWARD). Both autonomy and reward factors were within-participant manipulations. We created sum-to-zero contrasts for all the factors. In the model, we included autonomy and reward main effects as fixed effects. The model also included the two-way interaction effect between autonomy and reward as fixed effects. Additionally, the model had a full random effects structure, meaning that a random intercept and random slopes for all within-subject effects were included per participant (Barr, 2013; Barr et al., 2013). The LME model was fitted with 10,000 iterations and diagnosed with DHARMa (Hartig, 2020).

Similarly, we implemented the *brm* function of the package BRMS in R (Bürkner, 2017) to model recognition memory weighted accuracy, recognition memory sensitivity, and spatial memory hit rate as dependent variables with the same model structure. We used the default priors of the BRMS package (Cauchy priors and LKJ priors for correlation parameters). The model was fit running four chains with 10000 iterations each (5000 warm-ups) and inspected for convergence. Coefficients of the effects were deemed statistically significant if the associated 95% posterior credible intervals were non-overlapping with zero.

4.2.6.2 fMRI data analyses

GLM analysis within targeted brain mask - For each run for each participant, preprocessed fMRI data from the whole brain was modelled using an event-related GLM as the first-level analysis. We built the regressors by extracting time series based on the moment when a picture was revealed, and this picture was successfully recognized in the memory test. We defined events as occurring when the centre of the searchlight was located within 90 pixels (the searchlight radius) of the centre of an image. This ensured that events reflected only moments when participants were viewing complete images rather than navigating between images. Then, we separately modelled the events during which the picture was not successfully recognized during the memory test in the GLM, apart from the images that were remembered. These forgotten images were not included in the construction of the contrasts between experimental conditions. We constructed regressors respectively for each of the four encoding conditions: MOVE/REWARD, MOVE/NO-REWARD, FOLLOW/REWARD, and FOLLOW/NO-REWARD. Additionally, we included a regressor including all events corresponding to images that were not recognized in the memory test, labelled as FORGOTTEN. All five regressors for events were convoluted with double-gamma hemodynamic response function (HRF) in FSL. Eventually, the nuisance regressors, including the global signal, the five anatomical noise components, cosine regressors, and the motion components from ICA-Aroma, were included in the design matrix for each run.

Next, we conducted second-level analyses by combining the two runs for each participant, yielding contrast images for each condition, as well as for main effects, interaction effects, and post hoc comparisons. These participant-level contrasts were then entered into a third-level (group-level) analysis across all participants. Group-level results were thresholded at the voxel level with $z > 3.1$ ($p < 0.001$), followed by cluster-level family-wise error (FWE) correction at $p < 0.05$ within a mask of regions of interest (ROIs) based on previous studies. The current study aims to focus on the brain regions related to reward circuitry (Dubinsky & Hamid, 2024; Haber & Knutson, 2010). To define this mask, we combined regions identified in both studies as either core components of the reward system or as modulatory regions. The overlapping areas primarily comprised subcortical structures central to reward processing, including the substantia nigra (SN), ventral tegmental area (VTA), putamen, nucleus accumbens, and caudate. Additional regions known to modulate reward circuitry included the medial frontal cortex, orbitofrontal cortex, middle and superior frontal gyri, hippocampus, parahippocampal gyrus, and amygdala. We extracted probabilistic masks of these anatomical regions from the Harvard-Oxford cortical and subcortical structural atlases (Makris et al., 2006; Frazier et al., 2005; Desikan et al., 2006; Goldstein et al., 2007) from FSL using a 25% probability threshold (Craddock et al., 2012). Then, we binarized these masks by coding the voxels showing a probability for this specific region higher than or equal to 25% as "1" while the voxels with a probability below 25% as "0". We combined the binarized masks into a single mask encompassing all selected ROIs. Third-level analyses were conducted exclusively from within this combined mask. Note that the third-level analysis within the whole brain mask was conducted as well, and the results were put in Supplementary Material 4.1.

ROI analysis – To further confirm how each sub-region within the reward circuitry is involved in intrinsic and extrinsic motivation during learning, we conducted region-of-interest (ROI) analyses focusing on key reward-related regions separately (Dubinsky & Hamid, 2024; Haber & Knutson, 2010), including putamen, caudate, nucleus accumbens, VTA, and SN. Additionally, we included the hippocampus and parahippocampal gyrus since the current study focuses on memory encoding (Voss et al., 2011b). We used the same probabilistic anatomical masks as in earlier analyses, applying a 25% threshold. We extracted second-level z-values within each of these anatomical masks, separately. To account for spatial probability, we computed a weighted mean activation for each region by averaging the z-values of voxels weighted by their corresponding probabilistic values within the anatomical mask. These weighted mean z-values were then entered into an LME model to compare average activation across conditions for each brain region (Bates et al., 2015), including the main effect of autonomy and reward, the interaction effect between factors of autonomy and reward, and a random intercept to account for variability across participants.

$$\text{ROI activation} \sim \text{autonomy} \times \text{reward} + (1 \mid sub)$$

gPPI analysis – We then sought to characterize how memory system interacts with the rest of the brain depending on our manipulation of intrinsic and extrinsic motivations. Hence, a generalized psychophysiological interaction (gPPI) analysis was conducted, extending the approach used by Voss et al. (2011b), which focused solely on functional connectivity. Given our 2×2 factorial design, introducing both autonomy (MOVE vs. FOLLOW) and reward (REWARD vs. NO-REWARD) and interaction between these two factors, gPPI was more appropriate, since this allowed us to model both psychological conditions of autonomy and reward, and their interactions simultaneously with the dependent variable as the functional connectivity with the seed region as bilateral hippocampus.

For each subject and run, we constructed a gPPI design matrix beginning with five psychological regressors corresponding to the task conditions: MOVE/REWARD, MOVE/NO-REWARD, FOLLOW/REWARD, FOLLOW/NO-REWARD, and FORGOTTEN. To define our seed region, we extracted the bilateral hippocampal time series using the same anatomical probabilistic mask from the Harvard-Oxford atlas, thresholded at 25%. Voxels exceeding this threshold were included in the mask. The time series for each voxel within the mask was multiplied by its corresponding probability value, and a weighted average was computed across spatial dimensions, yielding a single time series for the bilateral hippocampus. This signal was then mean-centred (demeaned) for each run and served as the physiological regressor.

Next, we generated psychological-physiological interaction (PPI) regressors by multiplying the mean-centred hippocampal time series with each of the convolved psychological regressors, resulting in five PPI regressors. Altogether, the design matrix included 11 regressors: five psychological regressors, the physiological regressor from hippocampus activity, and five PPI regressors. Nuisance regressors identical to those used in the original GLM analysis within targeted brain mask were also included.

The gPPI GLM was implemented within the whole brain, excluding the hippocampus itself. First-level (within-run), second-level (within-subject), and third-level (group) analyses were then performed. Group-level results were thresholded using a voxel-wise threshold of $z > 2.3$, $p < 0.01$, followed by cluster-level correction with FWE at $p < 0.05$. This relatively liberal threshold was chosen because gPPI is generally weak in power and more susceptible to false negatives (O'Reilly et al., 2012).

4.3 Results

4.3.1 Behavioural results

We conducted the same statistical analyses using LME and BRM with the dependent variables as weighted hit rate and *d'* for recognition memory and the spatial hit rate (Table 4.1 & 4.2, Fig. 4.3). Using LME model, we found a significant main effect of autonomy across all three dependent variables, indicating that participants encoded both the images and their locations better when they could MOVE the searchlight by themselves compared to when they FOLLOW the searchlight with the joystick. Moreover, there was a significant main effect of reward on both weighted accuracy and *d'* calculated for recognition memory. This suggested that recognition memory performance was enhanced by extra monetary rewards. In contrast, the main effect of reward on spatial memory hit rate was only marginally significant. We did not find an interaction effect of autonomy and reward on any of the measurements. We obtained similar results using Bayesian regression modelling, with the exception that the main effect of reward on spatial memory hit rate reached significance as well (Table 4.1).

Table 4.1 Behavioural results on recognition memory, *d'* and spatial memory tests

Dependent variables	**LME/gLME**				**Bayesian statistics**
Recognition memory: weighted accuracy	*β*	*t*	*Chisq*	*p*	Credible interval
Autonomy	**-0.29**	**-8.95**	**82.49**	**<0.001**	**95%CI [-0.457, -0.289]**
Reward	**-0.05**	**-2.52**	**7.10**	**0.008**	**95%CI [-0.116, -0.003]**
Autonomy × Reward	0.002	0.17	0.03	0.86	95%CI [-0.049, 0.051]
Recognition memory: *d'*	*β*	*t*	*Chisq*	*p*	
Autonomy	**-0.37**	**-9.02**	**81.64**	**<0.001**	**95%CI [-0.354, -0.223]**
Reward	**-0.06**	**-2.05**	**4.25**	**0.04**	**95%CI -[0.093, -0.009]**
Autonomy × Reward	0.001	0.05	0.002	0.96	95%CI [-0.025, 0.029]
Spatial memory: hit rate	*β*	z	*Chisq*	*p*	
Autonomy	**-0.13**	**-4.78**	**23.25**	**<0.001**	**95%CI [-0.184, -0.077]**
Reward	-0.05	-2.04	3.70	0.05	**95%CI [-0.101, -0.001]**
Autonomy × Reward	-0.03	-1.36	1.86	0.17	95%CI [-0.084, 0.015]

Note: There are 2 factors included in this LME model, autonomy (MOVE/FOLLOW) and reward (REWARD/NO REWARD). Bold font indicates significant effects

Table 4.2 Descriptive statistics of weighted memory accuracy, d’, and spatial memory hit rate

	Weighted accuracy		**d'**		**Spatial memory hit rate**	
Main factors	***M***	***SD***	***M***	***SD***	***M (%)***	***SD***
MOVE	1.02	0.59	0.37	1.18	74.63	9.73
FOLLOW	0.45	0.70	-0.37	1.26	69.50	11.37
REWARD	0.78	0.63	0.06	1.21	73.08	10.98
NO REWARD	0.68	0.62	-0.06	1.20	71.73	9.41
Autonomy × Reward	***M***	***SD***	***M***	***SD***	***M (%)***	***SD***
MOVE/ REWARD	1.07	0.60	0.43	1.21	74.79	10.84
MOVE/NO REWARD	0.97	0.62	0.31	1.19	74.32	9.96
FOLLOW/REWARD	0.50	0.73	-0.43	1.29	70.78	12.96
FOLLOW/NO REWARD	0.40	0.72	-0.31	1.29	68.69	12.61

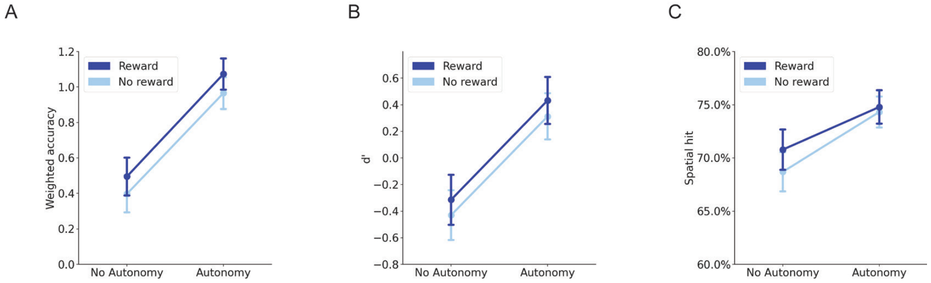

Figure 4.3 Behavioural results. Results from three measurements of memory (i.e., recognition memory weighted accuracy, d’, and spatial memory hit rate) are shown as a function of the two factors of interest: autonomy and reward. **A.** Recognition memory weighted accuracy is plotted as a function of autonomy and reward. The dark blue colour represents the reward condition, while the light blue colour represents the no reward condition. **B.** As in A, d’ is plotted as a function of autonomy and reward. The dark blue colour represents the reward condition, while the light blue colour represents the no reward condition. **C.** As in A, the spatial memory hit rate is plotted the same for the Dutch group. The dark blue colour represents the reward condition, while the light blue colour represents the no reward condition. In all panels, the error bars represent the standard error of the mean. Since the two-way interaction between the factors of autonomy and reward was not significant, we did not perform post hoc comparisons on the difference between autonomy conditions within reward or no reward conditions.

4.3.2 Neuroimaging results

4.3.2.1 Masked GLM analysis

First, we examined whether autonomy modulates brain activity within the mask from previous studies (Dubinsky & Hamid, 2024; Haber & Knutson, 2010). We found that among cortical regions, the right middle frontal gyrus, bilateral anterior cingulate cortex, and bilateral parahippocampal gyrus were activated more under the MOVE condition compared to the FOLLOW condition. Meanwhile, among the subcortical regions associated with reward processing (Haber & Knutson, 2010), we found that the right caudate and bilateral putamen were activated more under MOVE compared to the FOLLOW condition (Table 4.3, Fig. 4.4A). Additionally, there was greater activation under the FOLLOW condition compared to the MOVE condition in the right orbitofrontal cortex, bilateral middle frontal gyrus, bilateral superior frontal gyrus, and right amygdala. No significant clusters were observed in subcortical regions of the reward circuitry when comparing FOLLOW with MOVE conditions (Table 4.3, Fig. 4.4A).

Table 4.3 Brain regions showing differential activation in MOVE vs. FOLLOW in GLM analysis within targeted brain mask

Cluster Size	*zMax*	*p*	*x*	*y*	*z*	Hemisphere	Anatomical Region
MOVE - FOLLOW							
36	4.41	0.035	30	36	42	Right	middle frontal gyrus
1151	7.19	<0.001	8	22	36	Bilateral	anterior cingulate
67	4.32	0.003	-24	-42	-12	Left	parahippocampal gyrus
78	4.42	0.001	32	-28	-20	Right	parahippocampal gyrus
58	4.46	0.006	18	0	20	Right	caudate
596	6.06	<0.001	-24	4	8	Left	putamen
452	5.74	<0.001	22	12	-2	Right	putamen
FOLLOW - MOVE							
107	6.14	<0.001	50	30	-8	Right	frontal orbital cortex
119	4.35	<0.001	-40	4	54	Left	middle frontal gyrus
359	6.21	<0.001	50	6	52	Right	middle frontal gyrus
70	5.39	0.002	-12	-2	70	Left	superior frontal gyrus
74	3.86	0.002	6	40	44	Right	superior frontal gyrus
43	3.89	0.019	14	2	70	Right	superior frontal gyrus
74	5.07	0.002	22	-6	-14	Right	amygdala

Note: Coordinates correspond to the standard Montreal Neurological Institute (MNI) brain. We used a primary voxel threshold of $z > 3.1$, $p < .001$ (uncorrected) and a cluster-level correction of $p < .05$ (FWE).

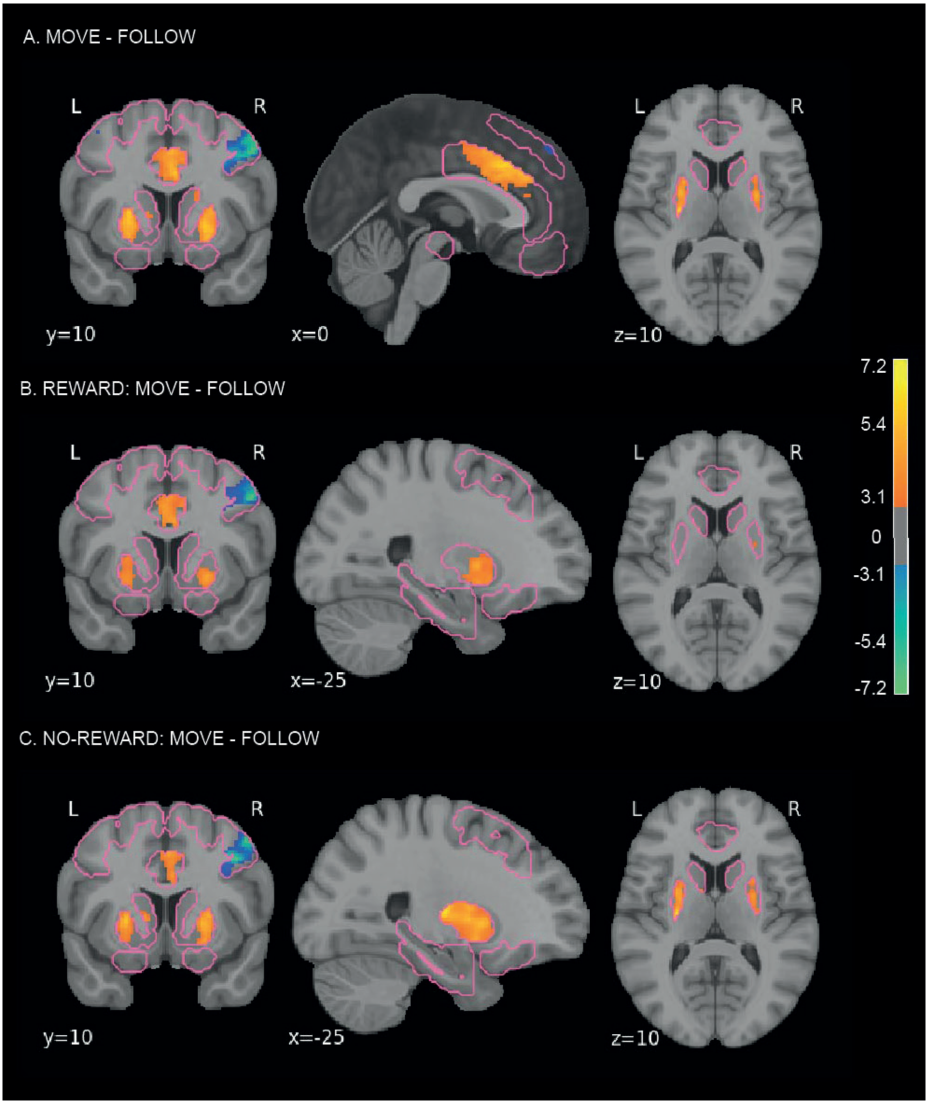

Figure 4.4 Brain regions showing differential activation in MOVE vs. FOLLOW in GLM analysis within targeted brain mask. **A.** Brain clusters showing significantly greater (orange) or reduced (blue) activation for the contrast MOVE > FOLLOW. We used a primary voxel threshold of $z > 3.1$, $p < .001$ (uncorrected) and a cluster-level correction of $p < .05$ (FWE) and displayed in standard MNI space. Colours indicate the direction of the effect (orange = MOVE > FOLLOW; blue = FOLLOW > MOVE), with intensity representing the z-statistic. The target brain mask is contoured with the pink lines. Neuroimaging data are plotted using nilearn toolbox (Abraham et al., 2014) with Python. **B.** Brain clusters showing significantly greater (orange) or reduced (blue) activation for the contrast MOVE > FOLLOW under the REWARD condition only. Other conventions are the same as Panel A. **C.** Brain clusters showing significantly greater (orange) or reduced (blue) activation for the contrast MOVE > FOLLOW under the NO-REWARD condition only. Other conventions are the same as Panel A.

To investigate whether autonomy modulates brain activity differently under the presence or the absence of monetary rewards, we conducted separate comparisons between MOVE and FOLLOW conditions within both the reward and no-reward conditions. When people were told that they would receive extra money for remembering the objects in a given grid, greater activation was observed in the right middle frontal gyrus, bilateral anterior cingulate, and bilateral putamen when comparing the MOVE condition to the FOLLOW condition (Table 4.4, Fig. 4.4B). In contrast, the right orbitofrontal cortex, right middle frontal gyrus, and bilateral superior frontal gyrus showed greater activation in the FOLLOW condition compared to the MOVE condition (Table 4.4, Fig. 4.4B). Meanwhile, under the absence of reward, we found higher activation of bilateral anterior cingulate and bilateral putamen when comparing the MOVE condition to the FOLLOW condition (Table 4.4, Fig. 4.4C). Also, the right frontal orbital cortex, bilateral middle frontal gyrus, bilateral superior frontal gyrus, and right amygdala were more activated when comparing the FOLLOW condition to the MOVE condition (Table 4.4, Fig. 4.4C).

Interestingly, although the putamen exhibited greater activation in the MOVE condition compared to the FOLLOW condition during memory encoding regardless of the reward condition, the putamen clusters identified in the MOVE versus FOLLOW contrast were noticeably larger under the absence of reward than with the presence of reward (Table 4.4, Fig. 4.4B & 4.4C). In contrast, the dorsal anterior cingulate cortex (dACC) was also significantly activated under MOVE versus FOLLOW in both reward and no-reward conditions, but with a larger cluster observed under the reward condition in this contrast compared to under the no-reward condition. These differences in cluster size for the putamen and dACC suggest that while autonomy engages both reward-related (putamen) and attentional control-related (dACC) regions, the relative involvement of these cognitive and neural mechanisms may vary depending on the presence or absence of rewards.

Table 4.4 Brain regions showing differential activation in MOVE vs. FOLLOW separately for reward and no-reward contexts in GLM analysis under targeted mask

Cluster Size	*zMax*	*p*	*x*	*y*	*z*	Hemisphere	Anatomical Region
REWARD							
MOVE - FOLLOW							
81	4.39	<0.001	30	36	42	Right	middle frontal gyrus
1069	7.03	<0.001	6	22	34	Right	anterior cingulate
218	4.79	<0.001	-26	4	2	Left	putamen
148	4.7	<0.001	22	12	-4	Right	putamen
FOLLOW - MOVE							
44	4.5	0.015	50	30	-8	Right	frontal orbital cortex
267	6.2	<0.001	50	6	52	Right	Middle frontal gyrus
81	5.72	<0.001	-10	-4	70	Left	superior frontal gyrus
50	4.09	0.009	14	0	72	Right	superior frontal gyrus
NO REWARD							
MOVE - FOLLOW							
665	6.24	<0.001	4	22	36	Right	anterior cingulate
536	6.38	<0.001	-26	-14	8	Left	putamen
372	5.38	<0.001	22	12	0	Right	putamen
FOLLOW - MOVE							
109	5.53	<0.001	48	32	-8	Right	frontal orbital cortex
109	4.57	<0.001	-40	4	52	Left	Middle frontal gyrus
315	5.74	<0.001	48	6	54	Right	Middle frontal gyrus
33	4.57	0.040	-14	-2	70	Left	superior frontal gyrus
128	4.34	<0.001	6	42	42	Right	superior frontal gyrus
61	4.57	0.003	28	-6	-22	Right	amygdala/hippocampus

Note: Coordinates correspond to the standard Montreal Neurological Institute (MNI) brain. We used a primary voxel threshold of $z > 3.1$, $p < .001$ (uncorrected) and a cluster-level correction of $p < .05$ (FWE).

4.3.2.2 ROI Results

In addition to the masked GLM analyses, we conducted statistical comparisons on brain activity extracted from ROIs, including nucleus accumbens, caudate, putamen, SN, VTA, hippocampus, and parahippocampal gyrus (Table 4.5). First, we found that the interaction between autonomy and reward was significant only in the activity extracted from the nucleus accumbens (Fig. 4.5A), suggesting a unique sensitivity of this region to the combined influence of intrinsic and extrinsic motivation. As a next step, we compared the activation in the nucleus accumbens between reward and no-reward conditions separately under MOVE or FOLLOW condition. Pairwise t-tests revealed that under the FOLLOW condition, reward slightly increased activation in the nucleus accumbens (β= 0.16, t = 1.64, p = 0.36), whereas under the MOVE condition, reward appeared to slightly suppress activation of nucleus accumbens (β = -0.14, t = 1.44, p = 0.48). Under the reward condition, autonomy (MOVE > FOLLOW) was associated with reduced activation in the nucleus accumbens (β = -0.25, t = -2.52, p = 0.06), exhibiting a marginally significant effect. In contrast, under the no-reward condition, autonomy led to no measurable effect on nucleus accumbens activation (β = 0.06, t = 0.56, p = 0.95). Moreover, autonomy was associated with increased activation in the caudate, SN, VTA, and putamen (Fig. 4.5B-E). However, no significant main effect of reward was observed in any of these reward-related brain regions. In addition, the interaction effect between autonomy and reward was not significant for activation from any other brain regions. Finally, we found that autonomy led to greater activation in the parahippocampal gyrus but not in the hippocampus (Fig. 4.5F-G).

