

NATIONAL RESEARCH UNIVERSITY HIGHER SCHOOL OF ECONOMICS

As a manuscript

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**An investigation into the modulation of learning processes by social context via
neuroimaging, computational modeling, and meta-analysis**

Dissertation Summary

for the purpose of obtaining academic degree

Doctor of Philosophy in Psychology

Academic supervisor:

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This dissertation was prepared at the Institute of Cognitive Neuroscience, National Research University Higher School of Economics. Three published articles were the studies selected for the defense:

1. Martinez-Saito, M., Konovalov, R., Piradov, M. A., Shestakova, A., Gutkin, B., & Klucharev, V. (2019). Action in auctions: neural and computational mechanisms of bidding behaviour. *European Journal of Neuroscience*, 50(8), 3327-3348
2. Martinez-Saito, M., Andraszewicz, S., Klucharev, V., & Rieskamp, J. (2022) Mine or Ours? Neural Basis of the Exploitation of Common-Pool Resources. *Social Cognitive and Affective Neuroscience*, 17(9):837-849
3. Martinez-Saito M, Gorina E (2022) Learning under social versus nonsocial uncertainty: A meta-analytic approach. *Human Brain Mapping*, 43(13), 4185-4206

1. Introduction

1.1 Research problem

Most decisions, such as saying what you think to a colleague or keeping it to yourself, or investing your savings in biotech stocks or real state, are fraught with uncertainty that is compounded by social factors. Understanding to what extent learning in social contexts is a specialized function is important not only because we could expedite adaptation to different social contexts, but also because this would shed light on the source of cognitive biases, many of which are grounded on social preferences.

The relevance of social cognition in evolution makes plausible that specialized mechanisms that compute learning signals under uncertainty of exclusively social origin operate in the brain. In this investigation, I inquire into whether there are learning mechanisms specialized in resolving uncertainty of exclusively social origin, while examining two illustrative examples that are fundamental to social neuroscience and behavioral economics: bargaining in auctions and consumption of common-pool resources.

1.2 Dissertation objectives

- 1 To study the neurocognitive mechanisms of learning during competitive (bidding) decisions;
- 2 To elucidate the functional and computational mechanisms underlying competitive decisions leading to exploitation behavior when facing scarce resources in social and non-social environments;
- 3 To investigate to what extent are learning what extent learning in social contexts is a specialized function with an anatomical and/or computational specialization, and if so, to determine their anatomic localization.

1.3 Theoretical and methodological basis

Theoretical basis

Adaptive behavior rests on appropriately assigning value to states and actions (Gold & Shadlen, 2007), which requires an elaborate internal representation of the world that includes conspecifics. Mapping internal states and their values to actions is in general an intractable task compounded by the need to predict the behavior of others (Frith & Frith, 2012; Yoshida et al., 2008). It is plausible that humans evolved specific mechanisms to approach the problem of efficiently deriving reliable values from social interactions (Fletcher & Carruthers, 2012). In this dissertation, I attempt to elucidate such value learning mechanisms in social contexts.

The studies included in this dissertation throw light on how generic learning processes are deployed and set up for specific complex situations that are not amenable to working out optimal choice or action policies.

In Study I, I show, that the learning heuristic based on a binary learning signal distinct from the conventional reward prediction error (RPE) signal furnishes a solution to the problem of repeated bidding in double auctions, which are competitive, dynamic, complex decisions (Martinez-Saito et al., 2019). Study II demonstrates, that the social context (a shared resource vs a private resource) modulates the neural signatures of the learning signal in the ventral striatum. This modulation by social factors expedites the development of efficient policies and a better understanding of global commons governance. In Study III, I verify whether learning and reward signals in social contexts generated by specialized, domain-general, or overlapping circuits.

Methodology

I used functional magnetic resonance imaging (fMRI), computational modeling of behavior and neuromagnetic signals, and meta-analysis of fMRI studies found in academic databases.