Table 4.5 Results from ROI analyses using LME model

Nucleus accumbens	***β***	***t***	***Chisq***	***p***
autonomy	0.03	1.39	1.93	0.17
reward	-0.003	-0.15	0.02	0.88
autonomy × reward	**-0.05**	**2.14**	**4.59**	**0.03**
Caudate				
autonomy	**-0.09**	**-4.42**	**19.50**	**<0.001**
reward	0.003	0.15	0.02	0.89
autonomy × reward	-0.01	-0.77	0.59	0.44
Substantia nigra				
autonomy	**-0.06**	**-5.54**	**30.73**	**<0.001**
reward	-0.001	0.05	0.002	0.96
autonomy × reward	0.01	1.07	1.14	0.29

Table 4.5 Continued

Nucleus accumbens	***β***	***t***	***Chisq***	***p***
Ventral tegmental area				
autonomy	**-0.04**	**-5.07**	**25.73**	**<0.001**
reward	-0.01	-1.23	1.52	0.22
autonomy × reward	0.003	0.42	0.17	0.68
Putamen				
autonomy	**-0.25**	**-7.85**	**61.56**	**<0.001**
reward	0.005	0.15	0.02	0.88
autonomy × reward	-0.06	-1.71	2.93	0.09
Hippocampus				
autonomy	0.008	0.58	0.33	0.57
reward	0.000	0.004	0.000	0.997
autonomy × reward	-0.004	-0.28	0.08	0.78
Parahippocampal gyrus				
autonomy	**-0.02**	**-3.58**	**12.79**	**<0.001**
reward	-0.006	-1.01	1.02	0.31
autonomy × reward	0.005	0.69	0.47	0.49

Note: There are 2 factors included in this LME model, autonomy (MOVE/FOLLOW) and reward (REWARD/NO REWARD). Bold font indicates significant effects

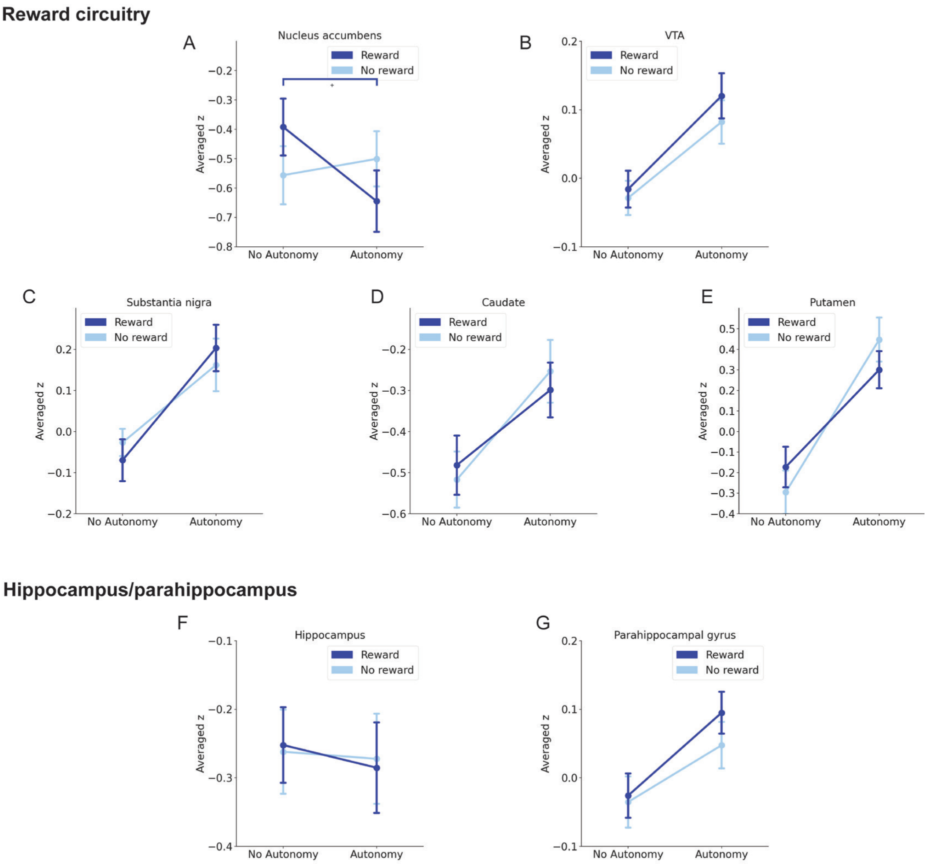

Figure 4.5 Results from ROI anlayses. Results from all the activation from each ROI are shown as a function of the two factors of interest: autonomy and reward. **A.** Activation of the nucleus accumbens is plotted as a function of autonomy and reward. The dark blue colour represents the reward condition, while the light blue colour represents the no reward condition. We found that the interaction between autonomy and reward on the activation of the nucleus accumbens is significant. We compared the activation between MOVE and FOLLOW under REWARD and NO-REWARD conditions separately, and we found that autonomy decreased the activation of the nucleus accumbens only when there were external rewards (β = -0.2528, t = -2.522, p = 0.0609; +, p<0.1). **B.** As in A, activation of the ventral tegmental area (VTA) is plotted as a function of autonomy and reward. **C.** As in A, activation of substantia nigra is plotted as a function of autonomy and reward. **D.** As in A, activation of the caudate is plotted as a function of autonomy and reward. **E.** As in A, activation of the putamen is plotted as a function of autonomy and reward. **F.** As in A, activation of the hippocampus is plotted as a function of autonomy and reward. **G.** As in A, activation of the parahippocampal gyrus is plotted as a function of autonomy and reward.

Note: In all panels, the error bars represent the standard error of the mean. Also, the dark blue colour represents the reward condition, while the light blue colour represents the no reward condition. We found autonomy was associated with increased activation in the VTA, substantia nigra, caudate, putamen, and parahippocampal gyrus. However, as no significant interaction effects were observed for these regions, no further comparisons of their activation were conducted.

4.3.2.3 gPPI results

Moreover, we examined how motivational factors of autonomy and rewards modulated hippocampal connectivity during memory encoding, extending the analysis by Voss et al. (2011b) to investigate how reward influences the autonomy-related functional connectivity patterns surrounding the hippocampus. As an exploratory analysis, we conducted a gPPI analysis to examine how functional connectivity between the hippocampus and brain regions across the whole brain was modulated by experimental conditions of autonomy and rewards with the current design. We found that functional connectivity between the seed region, bilateral hippocampus, and the left inferior frontal gyrus, as well as the bilateral supramarginal gyrus, was significantly stronger in the MOVE condition compared to the FOLLOW condition (Table 4.6, Fig. 4.6A). Conversely, comparing the FOLLOW condition to the MOVE condition, we found stronger functional connectivity between the hippocampus and the left temporo-occipital fusiform cortex, lateral occipital cortex, cuneal cortex, and cerebellum (Table 4.6, Fig. 4.6A). In addition, reward manipulation did not yield any significant changes in functional connectivity.

Table 4.6 Results from gPPI analysis using the hippocampus as seed region for MOVE vs. FOLLOW conditions

Cluster Size	***zMax***	***p***	**x**	**y**	**z**	**Hemisphere**	**Anatomical Region**
MOVE - FOLLOW							
454	4.22	<0.001	-52	10	14	Left	inferior frontal gyrus
301	4.23	<0.001	-60	-30	34	Left	supramarginal gyrus
254	3.91	0.001	62	-44	36	Right	supramarginal gyrus
FOLLOW - MOVE							
422	4.74	<0.001	-34	-52	-20	Left	temporal occipital fusiform cortex
333	3.66	<0.001	-32	-88	6	Left	lateral occipital cortex
229	4.33	0.003	-26	-80	24	Left	cuneal cortex
239	4.11	0.002	10	-68	-20	Right	cerebellum, VI

Note: Coordinates correspond to the standard Montreal Neurological Institute (MNI) brain. We used a primary voxel threshold of $z > 2.3$, $p < .01$ (uncorrected) and a cluster-level correction of $p < .05$ (FWE).

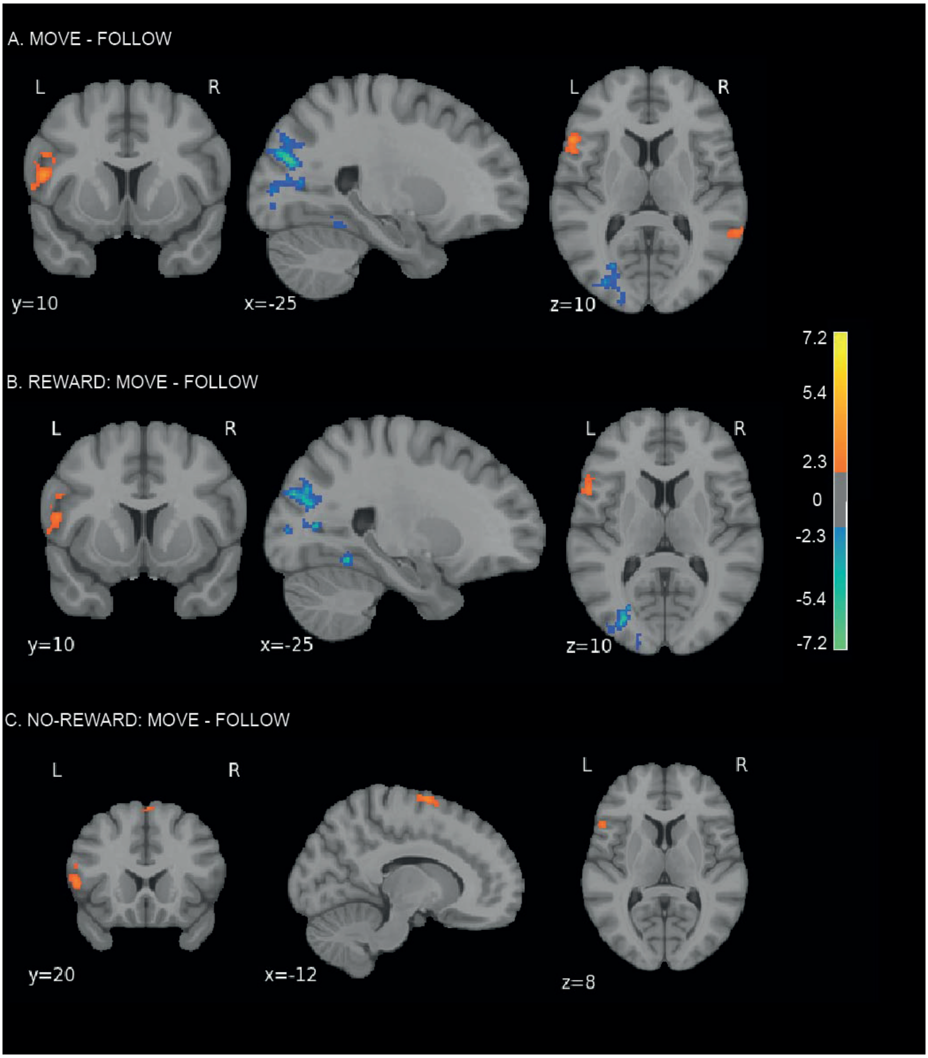

Figure 4.6 Brain Regions Showing Differential Functional Connectivity with the Hippocampus in MOVE vs. FOLLOW (gPPI Analysis). **A.** Brain clusters showing significantly increased (orange) or decreased (blue) functional connectivity with the hippocampus seed for the contrast MOVE > FOLLOW across all conditions. A primary voxel-wise threshold of $z > 2.3$, $p < .01$ (uncorrected) was applied, with cluster-level correction at $p < .05$ (FWE). Maps are displayed in standard MNI space. Colour hue reflects the direction of the effect (orange = greater connectivity during MOVE; blue = greater connectivity during FOLLOW), with intensity reflecting the z-statistic. The analysis was restricted to a targeted brain mask, outlined in pink. Plots were generated using the Nilearn toolbox (Abraham et al., 2014) in Python. **B.** Brain clusters showing condition-specific connectivity differences for the contrast MOVE > FOLLOW under the REWARD condition. Thresholding and conventions follow Panel A. **C.** Brain clusters showing condition-specific connectivity differences for the contrast MOVE > FOLLOW under the NO-REWARD condition. Thresholding and conventions follow Panel A.

Next, we assessed functional connectivity differences between the MOVE and FOLLOW conditions in the gPPI analysis separately for reward and no-reward grids. With the presence of monetary rewards, we found increased functional connectivity between the hippocampus and the inferior frontal gyrus and decreased functional connectivity between the hippocampus and the left temporal/occipital fusiform cortex, bilateral lateral occipital cortex, as well as the left cerebellum comparing the MOVE condition to FOLLOW condition (Table 4.7, Fig. 4.6B). In contrast, we found that the left superior frontal gyrus and inferior frontal gyrus exhibited stronger functional connectivity with the hippocampus, comparing MOVE to FOLLOW under no reward condition (Table 4.7, Fig. 4.6C). With the absence of reward, no brain regions demonstrated stronger functional connectivity with the hippocampus, comparing the FOLLOW to the MOVE condition (Table 4.7, Fig. 4.6C).

Table 4.7 gPPI analysis results using the hippocampus as the seed region: reward vs. no-reward conditions

Cluster Size	***zMax***	***p***	x	y	z	**Hemisphere**	**Anatomical Region**
REWARD							
MOVE - FOLLOW							
225	3.69	0.003	-56	14	8	Left	inferior frontal gyrus
FOLLOW - MOVE							
599	4.09	<0.001	-32	-50	-14	Left	temporal occipital fusiform cortex
628	4.26	<0.001	-38	-88	18	Left	lateral occipital cortex
169	3.88	0.023	32	-82	36	Right	lateral occipital cortex
157	4.05	0.036	-2	-80	-22	Left	Cerebellum Vermis VI
NO REWARD							
MOVE - FOLLOW							
180	3.82	0.015	-12	0	70	Left	superior frontal gyrus
161	3.59	0.031	-54	20	8	Left	inferior frontal gyrus
FOLLOW - MOVE							
-							

Note: Coordinates correspond to the standard Montreal Neurological Institute (MNI) brain. We used a primary voxel threshold of $z > 2.3$, $p < .01$ (uncorrected) and a cluster-level correction of $p < .05$ (FWE).

4.4 Discussion

Our study sheds light on the cognitive and neural mechanisms of how autonomy and reward simultaneously influence memory encoding. Behaviourally, both autonomy and reward independently enhanced memory encoding. However, the results from brain activity provided a more nuanced and integrated picture. First, we noticed the presence of autonomy led to stronger activation of ACC, subcortical reward circuitry, and parahippocampal gyrus. However, no subcortical reward circuitry was observed when comparing the no-autonomy to autonomy condition. Surprisingly, we did not find any significant discrepancies in brain activation comparing reward to no-reward conditions within reward-related ROIs. Second, although reward did not influence the beneficial effect of autonomy on memory accuracy, we observed a subtle shift in the neural signature of autonomy under different reward contexts. Specifically, in the masked GLM analysis, the presence of autonomy elicited a larger ACC cluster but a smaller putamen cluster activation under monetary reward compared to the no-reward condition. Third, exploratory functional connectivity analysis revealed involvement of frontal attentional control mechanisms alongside hippocampal activation during autonomous memory encoding and perceptual information integration between the visual cortex and the hippocampus during non-autonomous memory encoding.

4.4.1 Autonomy enhanced activation of reward-related brain regions during memory encoding

Firstly, the comparison between autonomy and no-autonomy conditions revealed significantly stronger BOLD activation in the caudate, putamen, ACC, and parahippocampal gyrus. Unsurprisingly, this pattern aligns with existing evidence that autonomous memory encoding, as a form of active learning, recruits the core components of the dopaminergic reward circuitry (Stuber, 2023), regions involved in modulation of the dopaminergic circuitry, namely the cortico-basal ganglia circuit, together with the memory system like the parahippocampal gyrus (Duan et al., 2020; Dubinsky & Hamid, 2024; Leotti & Delgado, 2011; Murty et al., 2015; Ripolles et al., 2016; Voss et al., 2011b). To start with, enhanced activation in the parahippocampal gyrus comparing autonomy to no-autonomy condition, together with reward circuitry, highlights the interplay between motivational and mnemonic processes during autonomous exploration. Notably, Kang et al. (2009) also found that the parahippocampal gyrus was related to memory encoding, and its activity was evoked during states of curiosity.

Moreover, Dubinsky and Hamid (2024) proposed a functional organization of cortical regions modulating reward circuitry, categorizing these brain regions into medial regions, intermediate regions, and lateral regions. Intermediate regions, like ACC, are related to cognitive functions like conflict monitoring, attentional control, and information valuation. This statement is consistent with recent work suggesting that active learning or making choices facilitates prediction processing toward upcoming information or solving uncertainty in learning contexts (Monosov & Rushworth, 2022). Additionally, lateral regions, like the superior frontal gyrus and the inferior frontal gyrus, are more commonly associated with sensorimotor control (Dubinsky & Hamid, 2024). However, we did not find significant activation in vmPFC comparing autonomy to no-autonomy condition. It was also indicated that vmPFC is primarily about emotional processing rather than in general memory encoding (Dubinsky & Hamid, 2024). Alternatively, vmPFC may be more prominent in paradigms where participants were required to remember the association between reward and stimuli, involving online processing of reward prediction error, rather than in tasks solely encoding images (Grabenhorst & Rolls, 2011; Wimmer et al., 2018).

When comparing no-autonomy to autonomy, we only found activation predominantly in the frontal lobe, including inferior and superior frontal gyri, with no engagement of subcortical dopaminergic reward circuitry. This pattern may be explained by the task demands in the FOLLOW (no-autonomy) condition, where participants were required to follow pre-determined movements, resulting in error monitoring and motor control. The presence of heightened activation in superior and inferior frontal gyri, located in the dlPFC, may reflect increased cognitive monitoring or control rather than heightened motivational drive under the no-autonomy condition compared to the autonomy condition (Duncan & Owen, 2000; Fu et al., 2023; Schall et al., 2002). Taken together, these findings contribute to evidence indicating that autonomy in memory encoding elicited intrinsic motivation during learning, which recruited reward-related processes and attentional control networks, supporting a dual role in promoting memory encoding.

Surprisingly, we did not observe any significant activation change in reward circuitry comparing the reward to the no-reward condition. One possible explanation is the temporal delay of reward in our task, which was only delivered after the memory tests. This is known to be a factor diminishing reward-related neural responses (Haber & Knutson, 2010; Kobayashi & Schultz, 2008). However, our ROI analyses revealed a significant interaction between factors of autonomy and reward in solely the activation of nucleus accumbens. Specifically, the reward effect in activation of the nucleus accumbens was more pronounced in the no-autonomy condition than in the autonomy condition. This pattern could provide evidence suggesting that external rewards may have a greater impact when there is no intrinsic motivation (van Lieshout et al., 2023).

4.4.2 Exploratory analysis showed the brain mechanisms of autonomy might be modulated by reward

Furthermore, there was no strong evidence that reward modulated the effect of autonomy in terms of brain activity. We examined brain responses to autonomy compared to no-autonomy conditions separately under reward and no-reward contexts. While both putamen and dACC were activated stronger by autonomy under both reward and no-reward conditions, we observed a notable difference in the cluster size showing different activations related to autonomy under reward and no-reward conditions. Specifically, autonomy elicited a larger bilateral putamen cluster under no-reward condition, suggesting that autonomy may be experienced as more inherently rewarding in the absence of external rewards. Conversely, dACC exhibited activation related to autonomy with a greater cluster size under reward conditions. Together, these resultthees support the view that the relationship between reward and autonomy should be conceptualized beyond the dichotomy of whether reward and autonomy, as motivations, are either additive or undermining behaviourally (Bardach & Murayama, 2025). Instead, it may be more appropriate to posit that distinct neural mechanisms underpin different types of motivational drives. These patterns could demonstrate a potential neural mechanism shift. Under no-reward conditions, autonomy may primarily engage reward circuitry (Leotti & Delgado, 2011), while under reward conditions, it may rely more heavily on cognitive control networks such as the dACC (Kennedy et al., 2024). However, since these observations of the cluster size in putamen and dACC showing activation differences were not supported by direct statistical comparisons, they should be interpreted with caution. Future work should investigate this further through conjunction or disjunction analyses or by directly comparing cluster sizes across conditions at the participant level to confirm whether these apparent neural shifts are robust.

A minor but noteworthy finding emerged from the ROI analyses, in which we found that autonomy could lead to deactivation of the nucleus accumbens, a key region in the reward circuitry, when monetary rewards were present. In contrast, this effect was not observed in the absence of monetary rewards. Such a pattern may partially align with the overjustification effect proposed by Lepper et al. (1973), demonstrating that intrinsic motivation, such as autonomy, could be diminished when extrinsic motivation was salient (Deci & Koestner, 1999). However, as this effect was limited to the nucleus accumbens and did not appear in other reward-related regions, this result alone should not be taken as conclusive evidence for undermining effect of extrinsic motivation on the intrinsic motivation during learning and memory encoding.

4.4.3 Exploratory functional connectivity analysis: attentional control in autonomy vs. perceptual processing in no-autonomy

To mirror the functional connectivity analysis that Voss et al. (2011b) conducted, we implemented an exploratory gPPI analysis with the hippocampus as the seed region. When comparing functional connectivity with the hippocampus under autonomy to no-autonomy conditions, we found increased hippocampal connectivity with frontal regions, including middle and inferior frontal gyri (Badre & Wagner, 2007; Eichenbaum, 2017; Tomita et al., 1999; Voss et al., 2011b; Zheng et al., 2021) and the supramarginal gyrus (Cristoforetti et al., 2022; Das & Menon, 2024; Guidali et al., 2019; Yue & Martin, 2021). These findings align with previous studies indicating that attention-related frontal-parietal networks enhance cognitive resource allocation during memory formation with active exploration (Voss et al., 2011b). In contrast, the reverse contrast comparing no-autonomy to autonomy revealed increased hippocampal connectivity with the occipital cortex, indicating a greater exchange of low-level perceptual information between visual and mnemonic brain regions (Bosch et al., 2014; Ranganath et al., 2005). This suggests that the presence of monetary incentives may have driven participants to process the visual stimuli, even when they lacked volitional control during learning. This could also be supported by the enhanced visual cortex activation found in whole-brain analysis (Supplementary material, Table S4.1&4.2). Notably, this enhanced low-level perceptual information exchange between the visual cortex and hippocampus brought by autonomy only existed with the existence of reward. However, when autonomy and reward were both deprived, participants likely had minimal engagement with the memory task, resulting in shallow perceptual processing and reduced hippocampal connectivity with the visual cortex.

4.4.4 Limitation

Whole-brain analyses were conducted and reported in the supplementary materials. As expected, differences in brain activation were observed in motor control regions, including the parietal lobe and cerebellum. This pattern is likely a result of the task design. In the autonomy conditions, participants naturally engaged in more motor activity to explore, while in the no-autonomy condition, they may have exerted less effort in following the movement of the searchlight window with the joystick. Further analyses should incorporate kinematic move regressors to determine whether activity in these motor control regions can be effectively regressed out, allowing for better control of potential motor-related confounds.

Second, the current chapter indicates an observation of a shift in cluster size within the putamen and ACC when comparing autonomy across reward and no-reward contexts. While suggestive, these observations were not supported by formal statistical comparisons. Future studies should test these effects more rigorously, for instance, by directly comparing cluster sizes across conditions at the participant level. Additionally, we used a relatively liberal threshold for the gPPI analysis. This decision was supported by previous studies suggesting that gPPI could be a relatively insensitive method, potentially leading to false negative results (O'Reilly et al., 2012). Although our approach closely followed the analysis conducted by Voss et al. (2011b), hence was hypothesis-driven. Nevertheless, future studies would benefit from incorporating more advanced connectivity analysis, which may allow for the capture of large-scale dynamic brain connectivity.

4.5 Conclusion

In conclusion, the current chapter demonstrated that autonomy during learning, as a form of intrinsic motivation, not only engaged dopaminergic reward circuitry but also activated brain regions associated with attentional control. Interestingly, the current study observed no modulation of reward on the beneficial effect of autonomy in memory accuracy, but there was a subtle neural shift: under no-reward conditions, autonomy engaged a larger size of subcortical reward regions, while under reward, dACC activation was more widely spread. Rather than supporting a strict dichotomy in which rewards either diminish or not with intrinsic motivation, this might point to a flow of motivation between intrinsic and extrinsic sources beyond a simple dichotomy. Last, the functional connectivity analysis indicated greater attentional control modulation between the hippocampus and the frontal lobe in the autonomy condition, while under no-autonomy condition, the brain exhibited more perceptual information exchange between the hippocampus and the visual cortex. Our findings hope to point out a future direction in conceptualizing extrinsic and intrinsic motivation as components of a dynamical system rather than opposing drives. In educational settings, both forms of motivation could be supported concurrently, with an emphasis on fostering intrinsic motivation, like autonomy, to promote more meaningful and sustainable learning.

4.6 Author Note

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4.7 Supplement– Whole brain GLM analyses

4.7.1 Methods

In Chapter 4, Section 4.2.7.2, we described a GLM analysis conducted within a targeted brain mask. To complement this, we also performed the same analysis across the whole brain to examine whether autonomy elicited brain regions outside of the predefined regions of interest to be activated. This supplementary whole-brain analysis allowed us to explore additional activation patterns beyond the targeted mask. Full methodological details are provided in Section 4.2.7.2.

4.7.2 Results

Specifically, we found extensive brain regions outside of the regions of interest from the main text to be activated by autonomy. All brain regions engaged by autonomy are listed in Tables S4.1 & S4.2. Importantly, we did not find any brain region to be activated by rewards throughout the whole brain.

Table S4.1 Brain regions showing differential activation in MOVE vs. FOLLOW in GLM analysis within whole brain

Cluster Size	***p***	***zMax***	**x**	**y**	**z**	**Hemisphere**	**Anatomical Region**
MOVE - FOLLOW							
6261	<0.001	8,06	-2	-64	-10	left/right	cerebellum
2576	<0.001	7,19	8	22	36	right	paracingulate/anterior cingulate gyrus
1343	<0.001	6,14	-38	-12	54	left	precentral gyrus
1060	<0.001	6,06	-24	4	-8	left	putamen
943	<0.001	5,74	22	12	-2	right	putamen
727	<0.001	5,36	-44	-64	-4	left	lateral occipital cortex
550	<0.001	5,46	-20	-82	46	left	lateral occipital cortex
379	<0.001	5,08	28	-68	34	right	lateral occipital cortex
264	<0.001	5,12	34	-50	62	right	superior parietal lobule
236	<0.001	5,09	-18	-44	-48	left	cerebellum
219	<0.001	5,18	24	-10	66	right	precentral gyrus

Table S4.1 Continued

Cluster Size	*p*	*zMax*	x	y	z	Hemisphere	Anatomical Region
188	<0.001	6,85	40	-12	52	right	precentral gyrus
149	<0.001	4,36	-48	-82	22	left	lateral occipital cortex
148	<0.001	4,22	-18	-60	22	left	precuneus cortex
118	<0.001	4,43	28	-98	-6	left	occipital pole
100	0.003	4,07	24	-58	18	right	precuneus cortex
84	0.007	4,59	-24	-54	56	left	superior parietal lobule
80	0.01	4,1	-4	-24	-4	left	thalamus
62	0.04	4,41	30	36	42	right	frontal pole/middle frontal gyrus
61	0.04	3,89	-28	54	12	left	frontal pole
61	0.04	5	4	-38	-42	right	brain stem
FOLLOW - MOVE							
5443	<0.001	7,62	60	-56	10	right	middle temporal gyrus
3882	<0.001	6,47	-52	-60	10	left	middle temporal gyrus
2013	<0.001	6,4	56	14	18	right	inferior frontal gyrus
684	<0.001	5,91	-16	-74	-38	left	cerebellum
655	<0.001	4,74	14	-38	78	right	postcentral gyrus
207	<0.001	4,34	54	4	-16	right	superior temporal gyrus
202	<0.001	4,14	-58	12	12	left	inferior frontal gyrus
170	<0.001	4,35	-40	4	54	left	middle frontal gyrus
98	0.003	3,86	6	40	44	right	anterior cingulate
80	0.01	5,39	-12	-2	70	left	superior frontal gyrus
80	0.01	5,07	22	-6	-14	right	amygdala
77	0.01	4,67	40	0	-16	right	insular cortex

Note: Coordinates correspond to the standard Montreal Neurological Institute (MNI) brain. We used a primary voxel threshold of $z > 3.1$, $p < .001$ (uncorrected) and a cluster-level correction of $p < .05$ (FWE).

Table S4.2 Brain regions showing differential activation in MOVE vs. FOLLOW separately for reward and no-reward contexts in GLM analysis within whole brain

Cluster Size	*p*	*zMax*	x	y	z	Hemisphere	Anatomical Region
REWARD							
MOVE - FOLLOW							
4544	<0.001	7,25	2	-76	-34	right	cerebellum
1851	<0.001	7,03	6	22	34	right	paracingulate/anterior cingulate gyrus
324	<0.001	4,41	-32	-36	66	left	postcentral gyrus
324	<0.001	5,98	-36	-14	50	left	precentral gyrus
318	<0.001	4,33	-42	-64	-6	left	LOC/ITG
313	<0.001	4,91	-24	-80	44	left	lateral occipital cortex
304	<0.001	6	-8	-22	46	left	precentral/posterior cingulate gyrus
270	<0.001	4,79	-26	4	2	left	putamen
180	<0.001	4,7	22	12	-4	right	putamen
169	<0.001	4,99	-16	-44	-48	left	cerebellum
138	<0.001	4,22	30	-70	34	right	lateral occipital cortex
133	<0.001	6,38	44	-10	56	right	precentral gyrus
124	<0.001	4,39	30	36	42	right	frontal pole/middle frontal gyrus
119	<0.001	4,69	32	-48	62	right	superior parietal lobule
98	0.002	4,38	24	-10	66	right	precentral gyrus/superior frontal gyrus
FOLLOW - MOVE							
4858	<0.001	7,13	56	-42	10	right	supramarginal gyrus
3033	<0.001	6,37	-52	-40	30	left	supramarginal gyrus
559	<0.001	5,54	58	22	18	right	inferior frontal gyrus
498	<0.001	6,2	50	6	52	right	middle frontal gyrus
462	<0.001	5,52	-16	-76	-40	left	cerebellum
339	<0.001	5,22	52	36	-12	right	frontal pole
283	<0.001	4,16	-52	2	20	left	precentral gyrus
100	0.002	5,72	-10	-4	70	left	superior frontal gyrus
81	0.007	4,23	2	-54	60	right	precuneus cortex
77	0.01	4,05	12	-38	78	right	postcentral gyrus
71	0.02	4,02	54	4	-14	right	superior temporal gyrus
61	0.03	4,06	-10	-50	56	left	precuneus cortex
61	0.03	4,38	40	-10	-12	right	planum polar
56	0.05	3,97	2	-36	66	right	postcentral gyrus

Table S4.2 Continued

Cluster Size	***p***	***zMax***	**x**	**y**	**z**	**Hemisphere**	**Anatomical Region**
NO REWARD							
MOVE - FOLLOW							
4524	<0.001	0	7,63	-66	-10	left/right	cerebellum
1521	<0.001	4	6,24	22	36	right	paracingulate/anterior cingulate gyrus
1015	<0.001	-38	6,17	-10	54	left	precentral gyrus
834	<0.001	-26	6,38	-14	8	left	putamen
709	<0.001	22	5,38	12	0	right	putamen
419	<0.001	34	4,75	-50	62	right	superior parietal lobule
374	<0.001	-20	4,78	-82	44	left	lateral occipital cortex
313	<0.001	-48	5,01	-60	-10	left	LOC/ITG
170	<0.001	40	6,63	-12	52	right	precentral gyrus
160	<0.001	26	4,56	-8	66	right	precentral gyrus/superior frontal gyrus
152	<0.001	-28	4,74	-38	66	left	postcentral gyrus
114	<0.001	-26	4,46	-56	56	left	superior parietal lobule
93	0.003	-26	4,39	-98	-14	left	occipital pole
92	0.003	28	4,53	-96	-6	right	occipital pole
85	0.005	30	4,8	-34	60	right	postcentral gyrus
FOLLOW - MOVE							
4157	<0.001	50	7,19	-42	22	right	supramarginal gyrus
2858	<0.001	-52	6,66	-60	10	left	middle temporal gyrus
771	<0.001	48	5,53	32	-8	right	frontal orbital cortex
528	<0.001	48	5,74	6	54	right	middle frontal gyrus
436	<0.001	-14	5,48	-80	-32	left	cerebellum
175	<0.001	6	4,34	42	42	right	superior frontal gyrus
145	<0.001	-40	4,57	4	52	left	middle frontal gyrus
114	<0.001	16	4,14	-42	72	right	postcentral gyrus
112	<0.001	-4	3,97	-42	58	left	postcentral gyrus/precuneus cortex
85	0.005	54	4,23	2	-16	right	superior temporal gyrus
61	0.03	28	4,57	-6	-22	right	right amygdala/right hippocampus

Note: Coordinates correspond to the standard Montreal Neurological Institute (MNI) brain. We used a primary voxel threshold of $z > 3.1$, $p < .001$ (uncorrected) and a cluster-level correction of $p < .05$ (FWE).
LOC: lateral occipital cortex
ITG: inferior temporal gyrus

Chapter 5

A cross-cultural comparison of intrinsic and extrinsic motivational drives for learning

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This chapter is adapted from:

Zhang, Z., van Lieshout, L. L., Colizoli, O., Li, H., Yang, T., Liu, C., Qin, S., & Bekkering, H. (2025). A cross-cultural comparison of intrinsic and extrinsic motivational drives for learning. Cognitive, Affective, & Behavioral Neuroscience, 25(1), 25-44.

Abstract

Intrinsic motivational drives, like the autonomous feeling of control, and extrinsic motivational drives, like monetary reward, can benefit learning. Extensive research has focused on neurobiological and psychological factors that affect these drives, but our understanding of the sociocultural factors is limited. Here, we compared the effects of autonomy and rewards on episodic recognition memory between students from Dutch and Chinese universities. In an exploratory learning task, participants viewed partially obscured objects that they needed to subsequently remember. We independently manipulated autonomy, as volitional control over an exploration trajectory, as well as the chance to receive monetary rewards. The learning task was followed by memory tests for objects and locations. For both cultural groups, we found that participants learned better in autonomous than non-autonomous conditions. However, the beneficial effect of reward on memory performance was stronger for Chinese than for Dutch participants. By incorporating the sociocultural brain perspective, we will discuss how differences in norms and values between Eastern and Western cultures can be integrated with the neurocognitive framework about dorsal lateral and ventral medial prefrontal cortex and dopaminergic reward modulations on learning and memory. These findings have important implications for understanding the neurocognitive mechanisms in which both autonomy and extrinsic rewards are commonly used to motivate students in the realm of education and urge more attention to investigate cultural differences in learning.

5.1 Introduction

Learning is a crucial aspect of life: it is the ability to acquire knowledge and skills that are essential for personal and professional development. Motivation is the driving force that initiates and sustains learning efforts (Murayama & Jach, 2024; Ryan & Deci, 2017). Considerable research has only concentrated on exploring the biological and psychological aspects influencing motivation for learning (e.g., Di Domenico & Ryan, 2017) but not on the equally crucial sociocultural factors, even though cultural backgrounds shape both behaviour and brain development (neuroplasticity) by changing values, beliefs, expectations, and cognitive processes (Han et al., 2013; Kitayama & Salvador, 2024; Park & Huang, 2010; Qu et al., 2021). In the current study, we aim to fill this research gap by investigating how diverse cultural backgrounds, taking Chinese and Dutch cultures as examples, interact with the beneficial effects of intrinsic and extrinsic motivation on learning.

One of the key theories about motivation, Self-Determination Theory (SDT), proposed to see motivation as a continuum ranging from extrinsic motivation to intrinsic motivation (Ryan & Deci, 2000; Ryan & Deci, 2020). Extrinsic motivation comes from external sources (e.g., monetary reward) and can improve learning performance (Adcock et al., 2006; Duan et al., 2020; Elliott et al., 2020; Mason et al., 2017; Murayama & Kuhbandner, 2011). Intrinsic motivation, in contrast, refers to the internal desire and enjoyment derived from engaging in an activity (Ryan & Deci, 2000a) and can also enhance learning performance (Duan et al., 2020; Gruber et al., 2014; Gruber & Ranganath, 2019; Jepma et al., 2012; Kang et al., 2009; Ripolles et al., 2016). Intrinsic motivation can be fostered by satisfying our basic psychological needs (i.e., the need for autonomy, competence, and relatedness; Deci & Ryan, 1985). Among these needs, autonomy, referred to as self-controllable to choose, stands out as a particularly critical element, since autonomy not only supports but also initiates behaviours (Leotti et al., 2010). Fulfilling the need of autonomy helps with learning and memory (Bramley et al., 2016; DuBrow et al., 2019; Izuma et al., 2010; Kaplan et al., 2012; Markant et al., 2014a; Markant et al., 2014b; Murty et al., 2015; Rotem-Turchinski et al., 2019; Voss & Cohen, 2017; Voss, et al., 2011a; Voss, et al., 2011b; Voss, et al., 2011c). In learning experiments, autonomy can be fostered by giving participants the choice of which button to press (Ding et al., 2021; DuBrow et al., 2019; Murty et al., 2015) or by allowing them to freely control their learning trajectory (Kaplan et al., 2012; Markant et al., 2014a; Markant et al., 2014b; Voss et al., 2011b).

Although Self-Determination Theory (SDT) posits that motivation can be categorized into intrinsic and extrinsic types, human functional neuroimaging research has revealed that the underlying mechanisms of both intrinsic and extrinsic motivation exhibit both dissociation and overlap. Reward-motivated learning could elicit functional activation and connectivity among a network of distributed regions, including the orbital (OFC) and ventral medial prefrontal cortex (VMPFC) and dopaminergic circuitry, including the ventral tegmental area (VTA), midbrain, and ventral striatum (Adcock et al., 2006; Sescousse et al., 2013; Shigemune et al., 2014; Wolosin et al., 2012). Autonomy-motivated learning, in contrast, not only elicits activation and connectivity of the abovementioned brain regions but also engages higher-order prefrontal network including the dorsal lateral prefrontal cortex (DLPFC; Murty et al., 2015; Voss, et al., 2011b). These findings suggest a complex interplay where motivational types are not entirely distinct but share common neural substrates. While there is considerable evidence investigating the mechanism of extrinsic and intrinsic motivation in learning, discourse on how cultural factors shape these motivational factors remains inconclusive, as these studies yielded diverse results.

There has been abundant evidence suggesting that cultural backgrounds can alter how people perceive extrinsic motivators, for example, monetary rewards. This was mostly discussed under the premise of working environments. For instance, Chinese employees would become more devoted to their tasks when their monetary income increased, while for American employees, their devotion to their jobs was not relevant to their income (Huang, 2013). Similarly, Tang et al. (2003) also found that Chinese employees had higher respect for money compared to American and British employees. Furthermore, it has been observed that individuals who identify themselves more closely with collectivistic cultures tend to be extrinsically motivated to achieve their career goals (Arshad et al., 2019). This finding was also validated by ample educational studies investigating differences in motivation for learning between Eastern and Western cultures. In Eastern educational contexts, factors that come from external environments are more emphasized than in Western educational contexts, like materialistic rewards, academic achievement, expectancy of success, and group benefits (Blevins et al., 2023; Chen et al., 2005; Iyengar & DeVoe, 2003; Telzer et al., 2017). This could result in students from the East exhibiting anxiety about their learning performance and achievement motivation (Essau et al., 2008). In contrast, the anxiety of students from Germany was found not correlated with learning performance. Years of emphasis on these different forms of external drives might lead to a stronger adoption of extrinsic motivation for students from Eastern culture. For instance, it was found that extrinsic motivation contributed to the achievement level in mathematics of Eastern students whereas it even had a detrimental effect on the achievement level of mathematics of Western students (Zhu & Leung, 2011). A neuroimaging study demonstrated that the activation and connectivity between the inferior frontal gyrus and the ventral striatum (part of the dopaminergic circuitry) exhibit greater stability and persistence among Asian students compared to American students. This was observed in response to a boring go/no-go task where Asian and American participants were asked to improve their performance. In the American group, this neural coupling and activation tended to decrease over time (Telzer et al., 2017). This was also in line with the neuroplastic theory of culture-brain interaction. Specifically, the cultural environment might have impact on top-down modulation of subcortical regions (e.g., dopaminergic circuitry) during emotional or motivational processes (Chiao, 2015).

However, recent studies have addressed that in some situations, Western participants might be more sensitive to rewards than Eastern participants (Liu et al., 2020a; Medvedev et al., 2024). For example, Medvedev et al. (2024) found that the drive for monetary rewards on task performance was stronger for participants from Western countries than those from Eastern countries. Furthermore, it was also found by one neuroimaging study that reward circuitry activation did not differ between cultural groups when participants received monetary rewards (Blevins et al., 2023). Therefore, the consensus on how extrinsic motivation influences behaviours across cultures is not uniform, prompting further exploration into this complex topic.

Similarly, evidence regarding cross-cultural differences in intrinsic motivation for learning presents a varied perspective. Some studies have suggested that personal choices are more valuable for students from Western cultures than for students from Eastern cultures (Iyengar & Lepper, 1999; Markus & Kitayama, 2003; Sastry & Ross, 1998). This could be explained by potential differences in the origins of intrinsic motivation to learn between Eastern and Western cultures (Liu et al., 2020a). They elaborated that for European students, intrinsic motivation usually comes from their own interest in learning (i.e., autonomy). However, for Eastern students who were deeply influenced by Confucian philosophy, their intrinsic learning motivation comes from the internalization of the importance of learning. In other words, they derived a strong personal belief that learning is important for their future development, social status, and career success, despite their lack of interest in the learning content. These differences in values also might shift learning styles and preferences. For example, Chinese students embrace teacher-led instruction, aligning with cultural norms of respect for guidance, whereas American students often view the same approach as constraining and prefer a more self-dependent learning style (Zhou et al., 2012).

Alternatively, there is sufficient evidence suggesting that the beneficial effect of autonomy for learning is universal across Eastern and Western cultures (Chirkov et al., 2003; Chirkov, 2009; Chirkov et al., 2010; Helwig, 2006; Nalipay et al., 2020; Ryan

& Deci, 2006; Vansteenkiste et al., 2006; Vansteenkiste et al., 2020; Vansteenkiste et al., 2005; Wichmann, 2011; Yu et al., 2016). Although it is more intuitive to think that autonomy is a Western philosophical concept, Eastern Confucian culture has also been emphasizing the importance of personal choices (i.e., autonomy) during learning, conceptualized as "self-cultivation" (Ryan & Deci, 2017). This was also in line with the Basic Psychological Needs Theory in SDT suggesting that autonomy is an instinctive psychological need, and it is not influenced by social contexts (Ryan & Deci, 2017; Vansteenkiste et al., 2020). In summary, further research is required to understand if there is a cultural difference in intrinsic motivation for learning between Eastern and Western cultures.

Interestingly, the interaction between extrinsic and intrinsic motivation on learning has been controversial. On one hand, several studies suggested that extrinsic motivation can undermine intrinsic motivation for learning (Deci & Koestner, 1999; Hidi, 2015; Murayama et al., 2010; van Lieshout et al., 2023), and vice versa. For instance, Murayama & Kuhbandner (2011) found that the effect of extrinsic motivation on learning would also be undermined when students are learning interesting content. This negative interaction between intrinsic and extrinsic motivation during learning was proposed by the over-justification hypothesis (Lepper et al., 1973). This hypothesis states that when people are rewarded externally for their behaviour, they lose interest and joy in their task (Deci & Koestner, 1999). This interaction between intrinsic and extrinsic motivation also corroborates the discovery of overlapping neural mechanisms engaged in both types of motivation (Voss, et al., 2011b; Wolosin et al., 2012). In other words, intrinsic and extrinsic motivation would influence each other because they engage a similar brain mechanism. When the reward circuitry is already activated by external stimuli, the additional enhancing effect of intrinsic motivation on brain activation becomes redundant. On the other hand, there is also abundant evidence supporting the notion that intrinsic and extrinsic motivation improve learning independently. That is, people feel intrinsically engaged in learning tasks regardless of external stimulants (Duan et al., 2020). The differing results in these studies may stem from an overgeneralization of the circumstances (Eisenberg, 2002). For instance, Cerasoli et al. (2014) found that rewards salient to task performances (e.g., end-of-year bonuses) could undermine intrinsic motivation, while rewards not related to task performances (e.g., basic salary) do not undermine intrinsic motivation. It was also proposed that the Eastern population might be more intrinsically motivated to work with external regulation from other people, whereas the Western population might be less intrinsically motivated to work with outside control (Eisenberg, 2002). However, there is still a research gap regarding how cultural backgrounds shape the interaction between extrinsic and intrinsic motivation within learning environments.

In the current study, we aimed to address a gap in the literature concerning how culture may interact with our motivation to learn. To do so, we investigated how intrinsic and extrinsic motivation improve learning under different cultural backgrounds, taking Chinese students and Dutch students as samples. An exploratory learning task from Voss et al. (2011b) was adopted, in which participants viewed partially obscured images that they needed to subsequently remember. The learning task was followed by a separate recognition memory test. Crucially, Voss et al., (2011b) found a robust main effect of autonomy on memory performance, comparing the condition when participants had control over their learning trajectory (MOVE, autonomous) with the condition in which they were asked to follow the exploratory trajectory of another participant (FOLLOW, non-autonomous). With this manipulation, we were able to control the visual information displayed as well as the movements of the joystick during the autonomous and non-autonomous conditions. In addition to the main effect of autonomy, we introduced an additional reward manipulation. Participants had the chance to receive additional monetary rewards for correctly remembering the objects during half of the exploratory learning task (extrinsic motivation; van Lieshout et al., 2023). In this way, we compared the effects of these two motivational factors (i.e., autonomy and reward) on learning between the two cultural groups of interest.

To preview, we found that extrinsic motivation (i.e., rewards) improved recognition memory for Chinese students more than for Dutch students. Furthermore, it was observed that the beneficial effect of autonomy on learning performance did not differ between Dutch and Chinese students. Lastly, based on previous literature (Liu et al., 2020b), we conducted exploratory analyses by separating each cultural group into high achievers and low achievers based on their memory test performance. For Chinese students, extrinsic motivation was beneficial for both high and low achievers regardless of the existence of intrinsic motivation. In contrast, for Dutch students, extrinsic motivation did enhance learning except for high achievers when they had autonomy during learning.

In summary, investigating how intrinsic and extrinsic motivational drives affect recognition memory performance across cultures can deepen our comprehension of individual differences in how these motivational factors shape learning and behaviour. This understanding can also shed light on how educational settings can be optimally improved by considering the impact of cultural background on motivation for learning. Our findings also spur debate about the neurocognitive mechanisms that underpin motivational drives and memory modulation in different cultures from the perspective of neuroplasticity and the socio-cultural brain (Han et al., 2013).

5.2 Methods

5.2.1 Preregistration and data availability

The study was preregistered on the Open Science Framework (osf.io/5bkte). All data and code used for the experimental procedure and data analyses are freely available on the Donders Repository (https://data.ru.nl/login/reviewer-2751056670/4ANHBXAEY7OVOMKNMOXKMO5SI2VHQIGWY6WCAQY). Part of the data on Dutch students came from the data collected by van Lieshout et al. (2023). We collected more data to match the power analysis for between-group comparison. The experimental procedure was repeated at Beijing Normal University, Beijing, China.

5.2.2 Participants

A power analysis was conducted to determine the sample size of the current study with MorePower (Campbell & Thompson, 2012). The power analysis suggested that we need at least 42 participants in each cultural group so that we can detect a medium effect size (partial $\eta^2 = 0.09$, alpha level $p<0.05$) with 80% power for the three-way interaction among the two within-group factors (autonomy and reward) and one between-group factor (cultural group) using a 2×2×2 mixed measures ANOVA.

Data from 37 Dutch participants were from van Lieshout et al. (2023), among which one participant exhibited a recognition memory test accuracy of lower than three standard deviations from the mean of the Dutch group. Additionally, we recruited 10 more Dutch participants to match the power analysis, among which one participant was excluded due to being reported as not attentive in the experiment. In the final analysis, 45 Dutch participants were included (age = 24.36 ± 5.18 years, female = 29, male = 15, non-binary = 1). Most participants were right-handed (eight left-handed, one ambidextrous). All Dutch participants had normal or corrected-to-normal vision. All Dutch participants gave written informed consent according to the declaration of Helsinki prior to participation. The experiment was approved by the local ethics committee (CMO Arnhem-Nijmegen, The Netherlands) under a general ethics approval protocol ("Imaging Human Cognition", CMO 2014/288) and was conducted in compliance with these guidelines. Participants were told that they would get 14 euros as standard participation compensation, while they might earn a maximum 5 euros extra based on their task performance. All participants in the Dutch group are living, studying or working in the Netherlands when they participated. According to official demographic information data on students at Radboud University, Nijmegen (https://www.ru.nl/en/about-us/organisation/facts-and-figures/education), we could estimate that about 90% of the Dutch participants in this dataset were local Dutch people and the rest 10 % with a majority of German students.

In Beijing, China, we recruited 55 participants, among which we excluded 11. Seven of these excluded participants only saw less than 2/3 of the objects in one of the conditions. Three participants were excluded due to being reported as not attentive in the experiment. We included 45 participants (age = 22.36 ± 1.92 years, female = 28, male = 17) in the final analysis for the Chinese group. All Chinese participants were right-handed and had normal or corrected-to-normal vision. All Chinese participants gave written informed consent according to the declaration of Helsinki prior to participation. The experiment was approved by the ethics committee of Beijing Normal University (ICBIR_A_0071_017). Participants were told that they would get 90 RMB as standard participation compensation, while they might earn a maximum of 30 RMB extra based on their task performance. Participant compensation adhered to the standard rates established by each university's regulations, with the remuneration provided in Beijing being marginally lower than that in the Netherlands. All participants in the Chinese group were local Chinese students.

During the experiment, there was a FOLLOW condition in which participants were asked to move the joystick following the searchlight trajectory shown on the screen. The trajectory in FOLLOW condition was the recorded searchlight trajectory in MOVE condition from the previous participant. This is the “yoking” system in the current design. Therefore, in each cultural group, the very first participant was considered a "seed” participant, (i.e., Participant 0) and this participant only did the MOVE condition. Their searchlight trajectory was shown to Participant 1, but data from Participant 0 was not included in the final analysis.

5.2.3 Materials

Six hundred images were selected for visibility, recognizability, and lack of lettering from the set “2400 Unique Objects” from Brady et al. (2008). These images were presented on 24-inch full HD LED thin-film-transistor liquid-crystal display screens (1920 × 1080 pixels) in a square 5×5 grid consisting of 25 images. Experimental conditions, such as the refresh rate of the screens used for presenting stimuli, were closely matched across the test environments in China and the Netherlands. The images were 120 pixels in height and covered by black and white Gaussian noise (SD = 3). The searchlight window that uncovered the images during the learning phase was a circle with a diameter of 180 pixels. Participants could control the searchlight window with a Logitech® Attack™ 3 joystick. The experiment was programmed using PsychoPy version 3 (Peirce & MacAskill, 2018).

5.2.4 Procedure

The procedure was kept the same between the Netherlands and China. The experiment was divided into two blocks (Fig. 5.1A). In each block, there was a learning phase and a recognition memory phase. Each learning phase consisted of six learning grids, during which participants were instructed to remember as many objects as possible. In the recognition memory phase, all objects in these six learning grids were tested, along with the same amount of filler objects that were not presented during this learning phase.

The current study implemented an exploration learning task (Fig. 5.1B; Voss, et al., 2011b) as described in a recent study by van Lieshout et al. (2023). In each learning grid, participants were shown a 5×5 grid of objects covered with Gaussian noise. There was an opening ("searchlight") that moved around to uncover the objects. Each participant was presented with 6 MOVE grids and 6 FOLLOW grids. In the MOVE condition (autonomous grids), participants were told that they could control the movement of this searchlight window by moving the joystick to explore the object grid. In a FOLLOW condition (non-autonomous grid), participants were told to follow the searchlight window (which would "move on its own") using the joystick. This is a commonly used procedure called "yoking" (e.g., Voss, et al., 2011b), meaning that the trajectory of the MOVE condition of the last participant was recorded and presented in the FOLLOW condition for the next participant. As such, the temporal and spatial movement of the searchlight windows were kept identical across MOVE and FOLLOW conditions. The learning task requirement was to remember as many objects as possible. The MOVE or FOLLOW condition came up one after another. The sequence of MOVE or FOLLOW grids was counterbalanced.

At the same time, REWARD or NO REWARD conditions were allocated to MOVE or FOLLOW learning grids randomly and equally between the two blocks. In each block, there would be three REWARD learning grids and three NO REWARD learning grids. In the REWARD grids, participants were told that if they remembered and successfully recognized the objects in these grids, they would get additional money (up to five euros in the Netherlands and 30 RMB in China) on top of the standard participation compensation. In the NO REWARD grids, participants were told that they still should try to remember these objects, but they would not get extra money for recognizing these objects.

Before each learning grid, participants would see an instruction screen indicating whether this was a MOVE (autonomous learning) or FOLLOW (non-autonomous learning) condition. In addition, for the REWARD condition, a picture of a 5-Euro banknote would be presented in the middle of this instruction screen with the text

(“Be aware: images from this grid are REWARDED!”) below the banknote. In China, participants would see a picture of a combination of a 20-RMB and a 10-RMB banknote with the same text. During the experiment, participants would not hear words like “volitional”, “voluntary” or “autonomous”, but instead, they would be told that “You can move/control the window by yourself”. Each of these instruction screens before each learning grid lasted for 20 seconds. Participants had 60 seconds in each learning grid, and each learning grid was divided into two parts of 30 seconds. In between the two parts, participants had 20 seconds to rest. Each block of the learning phase lasted exactly 10 minutes.

In each learning block, there were three REWARD and three NO REWARD conditions. Consequently, there would be two MOVE/REWARD grids and one FOLLOW/REWARD grid in one block, whereas there would be one MOVE/REWARD grid and two FOLLOW/REWARD grids in the other block. The trajectory from a MOVE/REWARD grid would be yoked to a FOLLOW/REWARD grid to the next participant. The same was the case for the NO REWARD grids. Hence, due to the nature of the yoking procedure, the condition allocation of MOVE/FOLLOW alternated between participants. Within one block, the order of rewarded grids was randomised over the MOVE grids. The order of the rewarded follow grids was determined by the randomisation over the previous (yoked-to) participant’s remaining move grids.