Image analysis for both Study I and II was performed with SPM12 (Friston et al., 1994). Images were realigned to the first image. Images were then corrected for differences in slice acquisition time, spatially normalized to the Montreal Neurological Institute (MNI) T1 template, resampled to $3 \times 3 \times 3$ mm³ voxels, and spatially smoothed with a Gaussian kernel of 8 mm full-width at half-maximum. Data were high-pass filtered, with cutoff at 1/128 Hz (Martinez-Saito et al., 2022). Separate regressors were constructed for each predictor of interest, and orthogonalized predictors where appropriate.

In Study I, six learning algorithms were implemented, fitted, compared and simulated. I compared different computational learning models of bidding: directional learning models (DL), where the model bid is “nudged” depending on whether it was accepted or rejected, along with standard reinforcement learning models (RL). The important parameters were the learning rate (a measure of how much weight was given to recent feedback with respect to older feedback) and the randomness of choice, embodied in the inverse temperature of the softmax function (a measure of degree of action selection randomness) for RL algorithms, and in the dispersion parameters for DL algorithms. In an fMRI analysis devoted to analysing the relationship between RPE and DL prediction error signals, two general linear model (GLM) regression matrices with three regressors each were constructed with the stimulus onset marker and the parametrically modulated regressors DL prediction error and RL prediction error orthogonalized one with respect to the other and vice versa, to disentangle their contributions to neural activity (Martinez-Saito et al., 2019).

In Study II, to explain the effect of the social and non-social contexts, I used variations of the reinforcement learning model (Sutton & Barto, 1998). I also tested these two learning models against another two competing models: a vanilla reinforcement learning model (Sutton & Barto, 1998) and a modified inequity aversion model (Fehr & Schmidt, 1999). I evaluated the learning algorithms by comparing them to the null (baseline) model, which assumed a uniformly random choice using the Bayesian Information Criterion (Schwarz, 1978) which is an approximation to model log-evidence that accounts for model complexity (Martinez-Saito et al., 2022).

Meta-analysis of fMRI studies allows to operationalize the question of whether the social aspect of value learning is functionally specialized enough to warrant functional segregation (Zeki & Shipp, 1988) within the neural substrates involved in general learning. In Study III, I accomplished a meta-analysis of fMRI studies with GingerALE 3.0.2 (Eickhoff et al., 2012), which implements the activation likelihood estimation method (ALE), a type of coordinate-based meta-analysis which uses solely coordinates of cluster peaks in statistical parametric maps. This is the most widely used approach for fMRI data meta-analysis (Samartsidis et al., 2017). ALE has shortfalls: it discards most of the full statistical image information. This can be partly alleviated by accounting for both activations and deactivations so that contradictory findings cancel each other (Radua & Mataix-Cols, 2009), and through the use of the peak t-statistics to estimate effect sizes, thus enabling random and fixed effects modeling, which increases reliability and accuracy (Bossier et al., 2018). These two features, together with subject-based permutation test to control FWER, feature in the algorithm Seed-based d-Mapping with Permutation of Subject Images (SDM-PSI; Albajes-Eizagirre, Solanes, Vieta, & Radua, 2019). Thus, in Study III, I also employed SDM-PSI to probe the robustness of ALE results.

1.4 Scientific novelty

In Study I, we studied the decision making mechanism in double auctions. Perceived market competition influences human bidding (van den Bos et al., 2008) and even the value of commodities traded by non-human animals. biological auctions are used to model competition between species and individuals (Reiter et al., 2015). Despite its key importance in social behavior and financial modeling, the neural mechanisms of decision-making under market competition are still unclear. In particular, how do we learn bidding strategies across different market scenarios? Here, we investigate the neural mechanisms underlying bidding under different conditions of competition (Martinez-Saito et al., 2019). Previous neuroimaging studies investigated bargaining games, but focused on strategic deception and uncertainty about trustworthiness (Bhatt et al., 2010) or examined the influence of loss contemplation under social contexts in overbidding (Delgado et al., 2008). In Study I, for the first time, we investigated the neural mechanism of bidding behaviour under different conditions of competition (Martinez-Saito et al., 2019).

In Study II, we hypothesized that the brain dopaminergic system, a set of brain areas involved in reward and performance monitoring, not only continuously monitors our own outcomes (Osten et al., 2017) during interactions but also monitors the outcomes of others. According to economic theory, non-excludable goods that anyone can enter and/or harvest are likely to be overharvested and destroyed (Martinez-Saito et al., 2022). However, behavioral economics also gives many examples in which people behave fairly and cooperatively contrary to the standard self-interest model (Fehr and Schmidt, 1999): under some conditions, in particular in two-person interactions, people often show high rates of cooperation (Fehr & Gächter, 2000). It has been shown that overharvesting is particularly prevalent in social groups containing a substantial number of ‘free riders’, that is, people who take benefits

without paying any costs (Camerer, 2003). One explanation for the tendency to overharvest common-pool resources refers to people's social preference for equity and reciprocal cooperation (Fehr & Schmidt, 1999): if others are cooperative, then people act cooperatively, but if others free ride, people correspondingly retaliate (Martinez-Saito et al., 2022). To find a computational explanation for resource depletion, we developed a computational model that posits a reward prediction error that compares a person's own outcome with the harvesting behavior of conspecifics. Therefore, we conducted the first fMRI study of competitive decisions in common-pool resource (CPR) dilemma. We hypothesize that the social comparison is encoded in the neural learning signal that facilitates overharvesting of the common natural resources (Martinez-Saito et al., 2022).

In Study III, we explored whether, mechanisms that compute learning signals under uncertainty of exclusively social origin operate in the brain. To test this hypothesis, we conducted the first meta-analysis of brain activation maps that compared learning in the face of social versus nonsocial uncertainty.

Theoretical novelty

I devised a heuristic algorithm (directional learning or DL) to describe bargaining behavior in double auction. DL was validated, both on behavioral and neural activity grounds, for double auctions set in markets with different levels of competition in Study I and in another set of experiments pertaining to another, unpublished, article (Martinez-Saito et al., 2020).

We also devised learning algorithms for the social and non-social conditions of Study II. These algorithms enacted exploitation of scarce resources in social and non-social contexts, respectively. The relevance of these two algorithms is propped up by

model fits to behavior, by the neural activity in learning regions associated with the proxy variables derived from the fitted models, and by model recovery analyses.

Practical significance

In the neuroimaging studies (Study I and II), computational models were fit through a conventional maximum likelihood procedure; however, this procedure was enhanced by running multiple optimizer subroutines, which increased the chances of finding better parameter fits. In regard to the behavioral paradigms, for the first time, we applied a double action bidding game and common-pool resource dilemma in model-based neuroimaging studies (Study I and II).

A large number of previous studies examined factors that favor natural shared resources preservation, including the best possible rules, institutions and communication. Results of our Study II show that the context of a shared resource vs a private resource modulates the neural activity of the ventral striatum: relative deactivation of the ventral striatum in response to resource depletion correlates positively with participants' attempts to preserve their own private resources and correlates negatively with their attempts to preserve the natural shared resource. Overall, the notion of the neurobiological underpinnings of resource overexploitation could help us to develop efficient boundary rules and a better understanding of global commons governance (Martinez-Saito et al., 2022).

We conducted the first the meta-analysis (Study III), that specifically focused on specialized mechanisms that compute learning signals under uncertainty of exclusively social origin operate in the brain. In the meta-analysis (Study III), I used the popular neuroimaging coordinate-based meta-analysis software GingerALE (Eickhoff et al., 2012). On top of that, I performed the same meta-analysis with another —less popular, but newer and in theory more powerful— meta-analysis software called SDM-PSI

(Albajes-Eizagirre, Solanes, Fullana, Ioannidis, et al., 2019), which allowed us to compare their performance on the same dataset. Furthermore, our meta-analysis employed a carefully selected set of criteria for paper eligibility that enabled examining whether areas in the brain exist that are functionally specialized to deal only with the effect of social uncertainty on learning.