After every six learning grids, participants were presented with a recognition memory test, consisting of a recognition memory test and a spatial memory test. During the recognition memory test, participants were tested on the 150 objects (“old” objects) presented in the last six learning grids (Fig. 5.1D), as well as an equal amount of foil objects (“new” objects). In each grid of the memory test, participants had to give a response on a 4-point Likert scale using the joystick (Fig. 5.1D). The four possible responses were “Definitely OLD”, “Probably OLD”, “Probably NEW”, and “Definitely NEW”. If participants responded to an object as “Definitely OLD” or “Probably OLD”, participants were presented with a trial of the spatial memory test. During this test, participants were asked to put the object at the location on the grid where they saw it during the learning phase (Fig. 5.1D; Markant et al., 2014a). In each trial of the spatial memory test, the object was initially presented in the middle of the screen with the 5×5 grid in the background (Fig. 5.1D). They could move the joystick to move the object to the correct location and had to confirm the positioning of the object by clicking the trigger button on the joystick with their index finger. The accuracy of the spatial memory test was not considered in the additional monetary reward calculation. Participants were only instructed to try their best and to go with their best guess of the position of each object.

Participants completed 12 learning grids, during which they were presented with a total of 300 objects. They also completed two memory tests (each test was administered after 6 grids), during which they were presented with 300 old and 300 new objects in total. At the end of the experiment, participants were informed how many objects they successfully recognized in the memory phases of the experiment (i.e., hits). They were also informed about the number of correctly recognized objects of the rewarded grids (i.e., rewarded hits) and the corresponding amount of extra monetary reward that they have won during the experiment. The calculation of the monetary rewards did not take the results of the spatial memory test into consideration. These numbers were presented on the screen.

The extra monetary reward was calculated as follows:

$$\textit{Extra monetary reward} = \textit{Maximum monetary reward} \times \frac{\textit{Rewarded hit objects}}{\textit{Number of rewarded objects}}$$

Before the formal experiment started, participants signed an informed consent form upon their arrival. Then, they were asked to read the instructions of the whole experiment printed on paper and explain the procedure verbally to the experimenters. This was done so that the experimenters could confirm that participants understood the task. Afterwards, participants performed a practice session, during which they were presented with four learning grids in a fixed order (one grid from each learning condition, a MOVE/NO REWARD grid, a FOLLOW/NO REWARD grid, a MOVE/REWARD grid and a FOLLOW/REWARD grid). The pictures presented during the practice session were cartoon images (Rossion & Pourtois, 2004), so that interference of memory would not occur between the practice session and the actual experiment. Afterwards, participants completed 20 practice trials of the memory test to ensure they understood the task, including both recognition memory and the spatial memory test. Participants were instructed to try their best to remember both the objects and the locations. No data was recorded during this practice session.

5.2.6 Data preparation

Data were prepared using MATLAB® R2019a (MathWorks, 2019). As mentioned before, participants were tested with 300 old objects (objects they had seen before) and 300 new objects (foil objects) during the memory phase of the experiment. All foil objects were deleted before the final analysis. Next, we calculated the viewing time duration of each object presented during the learning phases. Specifically, the viewing time duration was the amount of time that the searchlight window overlapped with an

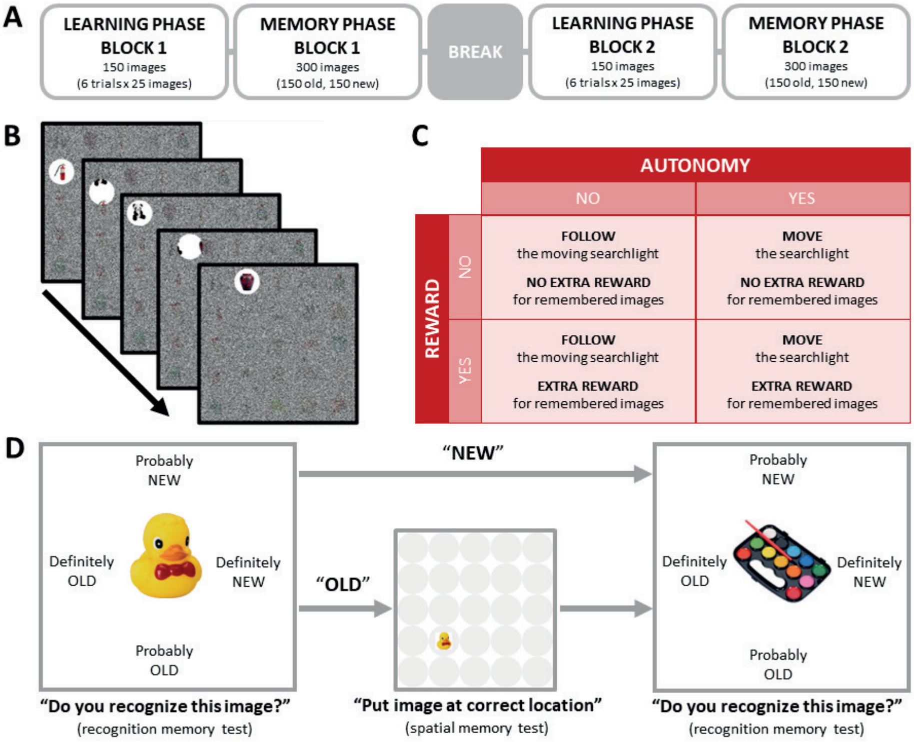

Figure 5.1 Experiment schematics. The figure is the same as Fig1 in van Lieshout et al. (2023). **A.** Experimental procedure. The whole experiment is divided into 2 blocks. Each block included one learning phase and one memory phase. In each learning phase, participants were shown 6 learning grids, and each learning grid was formed by a 5×5 grid containing 25 objects. After each learning phase, there would be a memory phase, in which participants would be shown 300 objects, including 150 presented objects in the last learning phase and 150 foil/new objects. **B.** Learning grid example. The paradigm was adapted from Voss, et al. (2011b) and previously used as described here in van Lieshout et al., (2023). In each learning grid, the 5×5 grid was covered by black-and-white Gaussian noise. The grid could be explored and uncovered by a moving searchlight window. Participants were told that they needed to remember as many objects as possible. **C.** Conditions in the learning phase. In MOVE (autonomous learning) grids, participants were instructed to control the searchlight window by moving the joystick. In FOLLOW (non-autonomous learning) grids, participants were told that the searchlight would move by itself, and they needed to use the joystick to follow the trajectory of the searchlight. Note that the trajectory of the searchlight in a FOLLOW grid was a MOVE grid trajectory recorded from the previous participant (according to a commonly used procedure called "yoking"). A learning grid might be REWARDED, in which participants would earn extra monetary rewards for recognizing the objects in that grid in the memory phase. If a learning grid was a NO REWARD grid, participants would not earn extra money for remembering these objects. Before each learning grid, participants would be shown an instruction screen, on which participants would be informed whether the following learning grid will be MOVE or FOLLOW and REWARD or NO REWARD. **D.** Memory trial example. Following the learning phase, there would be a memory phase in each block. In each memory phase trial, participants were asked to indicate whether the object was "Definitely OLD", "Probably OLD", "Probably NEW", or "Definitely NEW". During this recognition memory test, 4 reactions were located in 4 directions of the object, and participants could react by moving the joystick in the corresponding direction. If participants reacted such that the current object is "Definitely OLD" or "Probably OLD", a spatial memory test would be generated for this object. Participants would need to move the joystick to put the object back to where they saw it in the grid during the learning phase.

object picture (120 × 120 pixels) on the exploration grid. If the viewing time duration was smaller than 200 milliseconds, this object would also be recognized as “not seen” during the learning phase. These objects would be excluded from the final analysis. Consequently, all objects that were seen by the participants during the learning phase were included in the final analysis.

After removing the filler objects in the memory test, both the Chinese dataset as well as the Dutch dataset consisted of a total of 13,500 recognition memory test trials (over all participants). In the Chinese dataset, we identified 450 trials in which the objects were not seen by the participants during the learning phase. Consequently, 13,050 trials from the recognition memory test were valid and included in the final analyses. For Dutch participants, 441 objects were not seen by the participants. Therefore, we included 13,059 trials from the recognition memory test in the final analysis.

We calculated three dependent variables to quantify memory performance. For the primary analyses (as reported in the main text), we focused on recognition memory (i.e., whether objects were correctly identified as old objects). To this end, the Likert responses of the seen objects were collapsed into a binary variable. For all the seen objects, if participants responded with “Definitely OLD” or “Probably OLD”, they would be marked as 1 (hit). If they responded to these objects as “Probably NEW” or “Definitely NEW”, these objects would be marked as 0 (miss). Additionally, the spatial memory test performance was measured with two variables, spatial hit and spatial error. Data analysis protocols and results of spatial memory tests are reported in the Supplementary Material 1.

“Hit rate” was used as the performance measure to be consistent with previous studies with a similar paradigm (Markant et al., 2014a; Voss, et al., 2011b; Voss, et al., 2011c). The current experimental design precluded calculating false alarms for each experimental condition. In the memory test of each block (Fig. 5.1A), participants were shown all learned objects in random order, intermixed with an equal number of filler objects. These filler objects could not be assigned to any of the 4 experimental conditions. Therefore, it is not feasible to distinguish between condition-specific false alarms, prohibiting us from calculating d’ (hit rate – false alarm) for each condition with signal detection theory (Hautus et al., 2021). However, to address the concern of group differences in response biases, d’ (hit rate – false alarm) and C (-1/2[hit rate + false alarm]) were calculated and compared between cultural groups. Details were reported in the Supplementary Material 2.

5.2.7 Data analysis

5.2.7.1 Primary analysis

We conducted linear mixed effect (LME) modelling with lme4 toolbox (Bates et al., 2015) in R (R core team, 2022). The dependent variable of the model was “recognition memory accuracy”, a binomial variable. The independent variables were autonomy (MOVE, autonomous learning; FOLLOW, non-autonomous learning), reward (REWARD; NO REWARD) and cultural group (CHINESE; DUTCH). Among the 3 factors, autonomy and reward factors were within-participant manipulations, while the cultural group was a between-participant condition. We created sum-to-zero contrasts for all the factors. In the model, we included all three main effects as fixed effects, autonomy, reward and cultural group, respectively. The model also included two-way interaction effects between either two of these factors and the three-way interaction effect among all three factors as fixed effects. Additionally, the model had a full random effects structure, meaning that a random intercept and random slopes for all within-subject effects were included per participant (Barr, 2013; Barr et al., 2013). The LME model was fitted with 10,000 iterations and diagnosed with DHARMa (Hartig, 2020).

$$\begin{gathered} Memory\ accuracy \sim autonomy \times reward \times cultural\_group \\ + (1 + autonomy \times reward\ |sub) \end{gathered}$$

5.2.7.2 Exploratory analysis

Additionally, previous findings indicated that both Chinese and Western students with higher levels of intrinsic motivation outperformed their less intrinsically motivated peers in learning tasks. However, it was found that extrinsic motivation appears to bolster learning performance only when the task performance level is low for Chinese students, who were less willing to learn (Liu et al., 2020b). Moreover, a comparable result was also yielded on European students in a previous study (Murayama & Kuhbandner, 2011). It was found that for German students, their memory would only be boosted by money for boring materials, in other words, when they had no willingness to learn. These suggested that the effect of extrinsic motivation on learning may vary according to the learning performance of students or the willingness to learn. Hence, to explore the dataset, we separated each cultural group into two groups based on their performance on the recognition memory test (i.e., high achievers and low achievers). To split the participants by achievement level, we calculated the recognition memory hit rate for each participant as follows:

$$Hit\ rate = \frac{Number\ of\ hit\ objects}{Number\ of\ seen\ objects}$$

People who showed a higher or equal recognition memory hit rate than the median of their cultural group would be identified as high achievers, while people who showed a lower recognition memory hit rate than the median of their cultural group would be identified as low achievers. Consequently, we would have 23 participants in each cultural group as high achievers and 22 participants in each cultural group as low achievers. We will implement the same data analysis procedure as described for the full dataset on high achievers and low achievers separately.

5.3 Results

The current study aimed to investigate how intrinsic and extrinsic motivation improve learning under different cultural backgrounds. In an exploratory learning task, Chinese and Dutch participants viewed partially obscured images that they needed to subsequently remember. We compared the effects of autonomy (as volitional control over the exploration trajectory) and monetary reward on the subsequent recognition memory of the objects viewed between the two cultural groups of interest.

5.3.1 Primary results

Main effects and interactions between the factors of interest, autonomy (MOVE vs. FOLLOW), monetary reward (REWARD vs. NO REWARD), and cultural group (CHINESE vs. DUTCH), were assessed in a three-way LME model on the dependent variable of recognition memory accuracy. The model results with statistics are reported in Table 1 and the data are plotted in Fig. 5.2. The mean and standard deviation of recognition memory accuracy for the conditions of interest are reported in Table 2.

We found a main effect of autonomy and reward on recognition memory accuracy (Table 1). This indicated that participants learned better in the MOVE condition than in the FOLLOW condition. Also, participants learned better in the REWARD condition than in the NO REWARD condition. We did not find a main effect of cultural group on recognition memory accuracy. This suggested that Dutch students had a similar performance as Chinese students in the recognition memory test. For the two-way interaction effects of interest, we did not find an interaction between autonomy and reward on recognition memory accuracy. This indicated that, if we view the two cultural groups as one sample, the beneficial effect of autonomy on memory would not be affected by external rewards (Fig. 5.2). Interestingly, we found a significant two-way interaction effect between factors of reward and cultural group on recognition memory accuracy (Fig 5.3A-C). We did not find a two-way interaction effect on recognition memory accuracy between factors of autonomy and cultural group (Fig. 5.3D-F). This suggested that the beneficial effect of autonomy on recognition memory accuracy was similar between the Chinese and Dutch cultural groups. We also did not find a significant three-way interaction among autonomy, reward, and cultural groups.

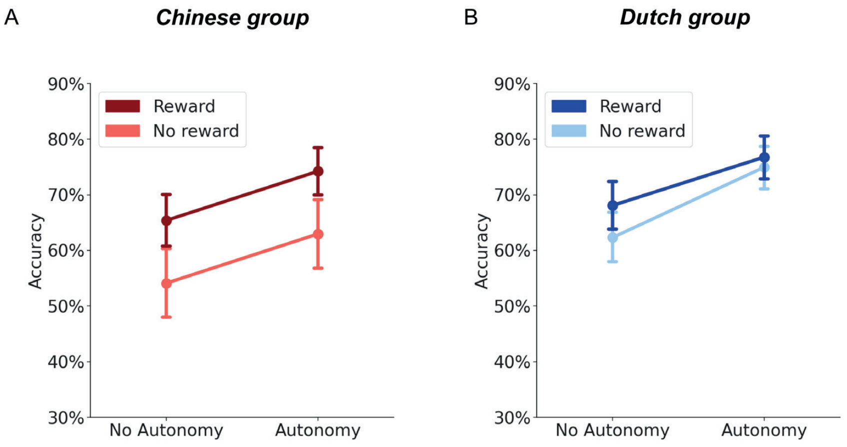

Figure 5.2 Primary results on recognition memory accuracy. Recognition memory (i.e., percentage of the correctly remembered objects) results are shown as a function of the three factors of interest: autonomy, reward, and cultural group. **A.** For the Chinese group, recognition memory is plotted as a function of autonomy and reward. The red colour represents the Chinese cultural group. The dark red colour represents the reward condition, while the light red colour represents the no reward condition. **B.** As in A, recognition memory is plotted the same for the Dutch group. The blue colour represents the Dutch cultural group. The dark blue colour represents the reward condition, while the light blue colour represents the no reward condition. In all panels, the error bars represent the standard error of the mean. Since the three-way interaction between the factors of autonomy, reward and cultural group was not significant, we did not conduct post hoc comparisons on the two-way interaction between autonomy and reward within each cultural group.

Table 5.1 Primary results on recognition memory accuracy

Effect of interests	β	z	p
Autonomy	-0.27	-8.74	<0.001***
Reward	-0.18	-5.81	<0.001***
Cultural group	-0.15	-1.81	0.41
Autonomy × Reward	-0.02	-1.09	0.29
Reward × Cultural group	-0.09	-2.85	0.004**
Autonomy × Cultural group	0.03	0.96	0.22
Autonomy × Reward × Cultural group	0.02	1.59	0.11

Note. There are 3 factors included in this LME model, autonomy (MOVE/FOLLOW), reward (REWARD/NO REWARD), and cultural groups (Chinese/Dutch).

Table 5.2 Descriptive results on recognition memory accuracy

					High Achievers				**Low Achievers**			
	Chinese		**Dutch**		**Chinese**		**Dutch**		**Chinese**		**Dutch**	
Main factors	*M* (%)	*SD*	*M* (%)	*SD*	*M* (%)	*SD*	*M* (%)	*SD*	*M* (%)	*SD*	*M*(%)	*SD*
MOVE	68.74	16.04	75.90	12.84	80.74	9.71	85.11	7.78	56.19	10.84	66.27	9.58
FOLLOW	59.76	17.25	65.24	14.37	72.81	11.24	80.74	9.71	46.11	10.47	54.42	10.95
REWARD	70.04	13.76	72.63	12.19	79.36	9.22	81.45	6.33	60.30	10.63	63.40	9.73
NO REWARD	58.64	21.05	68.75	13.19	74.50	10.85	79.31	6.52	42.06	15.55	57.70	8.36
Autonomy × Reward												
MOVE/REWARD	74.23	14.36	76.78	13.54	83.22	9.44	84.83	9.55	64.84	12.58	68.36	11.97
MOVE/NO REWARD	62.97	20.93	74.96	13.57	78.12	11.26	85.34	7.15	47.14	16.47	64.11	9.53
FOLLOW/REWARD	65.39	15.45	68.08	14.91	74.86	12.30	77.90	8.37	55.49	11.87	57.81	13.28
FOLLOW/NO REWARD	54.11	22.44	62.31	15.68	70.67	12.34	73.23	9.96	36.80	16.77	50.90	12.00

To disentangle the interaction between reward and cultural group further, we compared memory accuracy for the REWARD and NO REWARD conditions respectively for the Dutch group and the Chinese group (Fig. 5.3A) with the *emmeans* package in R (Lenth, 2022). It was found that the facilitatory effect of reward (REWARD – NO REWARD) on recognition memory was significant for both the Chinese group ($\beta = 0.55$, $z = 6.14$, $p < 0.001$) and the Dutch group ($\beta = 0.19$, $z = 2.11$, $p = 0.03$). Moreover, this reward effect on memory was found stronger for the Chinese group compared with the Dutch group (Fig. 5.3A). This difference between cultural groups is also apparent when plotting the reward effects of each participant in the Chinese (Fig. 5.3B) and Dutch group (Fig. 5.3C). Alternatively, we also compared recognition memory accuracy between the Chinese and Dutch groups under both REWARD and NO REWARD conditions respectively (Fig. 5.2). It was found that under reward conditions, the Dutch group and the Chinese group performed similarly ($\beta = -0.11$, $z = -0.73$, $p = 0.47$) in the recognition memory test. However, under the NO REWARD condition, the Dutch group performed better than the Chinese group ($\beta = -0.47$, $z = -2.48$, $p = 0.01$) in the recognition memory test.

For completeness, we also plotted the autonomy effect between cultural groups (Fig. 5.3D). The individual variability of autonomy effect on memory accuracy for the Chinese group is plotted in Fig. 5.3E. The same was done for the Dutch group in Fig. 5.3F.

Table 5.3 Statistical results of recognition memory accuracy from high achievers and low achievers

	High achievers			**Low achievers**		
Effect of interests	***β***	***t***	***p***	***β***	***t***	***p***
Autonomy	-0.29	-6.32	<0.001***	-0.24	-6.06	<0.001***
Reward	-0.11	-3.64	<0.001***	-0.27	-5.26	<0.001***
Cultural group	-0.09	-1.10	0.29	-0.21	-3.64	0.002**
Autonomy × Reward	-0.02	-0.74	0.50	-0.02	-0.92	0.36
Reward × Cultural group	-0.04	-1.53	0.16	-0.14	-2.76	0.005**
Autonomy × Cultural group	0.04	0.88	0.16	0.02	0.41	0.66
Autonomy × Reward × Cultural group	0.05	2.06	0.04*	0.01	0.26	0.80

Note. There are 3 factors included in the LME models above, autonomy (MOVE/FOLLOW), reward (REWARD/NO REWARD), and cultural groups (Chinese/Dutch).

5.3.2 Exploratory results: High achievers and low achievers

Additionally, we performed exploratory analyses to investigate whether the reported primary results differ based on participants' task performance. This was done because previous research has indicated that extrinsic motivation appeared to improve learning performance among Chinese students when their task performance was initially suboptimal (Liu et al., 2020b). However, for Western students, extrinsic motivation equally boosted learning for students regardless of task performance. This suggested that the reported effect of extrinsic motivation on learning might be modulated by both cultural group and task performance. To this end, we divided the Chinese and Dutch cultural groups into "high achievers" and "low achievers" and applied the same model used for the primary analysis to the high and low achiever groups separately.

When focusing on the high achievers only, we found a significant three-way interaction between the factors of autonomy, reward, and cultural group on recognition memory accuracy. To dig deeper into this three-way interaction, we compared the recognition memory accuracy between the two cultural groups under each condition of reward and autonomy with *emmeans* package in R (Lenth, 2022). We did not find significant differences between Chinese and Dutch high achievers (Chinese – Dutch) under the MOVE/REWARD condition ($\beta = -0.08$, $z = -0.34$, $p = 0.74$), FOLLOW/REWARD condition ($\beta = -0.11$, $z = -0.58$, $p = 0.56$), and FOLLOW/NO REWARD condition ($\beta = -0.09$, $z = -0.49$, $p = 0.63$). However, only for the MOVE/NO REWARD condition, we found that the Chinese high achievers exhibited a lower recognition memory accuracy than the Dutch high achievers ($\beta = -0.44$, $z = -2.19$, $p = 0.03$). Additionally, we also compared the reward effect on recognition memory accuracy (REWARD – NO REWARD) under either MOVE or FOLLOW conditions for each cultural group separately. For Chinese students, we found that reward improved learning under both MOVE ($\beta = 0.36$, $z = 3.33$, $p = 0.001$) and FOLLOW ($\beta = 0.24$, $z = 2.36$, $p = 0.02$) conditions (Fig. 5.4A). For Dutch participants, however, extra rewards only improved learning under the FOLLOW condition ($\beta = 0.26$, $z = 2.57$, $p = 0.01$) but not under the MOVE condition ($\beta = 0.01$, $z = 0.06$, $p = 0.96$; Fig. 5.4B).

Second of all, when focusing on the low achievers, we found a significant two-way significant interaction effect between reward and cultural group on memory accuracy (Fig. 5.4C & 5.4D). This was consistent with the results of the primary analysis. When breaking down this interaction effect, it was found that the facilitatory effect of reward on memory accuracy was larger for the Chinese low achievers ($\beta = -0.83$, $z = -5.66$, $p < 0.001$) than for the Dutch low achievers ($\beta = -0.26$, $z = -1.77$, $p = 0.08$). Alternatively, we also found that, under the REWARD condition, Dutch and Chinese

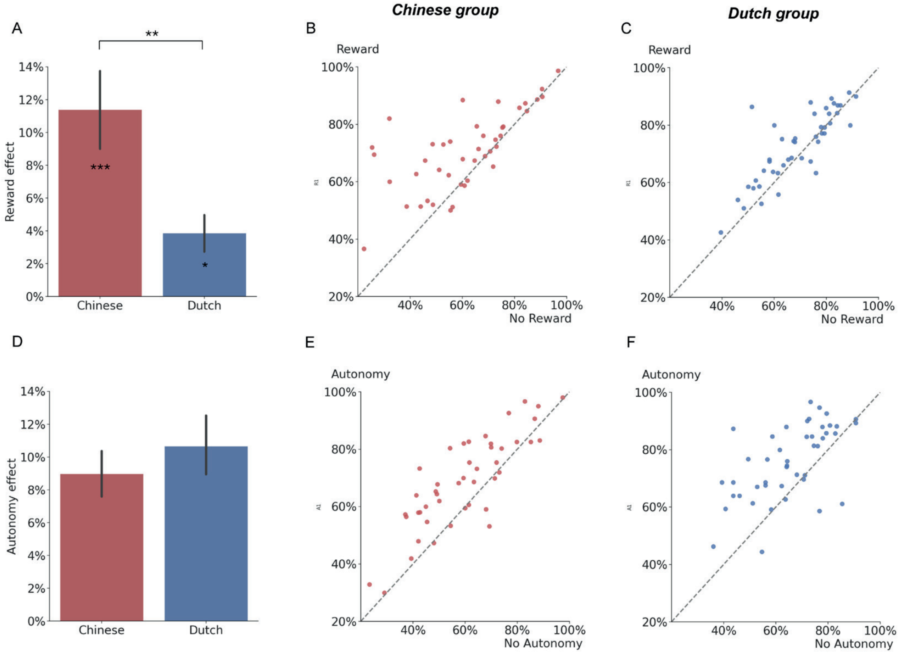

Figure 5.3. Individual variability in the beneficial effect of reward and autonomy based on recognition accuracy. In all graphs, the red colour represents the Chinese cultural group, while the blue colour represents the Dutch cultural group. **A.** The beneficial effect of reward on memory accuracy (Reward – No reward) is stronger for the Chinese group than for the Dutch group. The bars (y-axis) represented the beneficial effect of reward on recognition memory. The error bars represent the standard error of the mean of reward effect. Asterisks on the bars represent the significance of the beneficial effect of reward on the recognition memory accuracy of each group. ***$p < 0.001$; *$p < 0.05$. **B.** Chinese group individual variability in mean recognition memory accuracy for the REWARD condition (y-axis) compared with the NO REWARD condition (x-axis). Each dot represents a participant. Most dots tend to lie above the diagonal, illustrating that most of the Chinese participants had a higher recognition memory accuracy in the REWARD condition than in the NO REWARD condition. **C.** Dutch group individual variability in mean recognition memory accuracy for the REWARD condition (y-axis) compared with the NO REWARD condition (x-axis). Each dot represents a participant. While the dots lie close to the diagonal, more dots still lie above the diagonal. This illustrates the significant but smaller beneficial effect of reward on recognition memory than in the Chinese group. **D.** The beneficial effect of autonomy on learning did not differ between the Chinese and Dutch groups.The bars (y-axis) represented the beneficial effect of autonomy (MOVE – FOLLOW) on recognition memory. The error bars represent the standard error of the mean. **E.** Chinese groupindividual variability in mean recognition memory accuracy for the MOVE condition (y-axis) compared with the FOLLOW condition (x-axis). Each dot represents a participant. Most dots tend to lie above the diagonal, illustrating that most of the Chinese participants had a higher recognition memory accuracy in the MOVE condition than in the FOLLOW condition. **F.** Dutch group individual variability in mean recognition memory accuracy for the MOVE condition (y-axis) compared with the FOLLOW condition (x-axis). The distribution of the dots is similar to Fig. 5.3E, suggesting a similar beneficial effect of autonomy on learning between two cultural groups.

low achievers performed similarly (β = -0.14, z = -1.01, p = 0.31). However, under the NO REWARD condition, Dutch low achievers performed better in the recognition memory test than Chinese low achievers (β = -0.71, z = -4.11, p < 0.001).

To summarize, we found that reward improved memory accuracy for Dutch high achievers under FOLLOW condition (no autonomy), but not under MOVE condition. However, for Chinese high achievers, the reward effect was present for both MOVE and FOLLOW conditions. Meanwhile, Chinese low achievers were motivated to learn by monetary rewards more compared with Dutch low achievers. It was also evident that Chinese low achievers only performed less effectively compared to Dutch low achievers when without rewards.

5.4 Discussion

In our study, we delved into the impact of intrinsic and extrinsic motivation on learning across diverse cultural contexts, by focusing on the comparisons between Chinese and Dutch student populations. Participants engaged in an exploratory learning activity wherein they were presented with partially obscured images, which they were required to recall later. We manipulated autonomy (representing intrinsic motivation) by granting participants control over their exploration trajectory, and we also varied the opportunity for monetary rewards (representing extrinsic motivation) independently. Throughout the experiment, participants were tasked with memorizing as many objects as possible, followed by a subsequent memory assessment. By administering the same learning experiment to Chinese and Dutch students, the current study aimed to gain a better understanding of the cultural differences in intrinsic and extrinsic motivation for learning.

There are three key novel findings in this experiment. First, we found that the beneficial effect of extrinsic motivation (i.e., monetary reward) on memory encoding was stronger for Chinese students than for Dutch students (e.g., Zhu & Leung, 2011). Second, we found that there was no difference in the beneficial effect of intrinsic motivation (i.e., autonomy) on learning between Chinese and Dutch students (e.g., Ryan & Deci, 2006). Third, when including all participants, we did not find an interaction effect between autonomy and reward on learning in either cultural group, different from previous studies (e.g., van Lieshout et al., 2023). However, in an exploratory analysis taking learning achievement into account, we found that for Dutch high achievers, the beneficial effect of reward was diminished in autonomous learning compared to non-autonomous learning conditions (Fig. 5.4B; van Lieshout et

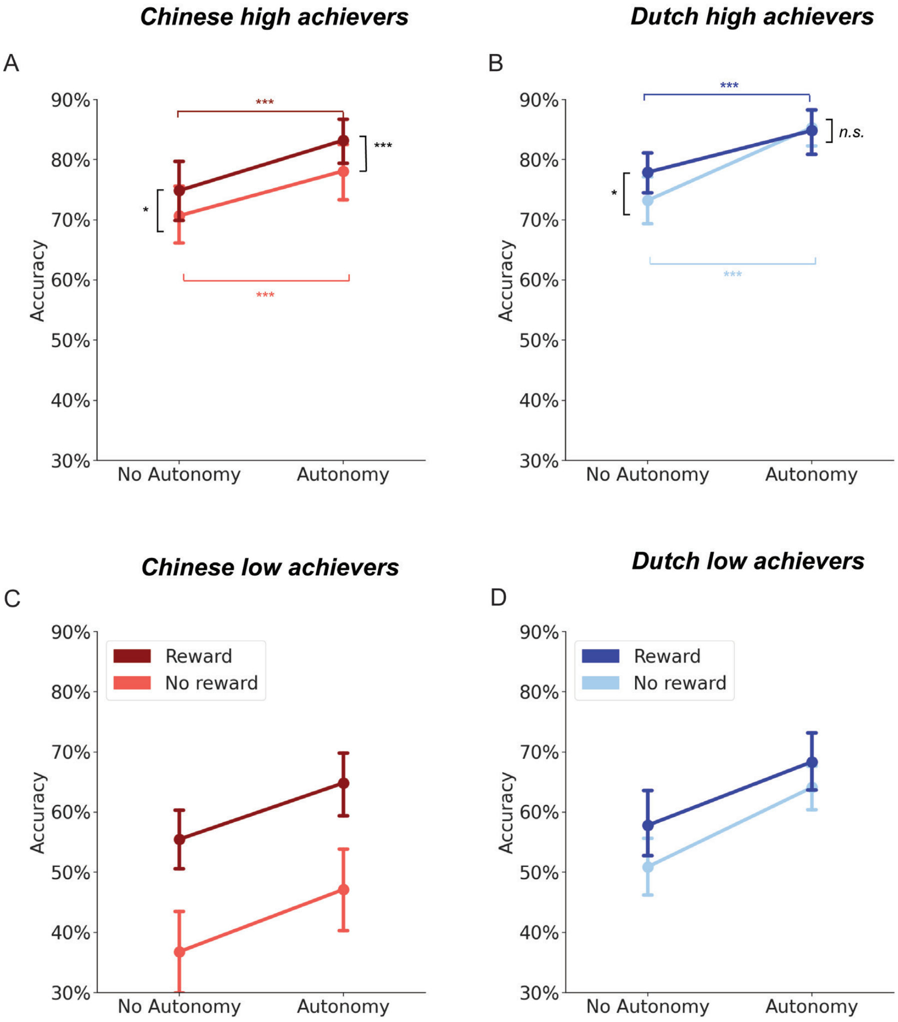

Figure 5.4 Results on recognition memory accuracy after splitting each cultural group into high and low achievers. **A.** For the Chinese high achievers, recognition memory is plotted as a function of autonomy and reward. The red colour represents the Chinese high achievers. The dark red colour represents the reward condition, while the light red colour represents the no reward condition. The coloured lines represent the effect comparison (MOVE FOLLOW) under REWARD or NO REWARD conditions. Asterisks near the red comparison lines indicated the significance of (MOVE – FOLLOW) under different reward conditions. Asterisks next to the black comparison lines indicated the significance of (REWARD – NO REWARD) under different autonomy conditions. The error bars represent the standard error of the mean (SEM). (***: $p < 0.001$; *: $p < 0.05$) **B.** For the Dutch high achievers, recognition memory is plotted the same. The blue colour represents the Dutch cultural group. The dark blue colour represents the REWARD condition, while the light blue colour represents the NO REWARD condition. The rest of the conventions were the same as in Fig. 5.4A. (***: $p < 0.001$; *: $p < 0.05$; n.s.: $p > 0.05$) **C.** Recognition memory accuracy for Chinese low achievers. All conventions are the same as in Fig. 5.4A. **D.** Recognition memory accuracy for Dutch low achievers. All conventions are the same as in Fig. 5.4B.

al., 2023). In contrast, reward improves learning regardless of autonomy for Chinese high achievers (see Fig. 5.4A). These results together support the idea that intrinsic motivation for learning may be culturally universal, while extrinsic motivation for learning is stronger for Chinese students than for Dutch students. Furthermore, the interaction effect between intrinsic and extrinsic motivation on learning needs to be discussed under different cultural groups and concerning different levels of learning outcomes.

5.4.1 The effect of reward on learning was stronger for Chinese than for Dutch students

In both cultural groups, participants remembered more objects in the reward condition than in the no-reward condition. However, Chinese students exhibited a stronger effect of reward on memory than Dutch students, indicated by a significant interaction effect between factors of reward and cultural group (Fig. 5.3A). When delving deeper into this interaction effect, it was found that Chinese students remembered fewer objects compared with Dutch students when there was no monetary reward. Students from the two cultural groups performed equally well for the rewarded objects.

This is consistent with findings from previous studies suggesting that people from a collectivistic cultural background would be more motivated by external sources (Huang, 2013). In our current setting, one of the goals was to obtain extra monetary rewards. However, the goals participants pursue do not necessarily have to consist of monetary rewards (e.g., Huang, 2013; Zhu & Leung, 2011); they can also encompass group benefits (Salili et al., 2012), or achievements (Telzer et al., 2017). Distinct from Western philosophy, Chinese cultural contexts emphasize academic success and attainment (Dekker & Fischer, 2008). The pursuit of education is traditionally intertwined with collective aspirations, such as upholding family honour and contributing to the broader society (Salili et al., 2012). This ethos stems from the Confucian principle of "Rushi" (入世) which promotes self-improvement and contribution to societal prosperity (Hao, 2018). In Confucian culture, factors that come from external environments are more emphasized than in non-Confucian Western educational contexts, like materialistic rewards, academic achievement, expectancy of success, and group benefits (Blevins et al., 2023; Chen et al., 2005; Iyengar & DeVoe, 2003; Telzer et al., 2017). Students with Confucian cultural backgrounds develop an intrinsic passion and commitment to learning after understanding the importance of learning in life-building and self-development (e.g., Liu et al., 2020a; Liu et al., 2020b), while in Western culture, learning is usually driven by interest. Furthermore, after separating participants into high and low achievers, it was observed that the cultural difference in the beneficial effect of reward on memory only existed for low achievers, but not for high achievers. This also matches with previous findings suggesting that students with a Confucian cultural background and low performance in learning showed a higher sense of extrinsic motivation for learning (Liu et al., 2020b).

To specify, Eastern culture deems norms of extrinsic motivation as more meaningful and essential compared with Western culture (Tao & Hong, 2013), shaping reward circuitry activity underlying specific behaviours. From the sociocultural brain perspective, neural responses toward external stimuli are shaped by both short- and long-term dynamic cultural experiences (Han, 2017; Han et al., 2013). For instance, previous studies have found that cultural backgrounds shape the activation of the ventral striatum toward monetary rewards (Kim et al., 2012). People with Eastern cultural backgrounds would have persistent reward circuitry activation even when the reward is delayed. Moreover, compared with American participants, Chinese participants showed more sustained reward circuitry activation (in the ventral striatum) during a go/no-go task when their goal was to improve their accuracy in this task (Telzer et al., 2017). In this situation, Chinese students were more motivated by gaining higher task achievement than American students were. This observation is consistent with the cultural valuation of achievement, which is notably higher for Chinese students compared to Western students (Tao & Hong, 2013). Integrating our findings and the sociocultural brain perspective, culture plays a critical role in shaping one's sensitivity towards various motivational factors, which is closely tied to the functioning of the reward system. In contrast, the cultural influences might not extend to the biological underpinnings of the reward system, such as dopamine receptors (Glazer et al., 2020).

Interestingly, there was a study specifically indicating that monetary reward does not cause different levels of activation on reward circuitry between different cultural groups (Blevins et al., 2023). However, it is crucial to emphasize that upon closer examination of their results, our current findings are in alignment with theirs. Although in their study, there were no differences in reward circuitry activation between Chinese and American groups when they received monetary rewards, American participants showed higher nucleus accumbens (NAcc) activity compared to Chinese participants when they received NO monetary rewards during the target-hitting task (Blevins et al., 2023; Supplementary material, Section 11, page 26). These findings resonate with the results presented in the current study, as we observed that Chinese participants demonstrated weaker recall for objects that were not rewarded in comparison to Dutch participants. Yet, this discrepancy was absent when rewards were involved. Hence, we hypothesize that cultural norms can shape functional engagement of certain brain systems during learning phase in the absence of rewards. From the perspective of neuroplasticity that is formed due to learning of culture norms (Han, 2017; Han & Ma, 2014), Chinese students might tend to use relatively more external-driven strategies during learning, leading them to exhibit a lower baseline activation in reward circuitry when they are learning for NO external drives or purposes. However, this hypothesis requires future research to be substantiated.

In summary, extrinsic motivation is universally recognized for enhancing behavioural performance. This is likely due to the regulatory effect of extrinsic motivation on activity in the reward circuitry (e.g., striatum). Our study further clarifies that this effect is more pronounced in Chinese individuals compared to Dutch individuals during learning tasks, suggesting cultural variability in cognitive and neural responses to extrinsic motivators.

5.4.2 The beneficial effect of reward on learning can be affected by context

In the current study, we found that only for Dutch high achievers, the effect of reward on learning was not present when their intrinsic motivation (autonomy) was invoked. However, the reward effect on learning always existed for Chinese high achievers. This finding aligned with the previous notion that the interaction between intrinsic and extrinsic motivation in learning is not always present and has been over-generalized (Eisenberg, 2002). One possible interpretation of the diminishing reward effect in Dutch high achievers with autonomy is that they do not need rewards to heighten their motivation, because autonomy as an intrinsic motivator is already sufficient (Cameron, 2001). Similar to results from Murayama and Kuhbandner (2011), when German students were learning interesting content (with intrinsic motivation to learn), money does not boost learning performance. Instead, money only improved learning when the content was boring. This notion is also supported by our finding, such that Dutch high achievers performed better than Chinese high achievers when they were learning autonomously but were not rewarded for their performance. However, their learning performance was equally high when both autonomy and rewards were provided. To rephrase, autonomy alone may suffice as a significant motivational driver for Dutch high achievers, enabling them to learn to the best of their ability. Conversely, for Chinese high achievers, the presence of autonomy does not fully maximize their motivational potential for learning, indicating that their learning motivation has not yet reached its peak.

An alternative interpretation is that the effect of autonomy is diminished in the presence of rewards compared to the absence of rewards for Dutch high achievers. This could be caused by the fact that Dutch high achievers perceived extrinsic rewards as controlling, which stands in stark contrast to experiencing autonomy during learning. Therefore, the advantageous impact of autonomy on the learning process is potentially diminished (i.e., overjustification; Hidi, 2015; Lepper et al., 1973). This is in line with educational studies indicating that extrinsic motivation is detrimental for academic achievement for Western students, while both intrinsic and extrinsic motivators are beneficial for Chinese students (Zhu & Leung, 2011).

Additionally, we also found that the beneficial effect of rewards on learning was stronger for Chinese students, but only for low achievers (Fig. 5.4C & 5.4D). This discovery aligns with the findings of prior research, suggesting that the influence of rewards on performance might be modulated by levels of achievement (Liu et al., 2020b). On the contrary, there are recent studies suggesting that the effect of rewards on behavioural performance is stronger for Western than for Eastern culture (Liu et al., 2020b; Medvedev et al., 2024). This was likely caused by the nature of their measurements, which were imbued with social or external values (i.e., helping the researcher to build up a machine-learning model or learning math). As we stated before, different fragments of motivation are stated and perceived as more meaningful in different cultural backgrounds. For instance, in the setting of Medvedev et al. (2024), a sense of relatedness (i.e., one of the components that foster intrinsic motivation, according to self-determination theory) was induced. Relatedness, defined as a feeling of connection with others, might be more meaningful for Chinese culture than for Western culture (e.g., Walker et al., 2020). Therefore, when relatedness is elicited, Chinese participants might rely less on additional extrinsic motivators than Western participants. This supports our claim that various intrinsic motivators can affect extrinsic motivation differently, depending on the cultural context.

Taken together, in line with the sociocultural brain perspective, for high achievers with Dutch cultural backgrounds, intrinsic motivation (i.e., autonomy) can reduce the effectiveness of extrinsic motivation on learning outcomes and vice versa. However, this interaction effect between intrinsic and extrinsic motivation on learning did not exist for Chinese participants nor Dutch low achievers. This highlights the mutual influence of various motivators throughout the learning process. Our findings align with and extend the sociocultural brain perspective (Han et al., 2013), highlighting that learning motivation is shaped not only by the cultural environment but also by levels of achievement in learning contexts.

5.4.3 Autonomy improved learning in both cultural groups

Furthermore, we did not find cultural differences in the beneficial effect of intrinsic motivation on learning. This was indicated by the strong effects of autonomy on memory performance, which were present for both Chinese and Dutch students.

These findings are congruent with the assertions of self-determination theory (SDT), which posits that autonomy is a fundamental psychological need and, akin to biological drives, is a universal phenomenon across different cultures (Helwig, 2006; Ryan & Deci, 2017). Moreover, intrinsic motivation, particularly autonomy, is closely linked to the pursuit of personal challenges (Di Domenico & Ryan, 2017). While intrinsic motivation and self-improvement are often highlighted in Western ideologies, these concepts are also deeply valued in Eastern tradition. For instance, Confucian philosophy emphasizes the importance of self-cultivation and personal reflection (Zusho, 2005), and Taoism emphasizes the sense of autonomy and freedom in personal behaviours (Wenzel, 2003).

Our study also corroborates neuroscientific evidence that both Chinese and Western individuals exhibit strong motivational brain responses linked to autonomy. For example, in both cultures, feedback-related negativity was stronger for self-relevant rewards compared to rewards relevant for others (Kitayama & Park, 2014; Zhu et al., 2016). Similarly, increased activation in the medial prefrontal cortex and anterior cingulate cortex is observed during self-related personality judgment tasks among participants from both Chinese and Western cultural backgrounds (Zhu et al., 2007). In our current setup, when participants were autonomously exploring the grid with objects, their personal connection to those objects was likely heightened. This might result in stronger brain activity in the dorsal lateral prefrontal cortex under autonomous conditions, thereby improving learning outcomes across diverse cultural backgrounds.

From a neuroscientific perspective, intrinsic motivation, like autonomy, might trigger not only activation and connectivity among a network of distributed brain regions including the OFC and VMPFC, subcortical dopaminergic circuitry, and hippocampus, but also enhance engagement of the dorsolateral prefrontal cortex (DLPFC), which is associated with attentional control (Voss, et al., 2011b). In contrast, extrinsic motivation, like monetary rewards, tends to specifically engage modulation from VMPFC and dopaminergic circuitry (e.g., VTA) influencing the hippocampus (Adcock et al., 2006; Wolosin et al., 2012). Combining with our current behavioural findings, we could hypothesize that cultural background shaped functional activation and connectivity among distributed regions including VMPFC, dopaminergic circuitry, and hippocampus of Eastern students to be more sensitive to rewards in learning tasks. However, with intrinsic motivation exerted on top of extrinsic motivation, DLPFC becomes engaged with a higher level of attentional control over this reward-related brain network, diminishing the cultural difference in intrinsic motivation. Interestingly, this also aligned with a meta-analysis on brain activity focusing on social cognitive processes, for instance, self-reflection tasks where people rate descriptions of their personalities. They found that East Asians exhibited a stronger activity in DLPFC, while

Westerners exhibited stronger activation in VMPFC (Han & Ma, 2014) in these social cognitive processes.

Taken together, our behavioural findings might shed light on both overlap (i.e., VMPFC, OFC, reward circuitry, the hippocampus) and potential dissociations (i.e., DLPFC) of the brain mechanism of intrinsic and extrinsic motivations in learning.

5.4.4 Future directions and limitations

In the end, there is still a lack of studies investigating brain mechanisms underlying the overlap, distinctions, and interactions between extrinsic motivation and intrinsic motivation on learning, particularly regarding the modulation of this process by individual differences. In the future, conducting the current behavioural study in conjunction with functional magnetic resonance imaging (fMRI) could provide valuable insights into the neural underpinnings of cultural differences affecting the interplay between extrinsic and intrinsic motivation during learning. To start with, our current findings, combined with previous neuroimaging studies, indicated that there might be cultural differences in both their behavioural performance and brain activation when participants are extrinsically motivated to learn. Previous research showed that extrinsic motivation elicits more connectivity among VMPFC, midbrain, VTA, and hippocampus (e.g., Adcock et al., 2006). We hypothesize that the beneficial effect of reward on this brain connectivity would be stronger for Chinese students compared to Dutch students. Second, we found that autonomy could enhance learning equally across cultural groups. Additionally, Voss, et al. (2011b) found that autonomous control (intrinsic motivation) could provoke connectivity between the hippocampus and brain areas related to attentional coordination, like the DLPFC. Hypothetically, this brain connectivity between the DLPFC and hippocampus might remain the same across cultural groups. Third, we found that the interaction effect between intrinsic and extrinsic motivation on learning does not uniformly apply across all participants. Regarding cultural differences in motivation, research indicated that Western individuals showed increased activity in both brain regions related to attentional control (i.e., DLPFC) and reward circuitry (i.e., VTA) during experiences of self-control. Conversely, Eastern individuals demonstrated similar brain activation patterns in scenarios where they felt under control from others (Freeman et al., 2009). As we discussed before, cultural backgrounds may shape individuals to perceive varying motivators as more meaningful. This revelation suggests that both the reward circuitry and the prefrontal cortex, related to different types of motivation, might be activated differently depending on cultural context. Hence, it would be intriguing to utilize the current design in an fMRI study to explore motivation-related connectivity among reward circuitry, the prefrontal cortex, and the hippocampus across cultures.

Regarding limitations, the current study did not collect questionnaires assessing the cultural norms and values of each participant. Therefore, we were unable to analyse which specific cultural perspectives might have contributed to the observed differences in learning motivation between cultural groups. Future research in this area should consider incorporating such assessments to deepen the understanding of these cultural attributions.

5.5 Conclusions

To summarize, our study yielded three significant insights. Firstly, extrinsic motivation was more beneficial for learning in Chinese compared with Dutch students. Secondly, intrinsic motivation positively impacted learning across both Western and Eastern cultures. Thirdly, while extrinsic motivation did not enhance learning for high-achieving Dutch students when their intrinsic motivation was fulfilled, it always enhanced learning for low-achieving Dutch students. In contrast, extrinsic motivation consistently improved learning for Chinese students, irrespective of their performance level. These outcomes enhance our comprehension of how cultural nuances affect our motivation to learn and underscore the importance of considering these differences in educational strategies.

5.6 Author note

5.6.1 Funding

The current project is funded by the Open Research Fund of the State Key Laboratory of Cognitive Neuroscience and Learning at Beijing Normal University, Chinese Scholarship Council (CSC), an interdisciplinary research fund provided by the Radboud Teaching and Learning Centre, and the National Natural Science Foundation of China (32130045). We thank Toon Holman and Florian Kühnert for contributions to the design and specification of the task used in this study. We thank Wilbert van Ham from the technical support group for programming the experiment and consulting on preprocessing data.

5.6.2 Availability of data, code and materials

All materials, data, and code used for the experimental procedure and data analyses are freely available on the Radboud Repository (https://doi.org/10.34973/tccj-j019).

5.7 Supplement

5.7.1 Supplementary Material 1: Spatial memory results

5.7.1.1 Methods

In the current experiment, during each trial of the memory test in which participants responded to an object as “Definitely OLD” or “Probably OLD”, they were additionally asked to put the object at the location where they saw it during the learning phase. This part of the memory test was called the spatial memory test. In this spatial memory test, there were three dependent variables calculated to represent the spatial memory performance, the spatial hit, the spatial error, and a general spatial test score.

The spatial hit was calculated and used as a binomial dependent variable, like the recognition accuracy described in the primary results. If participants managed to correctly put the object back to where they saw it during the learning phase, that trial would be counted as a “hit” (spatial hit as 1) in the spatial memory test. On the contrary, if they put it to a different location from the correct one, we counted that trial as a “miss” (spatial hit as 0).

Additionally, a spatial error was calculated, defined as the Euclidian distance between the responded location and the correct location. Hence, spatial error was a continuous variable.

$$Spatial\ error = \sqrt{(X_{respond} - X_{correct})^2 + (Y_{respond} - Y_{correct})^2}$$

We applied a logarithmic transformation to the spatial errors (after adding 1 to each value to avoid 0 in this variable) to achieve a normal distribution for the dependent variable in our inferential statistical analysis.

Last, we calculated a general spatial memory score by labelling objects where participants put back to the correct location and all 8 locations surrounding that correct location (Fig. S5.1) as “hit” (general spatial memory score as 1). On the contrary, if they put the object to the rest 16 locations from these 9 locations, we counted that trial as a “miss” (general spatial memory score as 0).

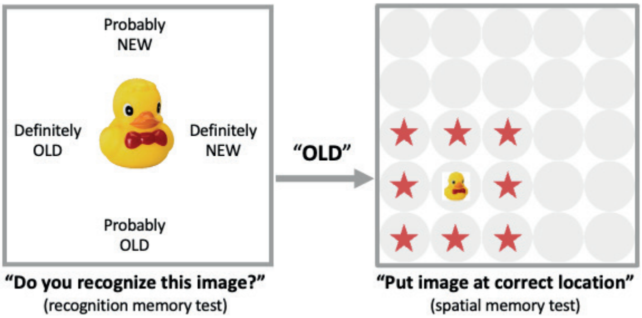

Figure S5.1 General spatial memory score calculation. In the memory test, participants were asked to put the OLD objects back to the locations they saw the object during learning. When computing the general spatial memory score, a margin of error was permitted. Specifically, an object was classified as a "hit" in the spatial memory test if participants positioned it either at the designated location (i.e., where the rubber duck was initially placed) or within any of the eight surrounding locations marked by red stars. If the object is put to the rest 16 locations on the grid (i.e., without any mark), we would count that trial as a "miss" in the spatial memory test. If the correct location of the object is on the corner, only 3 locations around the corner would be tolerated as "hit" locations. When the correct location of the object is on the border, only 5 locations around the correct location will be included as "hit" locations.

We conducted the same models with LME toolbox as the primary results only with spatial hit, spatial error, and general spatial memory score as the dependent variables (Barr, 2013; Barr et al., 2013; Bates et al., 2015). However, these models could not pass model diagnostics. For instance, the residuals of the models do not fit a normal distribution. Therefore, we implemented the *brm* function of the package BRMS in R (Bürkner, 2017) to model spatial hit, spatial error, and general spatial memory score as dependent variables. We used the default priors of the BRMS package (Cauchy priors and LKJ priors for correlation parameters). The model was fit running four chains with 10000 iterations each (5000 warm-ups) and inspected for convergence. Coefficients of the effects were deemed statistically significant if the associated 95% posterior credible intervals were non-overlapping with zero.

$$\begin{gathered} Spatial\ hit/Spatial\ error/General\ spatial\ memory\ score \sim autonomy \times reward \\ \times cultural\_group + (1 + autonomy \times reward \mid sub) \end{gathered}$$

To match the analysis with recognition memory accuracy, this same model was also conducted on the data set including all participants, high achievers and low achievers respectively.

5.7.1.2 Results

All results for the spatial memory test can be found in Table S5.1-5.3. The effects found significant with the models will be described in detail.

Spatial hit – When all participants were included, we found largely similar results for spatial memory (i.e. spatial hit) as for recognition memory (reported in the main text). Specifically, we found a significant autonomy effect, reward effect, and interaction effect between reward and cultural group on spatial hit (Table S5.1; Fig. S5.2A & S5.2B). This indicated that the presence of autonomy was beneficial for spatial hit. The same was true for the presence of rewards, also when dividing each cultural group into high and low achievers (Table S5.2; Fig. S5.3A-D). However, different from the recognition memory results reported in the main text, we also found a cultural group difference in spatial hit: the Chinese group had a lower spatial hit than the Dutch group. Since we also found an interaction effect between reward and cultural group on spatial hit, we conducted follow-up analyses with the *emmeans* package in R (Lenth, 2022). It was observed that the Chinese group performed worse on spatial hit than the Dutch group when they did not receive rewards (95%CI [-0.704, -0.140]), but not when they received rewards (95%CI [-0.443, 0.065]; Fig. S5.1).