1.6 Provisions for the defense: key ideas to be defended

- 1 The neural circuitry involved in learning is mostly, but not entirely, generic or independent from the social quality of the learning context, such that social-specialized frontal modules may tweak and modulate the generic learning scheme;
- 2 When exploiting a scarce resource, the functional role of the striatum—a prominent subcortical region involved in learning—is modulated by the social implications of the learning context, i.e. by whether the resource is public or private;
- 3 In iterated game playing (auctions) requiring estimation of values (prices) determined by the interactive action of multiple conspecifics, humans deploy a policy that harnesses generic striatal learning areas modulated by the category of social context via a signal from the frontopolar cortex.

1.7 Author contributions

Study I: Data collection, computational modeling, data analysis and interpretation, manuscript draft and revision.

Study II: Data collection, computational modeling, data analyses and interpretation, manuscript draft and revision.

Study III: Study conception and design, data collection, data analysis and interpretation, manuscript draft and revision.

1.8 Validation of the research

The dissertation was prepared at the Centre for Cognition and Decision Making, Institute of Cognitive Neuroscience, National Research University Higher School of Economics.

Peer-reviewed journals

The Ph.D. thesis consists of three studies that correspond to the following papers in first-tier journals¹:

- Study I (fMRI experiment): Martinez-Saito, M., Konovalov, R., Piradov, M. A., Shestakova, A., Gutkin, B., & Klucharev, V. (2019). Action in auctions: neural and computational mechanisms of bidding behaviour. *European Journal of Neuroscience*, 50(8), 3327-3348.
- Study II (fMRI experiment): Martinez-Saito, M., Andraszewicz, S., Klucharev, V., & Rieskamp, J. (2022) Mine or Ours? Neural Basis of the Exploitation of Common-Pool Resources. *Social Cognitive and Affective Neuroscience*, 17(9):837-849
- Study III (meta-analysis): Martinez-Saito M, Gorina E (2022) Learning under social versus nonsocial uncertainty: A meta-analytic approach. *Human Brain Mapping*

Conference presentations

The results were presented at the following conferences:

¹ First-tier publications include papers indexed in the Web of Science (Q1 or Q2) or Scopus (Q1 or Q2) databases, as well as peer-reviewed collections of conferences that appear in CORE rankings (ranks A and A*).

- 1 Society for Neuroeconomics (Sep 2015, Miami). Poster. The effect of economic competition on the neural mechanisms of decision-making. Martinez-Saito M, Gutkin B, Shestakova A, Klucharev V.
- 2 Society for Neuroscience (Oct 2015, Chicago). Poster. The effect of economic competition on the neural mechanisms of decision-making. Martinez-Saito M, Gutkin B, Shestakova A, Klucharev V.
- 3 Cognition, Computation, Communication and Perception (CCCP) Conference 2: “Theoretical and Neurobiological Bases of Higher Cognitive Functions” (Sep 2015, Moscow). The effect of economic competition on the neural mechanisms of decision-making. M. Martinez-Saito, A. Shestakova, V. Klucharev, B. Gutkin.
- 4 CCCP19: Russian-French Symposium on Neuroeconomics (Sep 2019, Moscow). Presentation. Neural Underpinnings of Exploitation of Common Goods. Martinez-Saito M, Shestakova A, Klucharev V.

2. Scientific content synopsis

In total, 79 participants took part in the fMRI experiments of Study I and Study II. All subjects were queried to exclude histories of neurological pathologies; none of the participants reported a history of drug abuse, head trauma, neurological or psychiatric illness. After a briefing, all subjects gave informed written consent; subjects were paid upon completion of the task. All protocols was performed in accordance with the Declaration of Helsinki with approval of the University Review Board of Higher School of Economics (Martinez-Saito et al., 2019). For Study III, I selected 50 neuroimaging studies, which included 28 social experiments and 31 non-social experiments, and that satisfied all eligibility criteria for the meta-analysis of Study III.