Spatial error – When looking at spatial error (Table S5.1; Fig. S5.2C & S5.2D), we found similar results for the main effects of autonomy, reward, and cultural group as for spatial hit. Compared with the results on spatial hit, there was also no interaction between cultural group and reward on spatial error. Additionally, we also implemented the same model after dividing participants into high and low achievers based on their recognition memory accuracy (Table S5.3; Fig. S5.3E-H), and similar results were yielded with the analysis including all participants.

General spatial memory score — When looking at the general spatial memory score, we found all 3 main effects of cultural group, autonomy, and rewards (Table S5.1; Fig. S5.2E & S5.2F) when including all participants. These effects remained significant after splitting each cultural group into high and low achievers (Table S5.4; Fig. S5.3I-L). Different from results with memory accuracy as the dependent variable, the Dutch group (63.16% ± 10.09) performed better on spatial memory tests than the Chinese group (56.55% ± 10.19).

5.7.1.3 Conclusions

Taken together, the results of the spatial memory test largely mirror the results of the recognition memory test reported in the main text. To be more specific, the beneficial effect of reward on memory was stronger for Chinese students than for Dutch students, whereas the influence of autonomy on memory demonstrated a uniform effect across different cultural groups. However, the results on spatial memory tests deviated from the results on recognition memory in one respect: we found Dutch students performed better than Chinese students in the spatial memory test. This group difference between Chinese and Dutch students on spatial memory performance might be explained by a finding that over-challenging tasks usually weaken learning motivation of Chinese students but not of Western students (Moneta, 2004). In our case, the spatial memory test was more difficult than the recognition memory test. This might explain why Chinese students had a worse performance than the Dutch students in the spatial memory test, but not in the recognition memory test.

Table S5.1 BRMS results with Spatial memory as the dependent variable

Effect of interests	All participants	High achievers	Low achievers
Dependent variable: Spatial hit			
Autonomy	**95%CI [-0.100, -0.026]**	**95%CI [-0.108, -0.017]**	95%CI [-0.134, 0.003]
Reward	**95%CI [-0.168, -0.077]**	**95%CI [-0.136, -0.050]**	**95%CI [-0.272, -0.079]**
Cultural group	**95%CI [-0.261, -0.001]**	**95%CI [-0.278, 0.018]**	**95%CI [-0.367, 0.075]**
Autonomy × Reward	95%CI [-0.042, 0.026]	95%CI [-0.053, 0.032]	95%CI [-0.072, 0.060]
Reward × Cultural group	**95%CI [-0.094, -0.005]**	95%CI [-0.058, 0.028]	**95%CI [-0.199, -0.007]**
Autonomy × Cultural group	**95%CI [0.003, 0.075]**	**95%CI [0.002, 0.093]**	95%CI [-0.045, 0.090]
Autonomy × Reward × Cultural group	95%CI [-0.023, 0.043]	95%CI [-0.037, 0.047]	95%CI [-0.051, 0.079]
Dependent variable: Spatial error			
Autonomy	**95%CI [0.011, 0.029]**	**95%CI [0.009, 0.032]**	**95%CI [0.005, 0.036]**
Reward	**95%CI [0.021, 0.045]**	**95%CI [0.016, 0.037]**	**95%CI [0.019, 0.069]**
Cultural group	**95%CI [0.006, 0.077]**	**95%CI [0.000, 0.086]**	95%CI [-0.011, 0.100]
Autonomy × Reward	95%CI [-0.002, 0.014]	95%CI [-0.005, 0.016]	95%CI [-0.007, 0.020]
Reward × Cultural group	95%CI [-0.001, 0.023]	95%CI [-0.008, 0.013]	95%CI [-0.001, 0.049]
Autonomy × Cultural group	95%CI [-0.018, 0.001]	95%CI [-0.021, 0.000]	95%CI [-0.021, 0.011]
Autonomy × Reward × Cultural group	95%CI [-0.013, 0.003]	95%CI [-0.014, 0.006]	95%CI [-0.020, 0.007]
Dependent variable: General spatial test score			
Autonomy	**95%CI [-0.115, -0.029]**	**95%CI [-0.127, -0.028]**	95%CI [-0.150, 0.011]
Reward	**95%CI [-0.148, -0.060]**	**95%CI [-0.149, -0.051]**	**95%CI [-0.205, -0.032]**
Cultural group	**95%CI [-0.330, -0.076]**	**95%CI [-0.358, -0.030]**	**95%CI [-0.410, -0.030]**
Autonomy × Reward	95%CI [-0.067, 0.004]	95%CI [-0.087, 0.015]	95%CI [-0.087, 0.025]
Reward × Cultural group	95%CI [-0.077, 0.011]	95%CI [-0.071, 0.027]	95%CI [-0.143, 0.034]
Autonomy × Cultural group	95%CI [-0.022, 0.063]	95%CI [-0.009, 0.089]	95%CI [-0.087, 0.025]
Autonomy × Reward × Cultural group	95%CI [-0.009, 0.063]	95%CI [-0.019, 0.085]	95%CI [-0.040, 0.071]

* Bold font indicates significant effects

Table S5.2 Mean and standard deviation for spatial hit

					High achievers				**Low achievers**			
	Chinese		**Dutch**		**Chinese**		**Dutch**		**Chinese**		**Dutch**	
Main factors	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***
MOVE	35.95	12.88	42.59	14.09	37.63	11.61	46.10	11.40	34.20	14.15	38.92	15.88
FOLLOW	35.06	13.54	38.18	15.06	37.37	11.57	40.81	11.87	32.65	15.23	35.42	17.67
REWARD	38.29	13.94	42.06	14.19	39.77	10.82	45.24	11.52	36.74	16.72	38.73	16.13
NO REWARD	30.17	13.57	39.16	14.19	34.92	12.35	41.99	11.05	25.21	13.26	36.20	17.14
Autonomy × Reward	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***	***M (%)***	***SD***
MOVE/ REWARD	38.69	15.47	43.82	14.29	39.83	11.90	47.57	12.08	37.49	18.72	39.90	15.72
MOVE/NO REWARD	30.35	13.96	41.26	15.25	35.20	13.47	44.67	11.40	25.28	12.87	37.69	18.04
FOLLOW/REWARD	37.77	14.78	39.75	15.89	39.96	12.05	42.54	13.62	35.48	17.17	36.84	17.81
FOLLOW/NO REWARD	29.92	15.97	36.17	16.19	34.34	13.41	38.85	11.66	25.30	17.38	33.37	19.77

Table S5.3 Mean and standard deviation for spatial error

					High achievers				Low achievers			
	Chinese		Dutch		Chinese		Dutch		Chinese		Dutch	
Main factors	***M***	***SD***	***M***	***SD***	***M***	***SD***	***M***	***SD***	***M***	***SD***	***M***	***SD***
MOVE	1.26	0.37	1.05	0.35	1.17	0.34	0.94	0.28	1.35	0.38	1.17	0.37
FOLLOW	1.31	0.38	1.17	0.39	1.22	0.34	1.07	0.30	1.42	0.40	1.27	0.44
REWARD	1.22	0.37	1.06	0.36	1.14	0.30	1.04	0.29	1.30	0.43	1.18	0.40
NO REWARD	1.42	0.43	1.14	0.36	1.25	0.38	0.96	0.29	1.59	0.42	1.25	0.40
Autonomy × Reward	***M***	***SD***	***M***	***SD***	***M***	***SD***	***M***	***SD***	***M***	***SD***	***M***	***SD***
MOVE/EXTRA REWARD	1.19	0.39	1.04	0.38	1.12	0.32	0.91	0.31	1.27	0.45	1.16	0.41
MOVE/NO EXTRA REWARD	1.39	0.43	1.07	0.34	1.23	0.38	0.96	0.28	1.54	0.44	1.18	0.38
FOLLOW/EXTRA REWARD	1.25	0.39	1.10	0.39	1.16	0.31	1.00	0.33	1.34	0.45	1.21	0.43
FOLLOW/NO EXTRA REWARD	1.47	0.51	1.24	0.43	1.29	0.42	1.13	0.34	1.67	0.53	1.36	0.49

Note: The mean represents the Euclidean distance calculated between the response location and the correct location of each object in the spatial memory test.

Table S5.4 Mean and standard deviation for general spatial score

					High Achievers				**Low Achievers**			
	Chinese		**Dutch**		**Chinese**		**Dutch**		**Chinese**		**Dutch**	
Main factors	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***
MOVE	68.78	12.27	76.48	10.95	72.35	10.81	80.45	9.57	65.04	12.83	72.32	10.95
FOLLOW	66.82	12.39	73.34	12.34	71.17	10.67	76.61	10.06	62.26	12.64	69.91	13.74
REWARD	70.05	11.56	76.05	11.62	73.96	9.25	79.64	9.84	65.97	12.51	72.29	12.35
NO REWARD	63.80	15.16	73.94	11.01	69.30	12.10	77.36	9.76	58.05	16.13	70.38	11.32
Autonomy × Reward	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***	***M* (%)**	***SD***
MOVE/EXTRA REWARD	71.02	12.37	76.49	12.70	74.79	9.80	80.59	10.79	67.08	13.72	72.22	13.35
MOVE/NO EXTRA REWARD	64.96	15.90	76.33	10.32	69.59	13.39	80.25	9.17	60.13	17.15	72.22	10.02
FOLLOW/EXTRA REWARD	69.12	13.04	75.50	12.79	73.48	10.67	78.71	11.00	64.57	13.95	72.14	13.89
FOLLOW/NO EXTRA REWARD	61.63	17.43	70.87	14.12	68.48	12.79	74.37	12.47	54.48	18.98	67.22	15.08

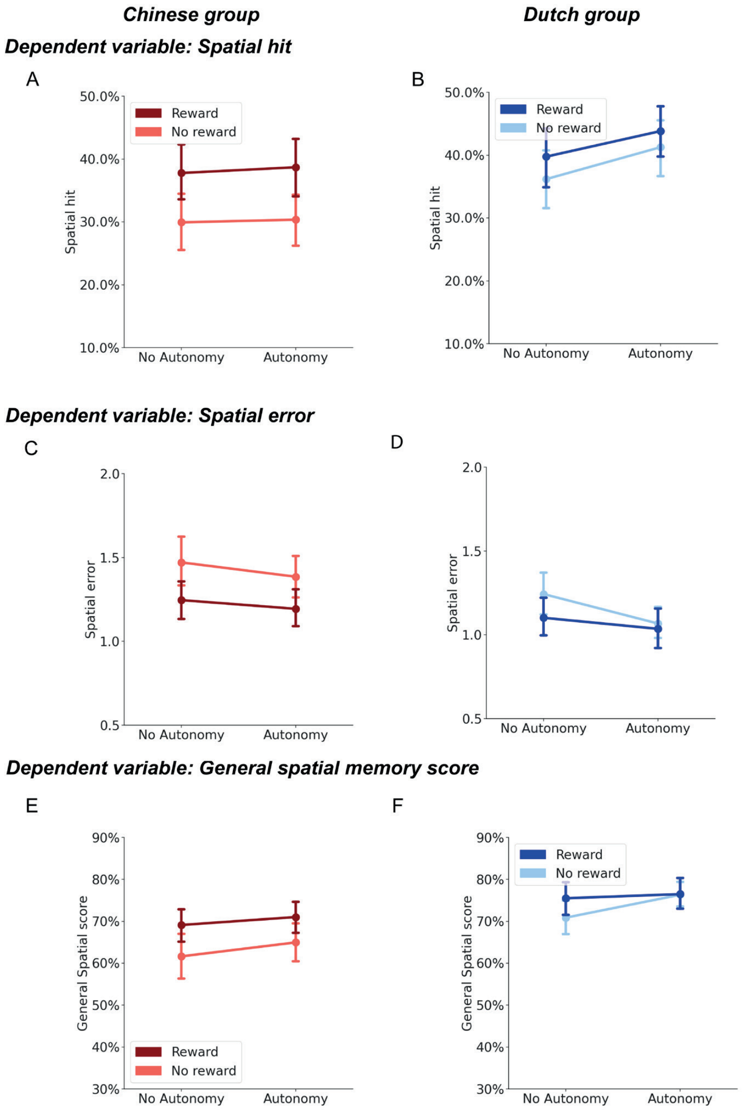

Figure S5.2 Results on spatial hits and spatial error (Table S5.1). **A.** For the Chinese group, the spatial hit is plotted as a function of autonomy and reward. The red colour represents the Chinese cultural group. The dark red colour represents the reward condition, while the light red colour represents the no reward condition. The error bars represent the standard error of the means (SEM). **B.** As in A, the spatial hit is plotted as a function of autonomy and reward for the Dutch group. The blue colour represents the Dutch cultural group. The dark blue colour represents the reward condition, while the light blue colour represents the no reward condition. Other conventions are the same as in Fig. S5.1A. **C.** For Chinese students, spatial error is plotted as a function of autonomy and reward. It should be noted that a lower spatial error reflects better spatial memory performance. All conventions are the same as in Fig. S5.1A. **D.** For the Dutch group, spatial error is plotted the same as in Fig. S5.1B. E & F. The conventions are the same as the panel of A & B, only with the y-axis representing general spatial memory score instead of spatial hit.

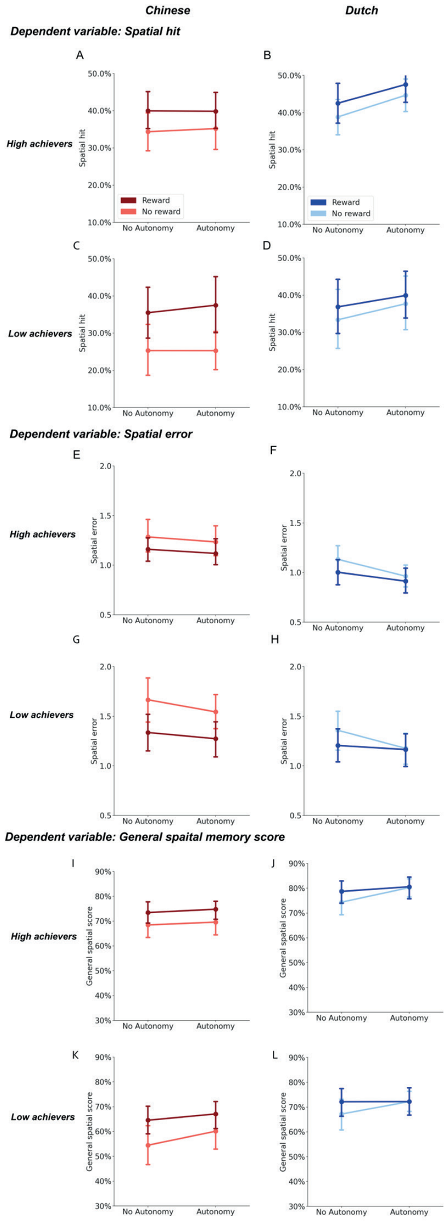

Figure S5.3 The results respectively on high and low achievers are listed in Table S3. All conventions are the same as in Fig. S5.1. **A.** For the Chinese high achievers, the spatial hit is plotted as a function of autonomy and reward. **B.** For the Dutch high achievers, the spatial hit is plotted as a function of autonomy and reward **C.** For Chinese low achievers, the spatial hit is plotted the same as in Fig. S5.2A. **D.** For the Dutch low achievers, the spatial hit is plotted the same as in Fig. S5.2B. **E-H.** The conventions are the same as the panel of A & B & C & D, only with the y-axis representing spatial error instead of spatial hit. **I-J.** The conventions are the same as the panel of A & B & C & D, only with the y-axis representing general spatial memory score instead of spatial hit.

5.7.2 Supplementary Material 2: signal detection theory based analysis

5.7.2.1 Methods

Meanwhile, there might be cross-cultural differences in response biases (Leger & Gutchess, 2021). This difference in response bias might contribute to the differences in reward effect on memory accuracy between cultural groups. To rule out this possibility, we employed signal detection theory to calculate both *d'* and *C* parameters, as detailed by Hautus et al. (2021; https://camel.psyc.vt.edu/models/recognition/index.shtml). In the current experiment, both the manipulation of autonomy (MOVE/FOLLOW) and rewards (REWARD/NO REWARD) were within-subject. Only the comparison of cultural groups was between-subject. In the learning phase of the experiment, each participant learned a total of 300 objects, divided into 75 objects per experimental condition. During the memory test, these objects were presented in random order, intermixed with 300 filler objects (foils). Since these foil items do not belong to any of the four conditions, we could only calculate *d'* and *C* at for overall performance at a participant level, but not per condition.

In order to compute *d'* and *C*, we first calculated the hit rate and false alarm for each participant.

$$Hit\ rate = Hit\ object\ number_{Old} / Total\ object\ number_{Old}$$
$$False\ alarm = Hit\ object\ number_{New} / Total\ object\ number_{New}$$

We implemented *z* transformation for Hit rate (Z_H) and False alarm (Z_{FA}) for each participant. Then, *d'* and *C* for each participant were computed as follows.

$$d' = Z_H - Z_{FA}$$
$$C = -1/2[Z_H + Z_{FA}]$$

According to signal detection theory, d' represents the discriminability/sensitivity. The higher the *d'* is for a participant, the better the participant is at discriminating between old and new objects. *C* represents the bias. If *C* is higher than 0, this suggests that participants had a conservative bias, meaning that participants tended to guess objects were NEW in the memory test. If *C* is lower than 0, this indicates that participants had a liberal bias, meaning that participants tended to guess objects were OLD in the memory test. With *d'* and *C* as dependent variables, we respectively conducted independent sample t-tests between Dutch and Chinese groups.

5.7.2.2 Results

In the results of *t*-tests, we found that the Dutch group (1.96 + 0.50) showed a higher *d'*(discriminability) than the Chinese group (1.51 + 0.58), t (86.40) = 3.90, $p < 0.001$. This suggests that Dutch students were better at discriminating between OLD and NEW objects than Chinese students. We also did the same analysis for *C* (bias) and found no difference between cultural groups (Dutch group: 0.40 + 0.30; Chinese group: 0.34 + 0.43.), t (78.67) = -0.79, $p = 0.43$. This suggested that there were no group differences in response bias, validating that our findings regarding the different effects of reward on memory accuracy between cultural groups could not be explained by bias alone.

The results partially aligned with previous work Leger and Gutchess (2021), in which they found that participants from North America were better at discriminating between OLD and NEW objects (*d'*) than participants from East Asia. They also found that participants from North America had a higher bias to respond to an object as OLD than East Asian participants. Moreover, in our study, we did not find differences in response bias (*C*) between cultural groups. To summarize, the cross-cultural differences in the reward effect might not be caused by differences in response bias between cultural groups. The current study builds upon the findings of Leger & Gutchess (2021), demonstrating that cultural differences extend beyond memory specificity also to include the effects of intrinsic and extrinsic motivation on memory.

5.7.3 Supplementary Material 3: Analysis of Recognition Memory Confidence

5.7.3.1 Methods

In the main manuscript, we labelled responses 1 and 2 were labelled as 'New,' and responses 3 and 4 were labelled as 'Old.' This binary classification was chosen to simplify the statistical analysis and to focus on the primary (preregistered) research question of whether participants could accurately distinguish between new and old items. In other words: it allows for a more straightforward interpretation of the recognition memory performance.

In this supplementary analysis, we implemented the same model as the main analysis on recognition memory accuracy on the Likert scale for memory confidence. We labelled “Definitely Old” -> 4, “Probably Old” -> 3, “Probably New” -> 2, “Definitely New” -> 1. Instead of using the glmer toolbox in R, we used the clmm toolbox (https://search.r-project.org/CRAN/refmans/ordinal/html/clmm.html) since the dependent variable was ordinal. In this way, the higher the Likert scale is, the more confident the participants are in remembering the objects. We did not report this in the main manuscript, since the results were very similar to the results using the binary format, but the results can be found in Supplementary Material 3.

5.7.3.2 Results

We also found the main effects of autonomy and reward and the interaction between the factor of cultural groups and rewards on the Likert scale. We did not report this in the manuscript since the results highly mirrored the results on memory accuracy. The results from this model are reported in tables here. These codes are also available in the open access codes for future researchers to check.

Table S5.5 CLMM results with the Likert scale for recognition memory as the dependent variable

Effect of interests	***β***	***z***	***p***
Autonomy	-0.23	-7.33	<0.001***
Reward	-0.17	-5.68	<0.001***
Cultural group	-0.12	-1.62	0.11
Autonomy × Reward	-0.02	-1.48	0.19
Reward × Cultural group	-0.08	-2.56	0.01*
Autonomy × Cultural group	0.04	1.25	0.21
Autonomy × Reward × Cultural group	0.02	1.29	0.14

*, $p< 0.05$; ***, $p<0.001$

Table S5.6 Mean and standard deviation for the Likert scale for recognition memory

	Chinese		**Dutch**	
Main factors	***M***	***SD***	***M***	***SD***
MOVE	3.07	0.40	3.27	0.36
FOLLOW	2.85	0.44	2.98	0.41
REWARD	3.11	0.36	3.18	0.34
NO REWARD	2.82	0.52	3.08	0.37
Autonomy × Reward	***M***	***SD***	***M***	***SD***
MOVE/EXTRA REWARD	3.21	0.38	3.29	0.37
MOVE/NO EXTRA REWARD	2.93	0.53	3.24	0.38
FOLLOW/EXTRA REWARD	3.00	0.41	3.06	0.43
FOLLOW/NO EXTRA REWARD	2.71	0.56	2.91	0.44

Notes: The dependent variable for this model is the Likert scale (e.g., “Definitely Old” -> 4, “Probably Old” -> 3, “Probably New” -> 2, “Definitely New” -> 1). The higher the Likert scale is, the more confident participants are that the objects were seen in the learning task.

To follow up, we also compared the Likert scale for the REWARD and NO REWARD conditions respectively for the Dutch group and the Chinese group with the *emmeans* package in R (Lenth, 2022). It was found that the facilitatory effect of reward (REWARD – NO REWARD) on Likert scale was significant for both the Chinese group ($\beta = 0.48$, $z = 5.82$, $p < 0.001$) and the Dutch group ($\beta = 0.19$, $z = 2.23$, $p = 0.03$). This reward effect on Likert scale was stronger for the Chinese group compared with the Dutch group. Alternatively, we also compared Likert scale between the Chinese and Dutch groups under both REWARD and NO REWARD conditions respectively (Fig. S5.5 & S5.6). It was found that under reward conditions, Likert scales were at a similar level between the Dutch and Chinese groups ($\beta = 0.09$, $z = 0.61$, $p = 0.54$). However, under the NO REWARD condition, the Dutch group performed with a higher confidence than the Chinese group ($\beta = 0.39$, $z = 2.20$, $p = 0.03$) in the recognition memory test.

In summary, the results of the CLMM model with Likert scale of recognition memory as the dependent variable mirrored the results from the main manuscript, where we used the binary dependent variable, recognition memory accuracy, as the dependent variable.

Chapter 6

General discussion

Although I learned traditional Chinese dance for eight years and practiced many different pieces, the only one I still vividly remember, even after 15 years, is the piece I chose to learn myself. This illustrates the power of autonomy, the regulation of one's own actions and experiences, in learning. When people take ownership of their choices, the resulting memory of the learning content becomes much stronger. The current thesis comprises four projects examining the cognitive and neural mechanisms that support the beneficial effect of autonomy on learning. Adopting an ecological psychology perspective (Vigliocco et al., 2024), the studies span three levels of analysis that could modulate the impact of autonomy on memory encoding: the internal predictive processing of the brain, external motivators, and socio-cultural contexts.

6.1 Main findings

In **Chapters 2 and 3**, autonomy was operationalized through a binary choice paradigm, combined with manipulations of predictability and surprise of the choice outcomes. Together, these two chapters focused on how making active choices influences memory encoding through its interaction with predictive processing. In **Chapters 4 and 5**, autonomy was manipulated through an exploration paradigm, in which participants were either allowed to actively explore a grid of objects or were required to follow predetermined paths. Monetary reward was concurrently manipulated for each exploration grid. Participants were asked to remember as many objects as possible in all the grids. **Chapter 4** implemented this paradigm in an fMRI scanner to examine how intrinsic and extrinsic motivational factors independently and interactively modulate brain activity during memory encoding, while **Chapter 5** explored how cultural contexts modulate the beneficial effect of autonomy and reward on learning. In this chapter, I will summarize the main findings from **Chapters 2-5**, discuss and integrate the most relevant findings, and highlight the relevance for future research directions.

In **Chapter 2**, we designed a binary choice paradigm to test the beneficial effect of autonomy on memory accuracy under different predictabilities of the choice outcomes. We found a significant beneficial effect of autonomy on memory accuracy for both high and low predictability conditions of choice outcomes. Importantly, the autonomy effect on memory accuracy was markedly smaller under the low predictability condition than under high predictability. In essence, these results are consistent with the hypothesis that making active choices enhances memory by fostering predictive processing.

In continuation of work from **Chapter 2**, **Chapter 3** introduced an experiment with more restricted control over predictive processing dynamics (Fig. 6.1A). Based on information theory, in Chapter 3, we held the entropy of the informational context constant, ensuring that participants were generally unable to predict which image would appear following their choice throughout the memory encoding session. Instead, we selectively manipulated Shannon surprise, the log probability of the category of the presented image being consistent or inconsistent with their prediction (Modirshanechi et al., 2022). We observed a significant interaction between autonomy and surprise in the model accounting for the memorability of the individual images. Follow-up analyses revealed that making active choices enhanced memory performance only in the no-surprise condition. This beneficial effect of choice on memory accuracy was eliminated under the surprise condition, suggesting that unexpected outcomes may disrupt the advantage conferred by autonomy.

In **Chapter 4**, we investigated the cognitive and neural mechanisms of how autonomy and reward, considered to be the micro-environment level in our framework (Fig. 6.1B), simultaneously influence learning. Participants engaged in a learning task wherein they were presented with grids of obscured images. We manipulated autonomy by granting participants control over their exploration trajectory over those grids of images, while we also varied the opportunity for monetary rewards for each image grid. Throughout the experiment, participants were tasked with memorizing as many objects as possible, followed by a subsequent memory assessment. Behaviourally, we found that both autonomy and reward independently enhanced learning, consistent with previous findings suggesting that intrinsic and extrinsic motivation operate in parallel without modulating one another (Duan et al., 2020). However, the results from brain activity provided a more nuanced picture. First, we noticed that the presence of autonomy led to stronger activation of dorsal anterior cingulate cortex (dACC), subcortical reward circuitry, and parahippocampal gyrus. However, no subcortical reward circuitry was observed when comparing the brain activity under the no-autonomy condition to the autonomy condition. Second, although reward did not influence the beneficial effect of autonomy on memory accuracy, we observed a subtle shift in the neural signature of autonomy under different reward contexts. Specifically, the presence of autonomy elicited a larger dACC cluster but a smaller putamen cluster activation under the reward compared to the no-reward condition. However, this result was not confirmed through statistical analysis; therefore, future studies are needed to investigate this mechanism further. We interpret our current findings with caution. Third, exploratory functional connectivity analysis revealed possible attentional modulation between the frontal cortex and the hippocampus during autonomous learning and more active perceptual information integration between the visual cortex and the hippocampus during non-autonomous learning.

In **Chapter 5**, by administering the same learning experiment in **Chapter 4** to Chinese and Dutch students, this study aimed to gain a better understanding of how autonomy and rewards simultaneously influence memory encoding under different cultural contexts, which is considered to be the macro-level in our framework (Fig. 6.1C). There are three key novel findings in this project. First, we found that the beneficial effect of monetary rewards on learning was stronger for Chinese students than for Dutch students. Second, we found that there was no difference in the beneficial effect of autonomy on learning between Chinese and Dutch students. Third, consistent with **Chapter 4**, we confirmed that the interaction between intrinsic and extrinsic motivation is not significant. This could indicate that when intrinsic and extrinsic motivators exist simultaneously, they have an additive effect, enhancing learning beyond the influence of either factor alone (Duan et al., 2020).

6.2 Interpretation of the findings

6.2.1 Autonomy supports learning by facilitating prediction over upcoming information

Taking **Chapters 2 and 3** together, we could conclude that making active choices, as a form of autonomy, supports memory encoding by facilitating prediction over upcoming information. This is supported by the attenuation of the beneficial effect of choice in memory encoding under the low predictability of choice outcomes. Also, it was found in **Chapter 3** that choices could only enhance learning when the image was presented under a no-surprise condition, while choices could not enhance learning when it was the surprise condition. Moreover, **Chapter 4** indicated results that autonomy could induce higher activation in dACC and enhanced functional connectivity between the hippocampus and attention-related frontal-parietal networks, including the inferior frontal gyrus and supramarginal gyrus. This also aligns with the notion that making active choices facilitates attentional tuning in anticipation of upcoming information, thereby enhancing the encoding process. Collectively, the findings from Chapters 2 to 4 allow us to address the research question posed in Chapter 1, Section 1.2: whether and how internal predictive processing modulates the beneficial effect of autonomy on memory encoding, and how this is reflected in the brain.

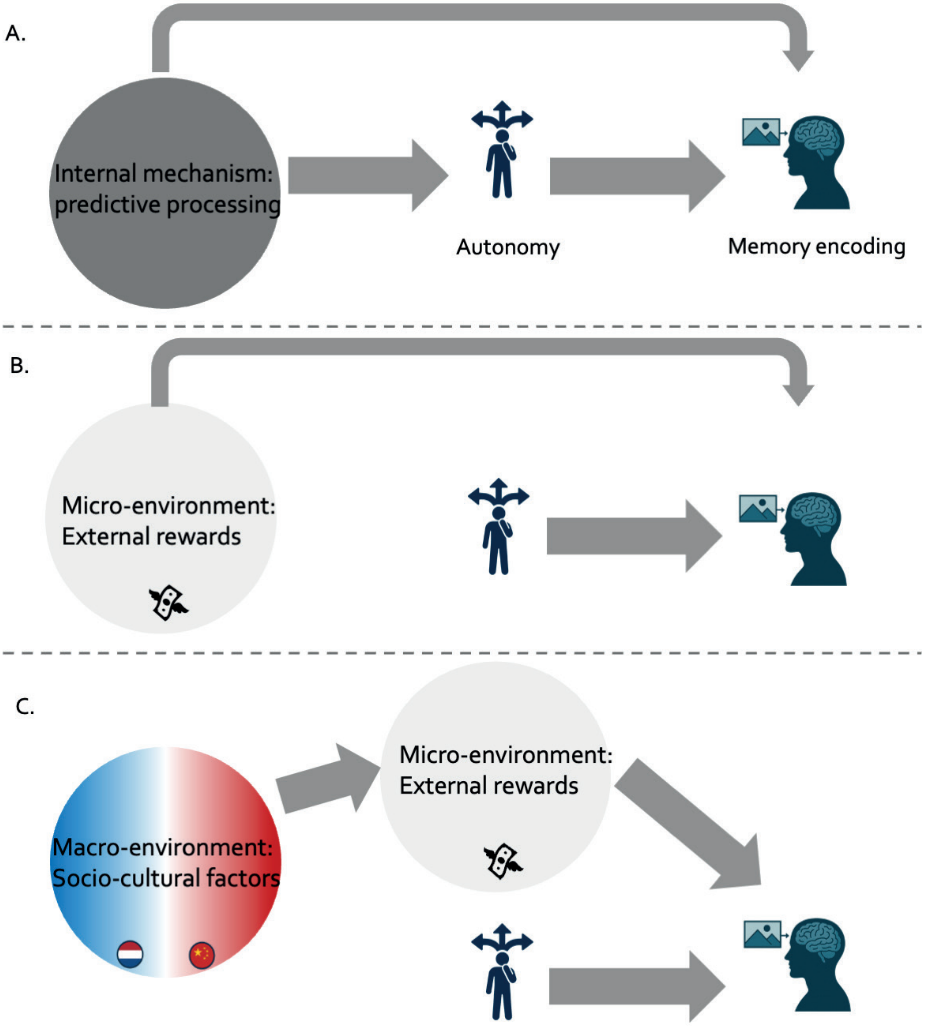

Figure 6.1 Summary of main findings relating back to the hierarchical structure of the factors that could influence autonomy and memory encoding. **A.** Combining findings from **Chapters 2 and 3**, we conclude that the internal mechanism of predictive processing interacts with autonomy to influence memory encoding. **B.** Based on **Chapters 4 and 5**, we find that the micro-environmental factor of reward does not modulate the effect of autonomy. However, autonomy and reward independently enhance memory encoding. Crucially, only autonomy increases activation in reward-related brain regions during encoding, while reward does not. **C. Chapter 6** reveals that macro-environmental socio-cultural factors shape how reward influences memory encoding, but do not affect the impact of autonomy. Nevertheless, both autonomy and reward continue to independently support memory performance.

6.2.1.1 Predictability modulates the choice effect in memory encoding

Across two experiments in **Chapter 2**, we found that the choice effect on memory accuracy was attenuated under low predictability compared to high predictability. This result echoes findings from educational research arguing that choice enhances motivation only under certain conditions (Katz & Assor, 2006). Specifically, autonomy enhances learning most effectively when the choices are made based on information that is meaningfully related to the content students will subsequently be exposed to, rather than being arbitrary or unrelated to the learning material. Our findings can be interpreted through three theoretical perspectives.

To start with, the act of choosing transforms the information process from passive perceiving to active predicting. Our brains are not old-fashioned computers that can only take passive inputs and produce responses. On the contrary, our brains are considered to be active inference agents that constantly predict upcoming events in the surrounding environments (Friston, 2010; Friston et al., 2016; Friston et al., 2017; Friston et al., 2013). Choices could enhance active inference, leading to a facilitation of reducing prediction error between predicted states and perceived information (Friston et al., 2013). Hence, when participants could not accurately predict the outcome of their choices, the sense of autonomy would also be attenuated (Friston et al., 2013). Meanwhile, there are also studies indicating that maybe just making a choice would bring an illusory sense of control (Sullivan-Toole et al., 2017). This is supported by our findings in **Chapter 2**, which showed that even under low predictability, when participants could not accurately anticipate the outcomes of their choices, making a choice still enhanced memory encoding, though the effect was notably weaker compared to the high-predictability condition.

Second, some studies also posit that choices would lead to a distortion of the information value after it was perceived. When people are choosing, they might feel that information is more valuable than when they could not choose (Assor et al., 2002; DuBrow et al., 2019; Izuma & Murayama, 2013; Meng & Ma, 2015; Sharot & Sunstein, 2020). Making an active choice could create a stronger information bias towards the positive valence of information (Chambon et al., 2020). As a result, the beneficial effect of choice emerged only when the information aligned with predictions before images appeared, as demonstrated in **Chapters 2 and 3**. However, the current design did not account for the subjective value or preference associated with the information. Future studies could incorporate individual preferences to examine how value influences memory encoding. In the present study, all stimuli were largely neutral in content.

Third, since people would more actively predict upcoming information when they could choose, they could also coordinate their attention beforehand. This is consistent with the mechanism of proactive interference and divided attention since more encoded cues might cause a higher cognitive load (Jacoby et al., 2010; Kane & Engle, 2000; Luo et al., 2022). This was supported by previous findings showing that even if people could only control *when* to adjust their attention to the next object, memory would already be boosted (Gureckis & Markant, 2012; Markant et al., 2014a). When comparing functional connectivity with the hippocampus under autonomy to no-autonomy conditions, we found increased hippocampal connectivity with frontal regions, including middle and inferior frontal gyri (Badre & Wagner, 2007; Eichenbaum, 2017; Tomita et al., 1999; Voss et al., 2011b; Zheng et al., 2021) and the supramarginal gyrus (Cristoforetti et al., 2022; Das & Menon, 2024; Guidali et al., 2019; Yue & Martin, 2021). These findings align with previous studies indicating that attention-related frontal-parietal networks enhance cognitive resource allocation during memory formation with active exploration (Voss et al., 2011b). As a result, the choice effect on memory accuracy became smaller under low predictability, in other words, when attentional tuning could not be successfully deployed due to the unpredictability of the upcoming content.

In summary, in **Chapter 2**, we found that the choice facilitatory effect on memory diminished under low predictability. This finding supported the hypothesis that choice improves learning by enhancing prediction over the consequences. Three potential explanations for this attenuation of the choice effect emerge. First, choices induced a more active prediction towards information. Second, choices evoked a sense of lower prediction error between the choice and the perceived information. Third, choices facilitated the attention coordination before the information was presented. This explanation was also supported by neuroscientific findings from **Chapter 4**, which showed greater engagement of the attentional control network during memory encoding when participants experienced autonomy compared to when they did not. In addition, one should observe that making choices still enhanced memory even under low predictability conditions (see **Chapter 2**), suggesting that the effect of choice was robust. This implies that choice may induce an illusion of control, enhancing memory even when outcomes are unpredictable.

6.2.1.2 Choice works only when it is not a surprise

Chapters 2 and 3 collectively demonstrate that the memory-enhancing effect of active choice depends on consistency between the choice and its outcome. In Experiment 2 of **Chapter 2,** the choice benefit disappeared for objects that were not selected under low predictability. Likewise, **Chapter 3** showed that choice only improved memory in the no-surprise condition; when the outcome violated expectations, the advantage of making a choice was entirely abolished.

Comparing the two experiments, Chapter 2 showed that when participants viewed both object names for a fixed duration, they may have formed competing predictions under low predictability, particularly in the no-choice condition. This could have led to confusion or false memory, reducing accuracy. In contrast, when participants actively made a choice, even under low predictability, they may have formed a stronger anticipatory representation of the selected object, mitigating the effect of competing predictions (Meng & Ma, 2015). Based on this result, we could demonstrate that when the upcoming information fits the prediction, even when the predictability was low, the choice effect on memory accuracy would not be attenuated. In Chapter 3, however, participants could only expect to see a consistent category, not specific items, thus forming weaker anticipatory predictions. Under these conditions, the memory benefit of choice was entirely eliminated. This aligns with previous findings suggesting that moderate violations of prediction can impair encoding (Csink et al., 2021; de Bruine et al., 2024; Frank et al., 2022). Together, these results support the interpretation that active choice enhances memory by strengthening predictive processes—a conclusion consistent with predictive coding accounts (Friston et al., 2013; Meng & Ma, 2015).

6.2.2 Reward does not influence the choice effect on memory behaviourally

Furthermore, in Chapter 1, we raised a second research question concerning the direct micro-environment, specifically, whether and how rewards modulate the beneficial effect of autonomy during memory encoding. To address this, we first examined the behavioural outcomes in **Chapters 4 and 5**. However, we did not find a significant interaction between autonomy and reward on memory performance. In other words, autonomy and rewards showed an additive rather than an undermining relationship in learning. That is, people feel intrinsically engaged in learning tasks regardless of external stimuli (Duan et al., 2020). Although some previous studies have found that the advantageous impact of autonomy on the learning process is potentially diminished by extrinsic motivation (i.e., overjustification; Hidi, 2016; Lepper et al., 1973; Murayama & Kuhbandner, 2011), the differing results in these studies may stem from an overgeneralization of the circumstances (Eisenberg, 2002). Cerasoli et al. (2014) proposed that extrinsic rewards are more likely to undermine intrinsic motivation when they are directly tied to task performance. Applied to our context, this would suggest that the beneficial effect of intrinsic motivation might be diminished if rewards were administered during the memory test phase rather than the encoding phase. However, in both our experiment and that of Duan et al.

(2020), intrinsic and extrinsic motivators were present simultaneously during the encoding phase. Under these conditions, we observed that autonomy and rewards enhanced memory in parallel, with no evidence of interference, thereby supporting the view that the timing and relevance of extrinsic incentives are critical moderators of motivational interactions.

Moreover, the interaction between intrinsic and extrinsic motivation should be interpreted in light of cultural context and individual differences in learning outcomes. One possible explanation for our findings is that the effect of autonomy may be diminished by the presence of rewards among Dutch high-achieving students. This may reflect their perception of extrinsic incentives as controlling, which undermines the sense of volition essential to autonomy. This interpretation aligns with educational research suggesting that extrinsic motivation can negatively impact academic achievement in Western contexts, whereas both intrinsic and extrinsic motivators contribute positively to learning outcomes in Chinese students (Zhu & Leung, 2011).

In summary, intrinsic and extrinsic motivation tend to operate in parallel for most individuals. However, among high-achieving students from Western cultural backgrounds, extrinsic rewards may be perceived as controlling, thereby undermining the beneficial effect of autonomy on learning. These findings underscore the importance of tailoring educational approaches to individual differences. As Confucius aptly noted, “Teaching in accordance with individual aptitude.”

6.2.3 Autonomy enhances memory encoding by eliciting reward circuitry activation

To further explore how autonomy and rewards jointly influence learning, we examined their interaction at the neural level in **Chapter 4**. It is worth mentioning that we did not observe any brain region activated by monetary rewards, while only observed that the reward circuitry was activated higher under the autonomy condition compared to the no-autonomy condition, even though we found main effect of autonomy and reward in behavioural results, suggesting that both motivational factors could boost memory encoding. The comparison between autonomy and no-autonomy conditions revealed significantly stronger BOLD activation in the caudate, putamen, ACC, and parahippocampal gyrus. Unsurprisingly, this pattern aligns with existing evidence that autonomous memory encoding, as a form of active learning, recruits the core components of the dopaminergic reward circuitry (Stuber, 2023), regions involved in modulation of the dopaminergic circuitry, namely the cortico-basal ganglia circuit, together with the memory system like the parahippocampal gyrus (Duan et al., 2020; Dubinsky & Hamid, 2024; Leotti & Delgado, 2011; Murty et al., 2015; Ripolles et al., 2016; Voss et al., 2011b). The divergent results from brain activation indicated that autonomy, as an intrinsic motivator, is more important and salient than monetary rewards during learning.

Although no behavioural evidence suggested that autonomy was more rewarding in the absence of external rewards, our exploratory neuroimaging results provided preliminary support that autonomy elicited a larger cluster of activation in reward-related regions, particularly the bilateral putamen, under no-reward conditions compared to reward conditions. While both the putamen and dorsal anterior cingulate cortex (dACC) were more active under autonomous conditions across reward contexts, their patterns diverged. Specifically, putamen activation associated with autonomy was more extensive in the no-reward condition, suggesting that autonomy may be perceived as more inherently rewarding in the absence of extrinsic incentives. Conversely, autonomy-related activation of the dACC was larger under reward conditions, pointing toward a shift in neural engagement from motivational (reward-related) to cognitive control (attentional and monitoring) systems depending on the reward context (Kennedy et al., 2024; Leotti & Delgado, 2011). However, since these observations of the cluster size in putamen and dACC showing activation differences were not supported by direct statistical comparisons, they should be interpreted with caution.

Taken together, these findings highlight the limitations of the traditional dichotomy, which views intrinsic and extrinsic motivation as either strictly additive or mutually exclusive (Bardach & Murayama, 2025). Thus, we advocate for a reconceptualization of motivational interactions that transcends the simple binary of enhancement versus undermining. While our neuroimaging findings point toward a potential shift in the underlying neural mechanisms of autonomy depending on the reward context, these conclusions remain exploratory. Because the observed cluster size differences in putamen and dACC were not supported by direct statistical comparisons, they should be interpreted tentatively. Future studies should incorporate conjunction or disjunction analyses and directly compare cluster sizes across participants to validate the robustness of these neural shifts.

6.2.4 Autonomy boosts learning universally across cultures, but external reward does not

6.2.4.1 Autonomy effect on learning does not differ between cultural groups

Furthermore, we did not find cultural differences in the beneficial effect of intrinsic motivation on learning. This was indicated by the strong effects of autonomy on memory performance, which were present for both Chinese and Dutch students. These findings are congruent with the assertions of self-determination theory (SDT), which posits that autonomy is a fundamental psychological need and, akin to biological drives, is a universal phenomenon across different cultures (Helwig, 2006; Ryan & Deci, 2017). Moreover, intrinsic motivation, particularly autonomy, is closely linked to the pursuit of personal challenges (Di Domenico & Ryan, 2017). While intrinsic motivation and self-improvement are often highlighted in Western ideologies, these concepts are also deeply valued in Eastern traditions. For instance, Confucian philosophy emphasizes the importance of self-cultivation, life building, self-development, and personal reflection (Liu et al., 2020a; Zusho, 2005), and Taoism emphasizes the sense of autonomy and freedom in personal behaviours (Wenzel, 2003).

6.2.4.2 Reward effect on learning is stronger for Chinese students compared to Dutch students

In both cultural groups, participants remembered more objects in the reward condition than in the no-reward condition. However, Chinese students exhibited a stronger effect of reward on memory than Dutch students, indicated by a significant interaction effect between factors of reward and cultural group (Fig. 5.3A). When delving deeper into this interaction effect, it was found that Chinese students remembered fewer objects compared with Dutch students when there was no monetary reward. Students from the two cultural groups performed equally well for the rewarded objects.

This is consistent with findings from previous studies suggesting that people from a collectivistic cultural background would be more motivated by external sources (Huang, 2013). Distinct from Western philosophy, Chinese cultural contexts emphasize academic attainment (Dekker & Fischer, 2008) and family honour (Salili et al., 2012). This ethos stems from the Confucian principle of "Rushi" (入世), which promotes self-improvement and contribution to societal prosperity (Hao, 2018). In Confucian culture, factors that come from external environments are more emphasized than in non-Confucian Western educational contexts, like materialistic rewards, academic achievement, expectancy of success, and group benefits (Blevins et al., 2023; Chen et al., 2005; Iyengar & DeVoe, 2003; Tao & Hong, 2013; Telzer et al., 2017).

From the sociocultural brain perspective, neural responses toward external stimuli are shaped by both short- and long-term dynamic cultural experiences (Han, 2017; Han & Ma, 2014; Han et al., 2013). For instance, compared with American participants, Chinese participants showed more sustained reward circuitry activation (in the ventral striatum) during a go/no-go task when their goal was to improve their accuracy in this task (Telzer et al., 2017). In this situation, Chinese students were more motivated by gaining higher task achievement than American students were. This observation is consistent with the cultural valuation of achievement, which is notably higher for Chinese students compared to Western students (Tao & Hong, 2013). Integrating our findings and the sociocultural brain perspective, culture plays a critical role in shaping one's sensitivity towards various motivational factors, which is closely tied to the functioning of the reward system.

In summary, extrinsic motivation is universally recognized for enhancing behavioural performance. This is likely due to the regulatory effect of extrinsic motivation on activity in the reward circuitry (e.g., striatum). Our study further clarifies that this effect is more pronounced in Chinese individuals compared to Dutch individuals during learning tasks, suggesting cultural variability in cognitive responses to extrinsic motivators. These results together support the idea that intrinsic motivation for learning may be culturally universal, while extrinsic motivation for learning is stronger for Chinese students than for Dutch students.

6.3 Limitations, Future Directions, and Implications

6.3.1 Limitations and Future Directions

One of the central findings of this thesis is that autonomy enhances learning by facilitating active predictions about upcoming information. While the current studies operationalized predictability and surprise through Shannon's information theory, future research could adopt more dynamic frameworks. For instance, incorporating models of stochasticity and volatility, as proposed by Piray and Daw (2024), may allow for a more nuanced understanding of how contextual uncertainty shapes the effect of choice on memory encoding. These computational approaches could be further complemented by neuroimaging methods such as fMRI and EEG to examine how brain activity is modulated by the interaction between autonomy and predictive processing during learning. Another potential approach would be to introduce specific emotional valence during the act of making active choices (Kaskan et al., 2022), allowing for a more precise examination of how the predictability of informational value interacts with active choice in shaping memory encoding.

Further analysis would offer deeper insights into the neural mechanisms underlying the effects observed in this thesis. For instance, future studies could implement advanced brain connectivity techniques such as BrainGNN (Li et al., 2021) to explore how autonomy shapes large-scale, dynamic brain networks. Incorporating such graph theory-based models may enable a more comprehensive understanding of how distributed neural systems interact during autonomous learning. Also, in **Chapter 4**, whole-brain analyses were conducted and reported in the supplementary materials. As expected, differences in brain activations were observed in motor control regions, including the parietal lobe and cerebellum. This pattern is likely a result of the task design. In the autonomy conditions, participants naturally engaged in more motor activity to explore, while in the no-autonomy condition, they may have exerted less effort in following the movement of the searchlight window with the joystick. Further analyses should incorporate kinematic move regressors to determine whether activity in these motor control regions can be effectively regressed out, allowing for better control of potential motor-related confounds.

In future research involving rewards, particularly when comparing cultural groups, it is important to assess how individuals value monetary incentives. The present study did not include questionnaires evaluating participants' cultural values or personal attitudes toward money, limiting our ability to interpret which specific cultural perspectives influenced learning motivation. To better understand the role of cultural norms and values in modulating motivational processes, future studies should incorporate such psychometric assessments as part of their design. Additionally, with the growing trend of large-scale population studies conducted via online platforms, it would be valuable to extend the study from **Chapter 5** online to gather data from a broader range of cultural groups, enabling a deeper investigation into how cultural norms specifically shape learning motivations.

6.3.2 Practical Implications

In the domain of education and learning, on one hand, our findings indicate that the benefits of choice for learning depend on the meaningfulness and manageability of the options. In educational settings, this suggests that when offering students choices, educators should ensure that options are not overwhelming or arbitrary. For instance, in educational settings, teachers should consider providing students with opportunities to structure their own study schedules. Allowing more autonomous study time may enhance learning and facilitate the reconsolidation of acquired knowledge. However, offering too many choices in class can lead to confusion and a sense of unpredictability, which may render students' decisions less meaningful and ultimately hinder their learning. Moreover, when students are given the autonomy to plan their studies, it is beneficial for teachers to first provide structured guidance or foundational information. This scaffolding enables students to form expectations about the material, promoting a greater sense of control and thereby supporting more effective learning. Crucially, learners must perceive that their selections have genuine consequences. In other words, frequent violations of their choices may undermine the motivational value of autonomy.

On the other hand, our results point to autonomy as a more stable and universally beneficial motivational force, whereas the effect of extrinsic rewards appears to be more context-dependent and variable. The influence of rewards may fluctuate based on individual valuation and environmental framing. In this light, while rewards should be implemented with caution, autonomy emerges as a more robust and reliable foundation for supporting learning. Thus, from an applied perspective, educators and caregivers are encouraged to prioritize the cultivation of autonomy, as its positive impact on engagement and memory encoding appears to be consistent and enduring. This principle can also be extended to parenting practices. For example, rather than using external incentives such as offering extra screen time to motivate children to complete their homework, parents might instead foster autonomy by allowing children to choose the book or subjects they want to focus on. Supporting such autonomy can promote intrinsic motivation and lead to more sustainable learning engagement. While this approach may require additional effort from parents in terms of guidance and structure, the long-term benefits to the child’s motivation and self-regulated learning are likely to be more meaningful and enduring.

Extending beyond the field of education and learning, our findings also offer insights into workplace motivation and strategies for promoting sustainable work practices. With the rise of remote and flexible working arrangements, providing employees with greater autonomy—such as allowing them to structure their own schedules—may enhance productivity and motivation. However, this approach warrants further investigation, particularly regarding how flexibility interacts with external incentives in professional contexts. Moreover, cultural differences must be taken into account, as our results suggest that the interplay between autonomy and rewards may vary significantly across socio-cultural backgrounds.

6.4 Conclusion

The current thesis is structured around three key findings, based on two operationalizations of autonomy, respectively, binary choices and active exploration. First, we show that active choices enhance learning by facilitating predictive processing for upcoming information in **Chapters 2 and 3**. Second, in **Chapter 4**, while behavioural results indicate that autonomy and reward operate independently, neural data reveal a more nuanced interaction: autonomy elicited stronger activation in reward-related brain regions when no external reward was present, and greater engagement of attentional control regions when rewards were introduced. Third, in **Chapter 5**, although the effect of autonomy on learning was not influenced by cultural context, the motivational value of rewards was. Specifically, students from Eastern cultural backgrounds demonstrated greater sensitivity to reward-based motivation than those from Western backgrounds. Together, these findings offer a comprehensive account of the cognitive and neural mechanisms supporting autonomy during learning, framed within an ecological psychology perspective.