2.1 Study I. Neural and computational mechanisms of bidding behaviour

People often exchange goods at prices determined by fluctuations in supply and demand. Perceived market competition influences human bidding and even the value of commodities traded by non-human animals. Despite its key importance in social behaviour, the neural mechanisms of decision-making under social competition are still unclear (Martinez-Saito et al., 2019). In particular, how do we learn bidding strategies across different market scenarios? To probe neural mechanisms of bid learning, I used a modified version of the double auction, a standard paradigm in multiplayer game theory where players try to maximize their respective benefit by means of a single-shot transaction (Fudenberg & Tirole, 1991). Subjects played the role of buyers in a double auction with first-price sealed bids and with opponents assigned by repeated random matching, in three different market types. The game paradigm required buyers to fix their bids in advance (Martinez-Saito et al., 2019). Their task was to buy fish on a market using a 10-point Likert scale.

The scanned images were processed using SPM12 (Friston et al., 1994; Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK). The first

four EPI volumes were discarded to allow for T1 equilibration, and the remaining images were realigned to the first volume (Martinez-Saito et al., 2019). Preprocessing of T2*-weighted volumes consisted of rigid-body model realignment within each session to a mean volume for head-motion correction, unwarping of the residual variance using the field map, slice timing correction centred at TR/2, bias-field correction, coregistration of T2*-weighted volumes to the corresponding structural image and segmentation and spatial normalization to a standard T2*-weighted template (Montreal Neurological Institute, MNI) for group analysis, spatial smoothing with an 8 mm Gaussian kernel and high-pass temporal (128s) filtering (Martinez-Saito et al., 2019).

We compared different computational learning models of bidding: DL models, where the model bid is “nudged” depending on whether it was accepted or rejected, along with standard reinforcement learning models (Figure 1). In total, I implemented, fitted, tested and simulated six flavors learning algorithms, including model-free and model-based RL and DL algorithms, with ad hoc parameters (Martinez-Saito et al., 2019).