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Summary

Nederlandse samenvatting

Al op jonge leeftijd, toen ik traditionele Chinese dans leerde, was ik gefascineerd door het feit dat ik alleen plezier beleefde aan het leren van de dansstukken die ik zelf had gekozen. Wanneer een dans was toegewezen voor een wedstrijd of examen, verloor ik mijn interesse. Nu, jaren nadat ik ben gestopt met dansen, herinner ik me nog steeds levendig de choreografie van het stuk dat ik zelf had gekozen om te leren. Dit illustreert de blijvende kracht van autonomie – het zelf reguleren van je eigen handelingen en ervaringen – in het leerproces. Zoals Carl Rogers ooit zei: “The only kind of learning which significantly influences behaviour is self-discovered, self-appropriated learning.” Deze uitspraak onderstreept de centrale rol van autonomie in leren en onderwijs. Toch is er verrassend weinig bekend over de cognitieve en neurale mechanismen die ten grondslag liggen aan de voordelen van autonomie bij geheugenopslag en leren. Mijn proefschrift heeft als doel om te onderzoeken hoe het gevoel van autonomie het coderen van informatie in het geheugen beïnvloedt, in samenhang met andere omgevingsfactoren die mensen omringen, met een focus op zowel cognitieve als neurale processen.

Om deze onderzoeksvraag te beantwoorden, heb ik een ecologisch psychologisch perspectief aangenomen om te betogen dat het begrijpen van de interactie tussen autonomie en andere modulerende factoren – variërend van interne mechanismen tot micro- en macro-omgevingsinvloeden – ons inzicht in hoe autonomie leren ondersteunt, kan verdiepen. Ik richt me specifiek op drie niveaus: (1) interne predictieve verwerking van aankomende informatie, die nauw samenhangt met welke kennis in het geheugen wordt opgeslagen; (2) het micro-omgevingsniveau, waaronder externe beloningen zoals geld of cijfers vallen die bedoeld zijn om leren te stimuleren; en (3) het macro-omgevingsniveau, dat bredere sociaal-culturele normen vertegenwoordigt die de motivatie en leertradities van mensen vormgeven.

In de hoofdstukken 2 en 3 onderzocht ik de interactie tussen autonomie en predictieve verwerking bij geheugenopslag. Wanneer mensen de mogelijkheid krijgen om te kiezen, verbeteren hun leerresultaten doorgaans. Toch zijn de onderliggende cognitieve mechanismen van dit effect zelden onderzocht. In Hoofdstuk 2 voerde ik twee experimenten uit met een geheugentaak waarin keuzevrijheid en voorspelbaarheid onafhankelijk van elkaar werden gemanipuleerd. In de helft van de blokken konden deelnemers kiezen welk object ze wilden zien (keuze), terwijl in de andere helft de selectie voor hen werd gemaakt (geen keuze). Daarnaast was in de helft van de blokken het getoonde object altijd het gekozen object (hoge voorspelbaarheid), terwijl in de overige blokken slechts 50% kans bestond dat het gekozen object werd getoond (lage voorspelbaarheid). Geheugen werd vervolgens getest met een herkenningstaak. De resultaten lieten zien dat keuze het geheugen verbeterde onder zowel hoge als lage voorspelbaarheid, hoewel het effect kleiner was bij lage voorspelbaarheid. Deze bevindingen suggereren dat keuze leren bevordert door zowel intrinsiek belonend te zijn als door predictieve verwerking te ondersteunen.

Al snel realiseerden we ons echter dat de manipulatie van voorspelbaarheid in Hoofdstuk 2 zowel entropie als verrassing beïnvloedde in de informatiecontext, zoals gedefinieerd in de informatietheorie. Hierdoor konden we niet bepalen of het verminderde keuze-effect werd veroorzaakt door verminderde entropie of door verhoogde verrassing. In Hoofdstuk 3 ontwikkelden we daarom een paradigma dat verrassing isoleerde, terwijl entropie constant werd gehouden. Deelnemers voerden opnieuw een geheugentaak uit, met dezelfde autonomie-manipulatie als in Hoofdstuk 2. De resultaten toonden aan dat autonomie het geheugen alleen verbeterde wanneer de uitkomsten consistent waren met de verwachtingen van de deelnemers; wanneer uitkomsten verrassend waren, verdween het voordeel van keuze. Samen suggereren Hoofdstuk 2 en 3 dat predictieve verwerking samenwerkt met autonomie om geheugenopslag te ondersteunen: keuze vergemakkelijkt voorspellingen, en voorspellingen versterken het leren wanneer ze worden bevestigd.

In Hoofdstukken 4 en 5 richtte ik me op het micro-omgevingsniveau, specifiek op de interactie tussen autonomie en extrinsieke motivatie, zoals geldelijke beloning. In Hoofdstuk 4 voerde ik een studie uit met gedrags- en fMRI-gegevens van 47 deelnemers die een exploratieve leertaken uitvoerden. Deelnemers bekeken gedeeltelijk verhulde beelden die ze later moesten onthouden. Zowel autonomie (vrijheid om het exploratiepad te bepalen) als beloning (wel of geen geldelijke prikkel) werden onafhankelijk van elkaar gemanipuleerd. De resultaten toonden aan dat zowel autonomie als beloning het geheugen onafhankelijk van elkaar verbeterden. Cruciaal was dat alleen autonomie verhoogde activiteit veroorzaakte in beloningsgerelateerde hersengebieden tijdens het leren, terwijl de beloningsmanipulatie geen invloed had op hersenactiviteit. Dit suggereert dat autonomie een krachtigere motivator is dan externe beloningen. Bovendien bleek uit exploratieve functionele connectiviteitsanalyses dat autonomie gepaard ging met verhoogde connectiviteit tussen de hippocampus en aandachtsregio's, terwijl passief leren leidde tot meer connectiviteit met lagere perceptuele gebieden. Deze bevindingen benadrukken de verschillende neurale mechanismen van intrinsieke versus extrinsieke motivatie en geven waardevolle inzichten voor het ontwerpen van effectieve leeromgevingen.

Tot slot onderzocht ik in Hoofdstuk 5 het macro-omgevingsniveau door middel van een crossculturele studie met studenten van Nederlandse en Chinese universiteiten. Met hetzelfde paradigma als in Hoofdstuk 4 onderzocht ik of sociaal-culturele context de invloed van autonomie en beloning op leren modereert. De resultaten lieten zien dat beide cultuurgroepen baat hadden bij autonomie in het leerproces, wat suggereert dat het positieve effect van autonomie universeel is. De effecten van beloning daarentegen verschilden: Chinese deelnemers lieten een sterker geheugenvoordeel zien van beloning dan Nederlandse deelnemers. Deze bevindingen onderstrepen het belang van sociaal-culturele context in hoe mensen reageren op motivatie en pleiten voor meer aandacht voor culturele diversiteit in onderwijsonderzoek.

Deze dissertatie presenteert vier empirische studies die systematisch de cognitieve en neurale mechanismen onderzoeken waarmee autonomie het leren en geheugen versterkt. Gebaseerd op een ecologisch psychologisch kader onderzocht ik hoe interne voorspellende processen, micro-omgevingsfactoren en sociaal-culturele invloeden samen met autonomie de leerresultaten beïnvloeden. Over verschillende operationalisaties van autonomie – binaire keuzes en actieve exploratie – laten de resultaten consequent zien dat: (1) autonomie leren bevordert via voorspellende verwerking (Hoofdstukken 2 en 3); (2) autonomie beloningsgerelateerde hersengebieden actiever maakt dan geldelijke prikkels (Hoofdstuk 4); en (3) culturele achtergrond de effectiviteit van externe beloningen beïnvloedt, maar niet die van autonomie (Hoofdstuk 5). Samen dragen deze bevindingen bij aan een genuanceerder begrip van motivatie in leren en onderstrepen ze dat autonomie, als intrinsieke motivatie, een stabiel en krachtig effect heeft op geheugenopslag. In praktische zin pleiten deze resultaten voor onderwijsmethoden die studenten meer autonomie geven in hun leerproces, omdat dit kan leiden tot dieper en langduriger leren.

English summary

Even as a child learning traditional Chinese dance, I was fascinated by how I only enjoyed learning the pieces I chose myself. When a dance was assigned for a competition or exam, I would lose interest. Today, years after I stopped dancing, I still vividly remember the choreography of the one piece I chose to learn, demonstrating the lasting power of autonomy, the self-regulation of one's actions and experiences, in learning. As Carl Rogers famously said, "*The only kind of learning which significantly influences behaviour is self-discovered, self-appropriated learning.*" This sentiment captures the central role of autonomy in learning and education. However, surprisingly little is known about the cognitive and neural mechanisms underlying the benefits of autonomy in memory encoding and learning. My dissertation aims to investigate how the sense of autonomy influences memory encoding, in conjunction with other environmental factors that surround individuals, focusing on both cognitive and neural mechanisms.

To address this research question, I adopted the perspective of ecological psychology to argue that understanding the interaction between autonomy and other modulating factors, spanning from internal mechanisms to micro- and macro-level environmental influences, can deepen our understanding of how autonomy supports learning. Specifically, I focused on three levels: (1) internal predictive processing of upcoming information, which is closely tied to what knowledge will be encoded into memory; (2) the micro-environmental level, which includes external rewards such as money or grades that are designed to encourage learning; and (3) the macro-environment, representing broader socio-cultural norms that shape motivational priorities and learning traditions.

To begin with, **Chapters 2 and 3** examined the interaction between autonomy and predictive processing in memory encoding. When individuals are offered the opportunity to choose, learning outcomes typically improve. Yet, the underlying cognitive mechanisms of this effect have been rarely studied. In **Chapter 2**, I conducted two experiments using a memory encoding task that independently manipulated choice and predictability of the choice outcomes. In half of the blocks, participants could choose which object to view (choice), while in the other half, selections were made for them (no choice). Additionally, in half of the blocks (both choice and no-choice), the image participants saw was always the one selected (high predictability), while in the remaining blocks, there was only a 50% chance of seeing the selected object (low predictability). Memory was then tested with a recognition task. Results showed that choice enhanced memory under both high and low predictability conditions, though the effect was smaller when predictability was low. These findings suggest that choice benefits learning both by being intrinsically rewarding and by supporting predictive processing.

However, we soon realized that the manipulation of predictability in **Chapter 2** affected both entropy and surprise in the informational context, as defined by information theory. This made it difficult to determine whether the diminished choice effect in low-predictability blocks was due to reduced entropy or to induced surprise when information was encountered. **Chapter 3** addressed this by designing a paradigm that isolated surprise while holding entropy constant. Participants again performed a memory encoding task, with autonomy manipulated as in **Chapter 2**. Results revealed that autonomy enhanced memory only when the outcomes were consistent with participants' expectations; when outcomes were surprising, the benefit of choice disappeared. Together, **Chapters 2 and 3** suggest that predictive processing interacts with autonomy to support memory encoding: choice may facilitate prediction, and predictions, in turn, strengthen learning when they are confirmed.

In **Chapters 4 and 5**, I turned to the micro-environmental level, specifically examining how autonomy interacts with extrinsic motivators such as monetary rewards. In **Chapter 1**, I conducted a study using behavioural and functional magnetic resonance imaging (fMRI) data from 47 participants who performed an exploratory learning task. Participants viewed partially obscured images they needed to remember, with both autonomy (volitional control over exploration) and reward (presence or absence of monetary incentives) independently manipulated. Results showed that both autonomy and reward independently enhanced memory performance. Crucially, only autonomy elicited increased activation in reward-related brain regions during memory encoding, while the reward manipulation did not affect activation of the brain. This suggests that autonomy may be a more salient motivator than external rewards. Additionally, exploratory functional connectivity analyses revealed that autonomy was associated with increased connectivity between the hippocampus and attentional control regions, while passive learning was linked to greater connectivity with lower-level perceptual regions. These findings highlight distinct neural mechanisms underlying intrinsic and extrinsic motivation and provide valuable insights for designing effective educational environments that combine these motivational factors.

Finally, in **Chapter 5**, I investigated the macro-environmental level by conducting a cross-cultural study comparing results yielded from students in Dutch and Chinese universities. Using the same paradigm as in **Chapter 4**, I examined whether socio-cultural context modulates the influence of autonomy and reward on learning. Results showed that both cultural groups benefited from autonomy to learn more efficiently, indicating that its positive impact on learning is universal. However, the effect of rewards differed: Chinese participants showed stronger reward-based memory enhancement than Dutch participants. These findings underscore the importance of socio-cultural context in shaping how individuals respond to motivational factors and call for greater attention to cultural diversity in educational research.

Altogether, this thesis presents four empirical projects that systematically investigate the cognitive and neural mechanisms by which autonomy enhances learning and memory. Drawing on an ecological psychology framework, I examined how internal predictive processes, micro-environmental motivators, and socio-cultural factors interact with autonomy to influence learning outcomes. Across different operationalizations of autonomy—binary choices and active exploration—the findings consistently show that: (1) autonomy enhances learning through predictive processing (**Chapters 2 and 3**); (2) autonomy activates reward-related brain regions more reliably than monetary incentives (**Chapter 4**); and (3) cultural background influences the effectiveness of external rewards but not of autonomy (**Chapter 5**). Together, these findings contribute to a more nuanced understanding of motivation in learning and emphasize that autonomy, an intrinsic motivator, has a stable and powerful effect on memory encoding. In practical terms, these results advocate for educational practices that empower students with more autonomy in their learning process, as doing so may foster deeper and longer-lasting learning.

Research data management

This research followed the applicable laws and ethical guidelines. Research data management was conducted according to the FAIR principles. The paragraphs below specify in detail how this was achieved.

Ethics

This thesis is based on the results of human studies, which were conducted in accordance with the principles of the Declaration of Helsinki. The experiments conducted in Chapter 2 was approved by the Ethics Committee of the Faculty of Social Sciences (ECSW) at Radboud University, Nijmegen, under the general ethics approval for standard studies conducted at the Donders Centre for Cognition (ECSW.2018.115). Chapters 3-5 included data collected at Donders Centre for Neuroimaging, Nijmegen, the Netherlands, which were approved by the local ethics committee (CMO Arnhem-Nijmegen, The Netherlands) under a general ethics approval protocol ("Imaging Human Cognition", CMO 2014/288) and were conducted in compliance with these guidelines. Chapter 5 included data collected in Beijing, China, which was approved by the ethics committee of Beijing Normal University (ICBIR_A_0071_017). Informed consent was obtained on paper following the Centre procedure. The forms are archived in the central archive of the Centre for 10 years after termination of the studies.

Data collection and privacy

During this PhD trajectory, data collection was performed at the Doners Centre for Cognitive Neuroimaging (behavioural data and fMRI data), the Donders Centre for Cognition, and Beijing Normal University in China. A unique participant code was created for each participant, warranting the privacy of the participants. The code and data are stored separately.

Data storage

The table below details where the data and research documentation for each chapter can be found on the Radboud Repository.

Chapter	DAC	RDC	DSC
2	di.dcc.DAC_2025.00058_980	di.dcc.RDC_2025.00058_053	di.dcc.DSC_2023.00164_093
3	di.dccn.DAC_3018082.01_365		
4	di.dcc.DAC_2024.00007_065	di.dcc.RDC_2024.00152_683	
5	di.dcc.DAC_2023.00152_046	di.dcc.RDC_2023.00152_377	https://doi.org/10.34973/tccj-j019

Interoperable, Reusable

The raw data are stored in the DAC in their original form. For RDC and DSC long-lived file formats (e.g., .csv, .tif) have been used ensuring that data remains usable in the future. Results are reproducible by the provision of the descriptions of the experimental setup, raw data and analysis scripts or pipelines.

The data will be saved for 10 years after termination of the studies (2025).

Supplements

About the author

Zhaoqi Zhang (张兆祺), known as Claire in the Netherlands, was born and raised in Harbin, a city in northeastern China, famously nicknamed the “City of Ice.” It was during her second year of high school that she made a bold decision to dive deep into the science of the human mind, psychology.

Her determination paid off when she was accepted into the most prestigious undergraduate psychology program in China at Beijing Normal University (BNU). There, she got her first taste of research, working with Dr. Gonggu Yan on psychometrics. But the more she learned about the human mind, the more curious she became about the mechanism of these complex thoughts and ideas, so began her journey into cognitive neuroscience.

Claire pursued her Master’s at the State Key Laboratory of Cognitive Neuroscience and Learning at BNU, joining prof. dr. Taomei Guo’s lab to study bilingualism and psycholinguistics. A chance encounter with prof. dr. Harold Bekkering during his first visit to BNU in 2018 sparked a new opportunity.

In the middle of the COVID pandemic, Claire remotely joined Harold’s lab in Nijmegen, and soon after teamed up with dr. Lieke van Lieshout to co-develop a grant proposal on autonomy in learning. With this successful proposal, she secured a four-year doctoral fellowship funded by the China Scholarship Council, allowing her to move to the Netherlands and start her PhD trajectory at the Donders Institute for Brain, Cognition, and Behaviour.

Throughout her PhD, Claire fully immersed herself in research, focusing on how autonomy and prediction influence learning and memory. Given the central role of predictive processing in her work, she later joined the Predictive Brain Lab, where she was then supervised by prof. dr. Floris de Lange and collaborated closely with dr. Olympia Colizoli as co-supervisor, who provided valuable methodological guidance and expertise in neuroimaging. Beyond her research in the Netherlands, Claire was also committed to fostering international collaboration. She initiated a cross-cultural comparison project with prof. dr. Shaozheng Qin at Beijing Normal University, further strengthening academic ties between the Donders Institute and one of China’s leading institutions in psychology and education research.

Claire is now continuing her scientific journey as a postdoctoral researcher at Donders Institute.

List of Publications

Zhang, Z., Colizoli, O., van Lieshout, L., Bekkering, H., de Lange, F. (in prep). Surprise modulates the beneficial effect of choice in memory encoding.

Zhang, Z., van Lieshout, L., Yang, T., Li, B., Liu, C., Colizoli, O., Qin, Q., Bekkering, H. (in prep). Cultural differences in neural mechanisms underlying intrinsic and extrinsic motivation for learning.

Zhang, Z., van Lieshout, L., Bekkering, H. (accepted). Autonomy in learning: Predictability modulates the effect of choice on learning.

van Lieshout, L. L., **Zhang, Z.**, Friston, K. J., & Bekkering, H. (2025). Predictive processing: Shedding light on the computational processes underlying motivated behavior. *Behavioral and Brain Sciences*, *48*, e46.

Zhang, Z., van Lieshout, L. L., Colizoli, O., Li, H., Yang, T., Liu, C., Qin, S., & Bekkering, H. (2025). A cross-cultural comparison of intrinsic and extrinsic motivational drives for learning. *Cognitive, Affective, & Behavioral Neuroscience*, *25*(1), 25-44.

Zhang, Z.*, Ma, F.*, & Guo, T. (2023). Proactive and reactive language control in bilingual language production revealed by decoding sustained potentials and electroencephalography oscillations. *Human Brain Mapping*, *44*(15), 5065–5078.

Dang, Q., Ma, F., Yuan, Q., Fu, Y., Chen, K., **Zhang, Z.**, Lu, C., & Guo, T. (2023). Processing negative emotion in two languages of bilinguals: Accommodation and assimilation of the neural pathways based on a meta-analysis. *Cerebral Cortex*, bhad121.

Wu, Y. J., Dang, Q., **Zhang, Z.**, Zhang, H., & Guo, T. (2023). Multivariate decoding methods reveal how speaking two dialects affects executive functions. *European Journal of Neuroscience*, *57*(5), 840-853.

Yuan, Q., Li, H., Du, B., Dang, Q., Chang, Q., **Zhang, Z.**, Zhang, M., Ding, G., Lu, C., & Guo, T. (2023). The cerebellum and cognition: further evidence for its role in language control. *Cerebral Cortex*, *33*(1), 35-49.

Zinszer, B. D., Yuan, Q., **Zhang, Z**., Chandrasekaran, B., & Guo, T. (2022). Continuous speech tracking in bilinguals reflects adaptation to both language and noise. *Brain and language*, *230*, 105128.

Wu, J., Zhang, M., Dang, Q., Chang, Q., Yuan, Q., **Zhang, Z.**, Ding, G., Lu, C., & Guo, T. (2022). Nonverbal cognitive control training increases the efficiency of frontal-subcortical collaboration for bilingual language control. *Neuropsychologia*, *169*, 108204.

Zhang, Z., Yuan, Q., Liu, Z., Zhang, M., Wu, J., Lu, C., Ding, G., & Guo, T. (2021). The cortical organization of writing sequence: evidence from observing Chinese characters in motion. *Brain Structure and Function, 226,* 1627–1639.

Chen, M., Ma, F., **Zhang, Z.** , Li, S., Zhang, M., Yuan, Q., Wu, J., Lu, C., Guo, T. (2021). Language switching training modulates the neural network of non-linguistic cognitive control. *PLoS One 16*(4), e0247100.

Yuan, Q., Wu, J., Zhang, M., **Zhang, Z.**, Chen, M., Ding, G., Lu, C., & Guo, T. (2021). Patterns and networks of language control in bilingual language production. *Brain Structure and Function*, *226*, 963-977.

Yuan, Q., Ma, F., Zhang, M., Chen, M., **Zhang, Z.**, Wu, J., Lu, C., & Guo, T. (2021). Neural interaction between language control and cognitive control: Evidence from cross-task adaptation. *Behavioural Brain Research*, *401*, 113086.

Wu, J., **Zhang, Z.**, Chen, M., Yuan, Q., Zhang, M., Yang, J., Lu, C., & Guo, T. (2020). Language context tunes brain network for language control in bilingual language production. *Neuropsychologia*, *147*, 107592.

Chen, M., Ma, F., Wu, J., Li, S., **Zhang, Z.,** Fu, Y., Lu, C., & Guo, T. (2020). Individual differences in language proficiency shape the neural plasticity of language control in bilingual language production. *Journal of Neurolinguistics*, *54*, 100887.

Wu, J., Yang, J., Chen, M., Li, S., **Zhang, Z.**, Kang, C., Ding, G., & Guo, T. (2019). Brain network reconfiguration for language and domain-general cognitive control in bilinguals. *NeuroImage*, *199*, 454-465.

PhD Portfolio

Name PhD candidate: Zhaoqi Zhang
Graduate School: Donders Graduate School
PhD period: 01-09-2021 – 31-08-2025
Supervisors: Floris de Lange, Harold Bekkering, Lieke van Lieshout, Olympia Colizoli

Course & Workshops

Course	*Organizer*	*Hours*
Graduate School Introduction Day (2021)	Donders Graduate School	7
Project Management for PhD Candidates (2021)	Radboud University	52
Programming with presentation (2022)	Donders Centre for Neuroimaging	20
Linear Mixed Effect Modelling (2022)	Faculty of Arts	56
Effective Writing Strategies (2022)	Radboud University	75
Design and Illustration (2022)	Radboud University	26
Writing and Argumentation for Academic Papers (2022)	Radboud University	84
Graduate School Day (2023)	Donders Graduate School	7
Analysing Longitudinal and Multilevel Data Using R (2023)	Radboud University	96
Scientific Integrity Course (2024)	Donders Graduate School	7
Career Guidance for International PhDs (2024)	Radboud University	20
Digital Tools (2024)	Radboud University	4
Art of Finishing Up (2025)	Radboud University	10
Analytic Storytelling (2025)	Radboud University	20
Science Journalism and Communication (2025)	Radboud University	40
Getting Ready for Your First Grant Application (2025)	Radboud University	32

Conferences & Summerschools

Course	*Location*
NvP Winter Conference (2022)	Egmond aan Zee, the Netherlands
NvP Winter Conference (2023)	Egmond aan Zee, the Netherlands
CAOS (2024)	Rovereto, Italy
Neuro-AI Summer School (2024)	Amsterdam, the Netherlands
Information Theory Workshop (2024)	Amsterdam, the Netherlands
Donders Discussion (2024)	Nijmegen, the Netherlands
Foraging Conference (2024)	Lyon, France

Teaching activities

Internship supervision	*Study program*	*Hours*
Parker Winkel (2022)	Bachelor Psychology	4 months
Markéta Mičková (2022)	Bachelor Psychology	4 months
Natasza Adamus (2025)	Master Cognitive Neuroscience	8 months
Mingyao Sun (2025)	Master Cognitive Neuroscience	8 months

Teaching Activity	*Study Program*
Brain and Cognition: I (2022)	Bachelor Psychology

Committees

Member of Education Committee, PhD Organization Nijmegen (PON, 2022-2023)

Outreach & Societal Impact

Organizer of Pint of Science, Nijmegen (2023)

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Donders Graduate School

For a successful research Institute, it is vital to train the next generation of scientists. To achieve this goal, the Donders Institute for Brain, Cognition and Behaviour established the Donders Graduate School in 2009. The mission of the Donders Graduate School is to guide our graduates to become skilled academics who are equipped for a wide range of professions. To achieve this, we do our utmost to ensure that our PhD candidates receive support and supervision of the highest quality.

Since 2009, the Donders Graduate School has grown into a vibrant community of highly talented national and international PhD candidates, with over 500 PhD candidates enrolled. Their backgrounds cover a wide range of disciplines, from physics to psychology, medicine to psycholinguistics, and biology to artificial intelligence. Similarly, their interdisciplinary research covers genetic, molecular, and cellular processes at one end and computational, system-level neuroscience with cognitive and behavioural analysis at the other end. We ask all PhD candidates within the Donders Graduate School to publish their PhD thesis in de Donders Thesis Series. This series currently includes over 600 PhD theses from our PhD graduates and thereby provides a comprehensive overview of the diverse types of research performed at the Donders Institute. A complete overview of the Donders Thesis Series can be found on our website: https://www.ru.nl/donders/donders-series

The Donders Graduate School tracks the careers of our PhD graduates carefully. In general, the PhD graduates end up at high-quality positions in different sectors, for a complete overview see https://www.ru.nl/donders/destination-our-former-phd. A large proportion of our PhD alumni continue in academia (>50%). Most of them first work as a postdoc before growing into more senior research positions. They work at top institutes worldwide, such as University of Oxford, University of Cambridge, Stanford University, Princeton University, UCL London, MPI Leipzig, Karolinska Institute, UC Berkeley, EPFL Lausanne, and many others. In addition, a large group of PhD graduates continue in clinical positions, sometimes combining it with academic research. Clinical positions can be divided into medical doctors, for instance, in genetics, geriatrics, psychiatry, or neurology, and in psychologists, for instance as healthcare psychologist, clinical neuropsychologist, or clinical psychologist. Furthermore, there are PhD graduates who continue to work as researchers outside academia, for instance at non-profit or government organizations, or in pharmaceutical companies. There are also PhD graduates who work in education, such as teachers in high school, or as lecturers in higher education. Others continue in a wide range of positions, such as policy advisors, project managers, consultants, data scientists, web- or software developers, business owners, regulatory affairs specialists, engineers, managers, or IT architects. As such, the career paths of Donders PhD graduates span a broad range of sectors and professions, but the common factor is that they almost all have become successful professionals.

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