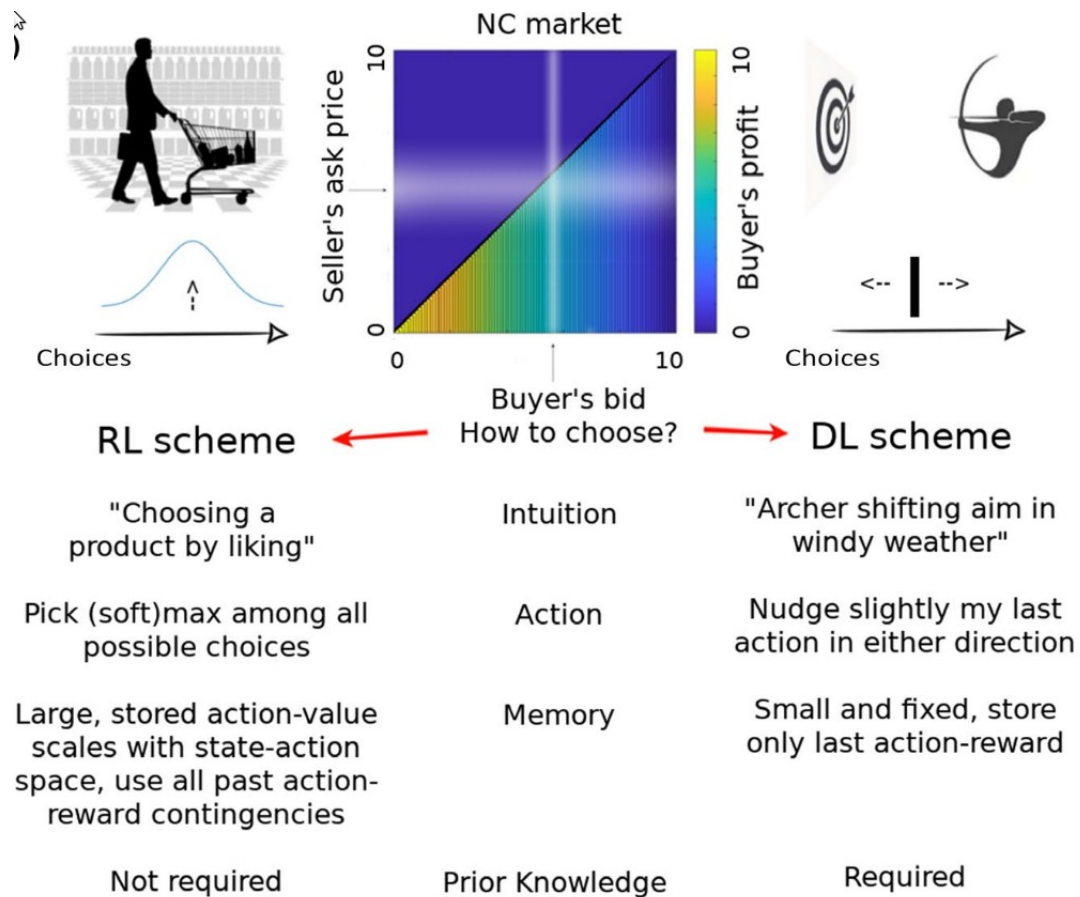


Figure 1 | RL- and DL-type algorithms comparison. Normal form (top centre) of a one seller versus one buyer (NC market) game: matrix cell colours represent the buyer's payoff. The buyer holds an estimate of the (possibly varying) seller's ask price (horizontal fuzzy white stripe) and tries to maximize profit by choosing the lowest possible bid that does not fall in a cell of the zero-profit yielding upper right triangle (adapted from Martinez-Saito et al., 2019).

The ability to recognize market types is also critical for successful bidding. At the beginning of each trial, activity in the bilateral superior posterior parietal cortex was stronger in trials with higher social competition (Martinez-Saito et al., 2019). This activation could reflect neural activity monitoring the competitiveness in the current trial or retrieving relevant information (Vilberg & Rugg, 2008) about the current market

type (i.e., the preferred bid). We found that a reward-prediction error-like signal was observed in the anterior and ventral striatal areas, whereas the DL error signal was represented in the dorsal posterior striatal areas, particularly in the posterior putamen (Figure 3). According to the Bayesian model comparison analysis, the variability of the striatal activity was explained by DL better than by RL, supporting the pertinence of DL-based bidding (Martinez-Saito et al., 2019). This finding concurs with previous suggestions that neural learning signals in motivated decision-making are not necessarily always reward prediction error-like (Behrens et al., 2008, supplement) and that a region of striatum is involved in learning stimulus–response associations and action selection (Jessup & O'Doherty, 2011). The DL-type learning strategy requires a representation of an internal number line where the preferred bids are stored and actively updated. Our results indicate that this representation is implemented in the parietal cortex (Martinez-Saito et al., 2019).

In summary, we found that DL fit the behaviour best and resulted in higher payoffs. We found the binary learning signal associated with DL to be represented by neural activity in the striatum distinctly posterior to a weaker reward prediction error signal. Consistent with the proposal that DL is an efficient heuristic for valuation when the action or bid space is continuous, the posterior parietal cortex represented the continuous action space of the task, and the frontopolar prefrontal cortex distinguishes among conditions of social competition (Martinez-Saito et al., 2019). Therefore, we can conclude that in the iterated game requiring estimation of values (prices) determined by the interactive action of multiple conspecifics, humans deploy a policy that harnesses generic striatal learning areas modulated by the category of social context via a signal from the frontopolar cortex.

2.2 Study II. Neural basis of the exploitation of common-pool resources

To investigate why people often exhaust unregulated common natural resources but manage to preserve similar private resources, we combined a neurobiological, economic and cognitive modeling approach.

Participants had to manage a common-pool resource in the form of fish stock, by imagining that they were fishing by a lake together with two other fishermen. Their task was to collect as much fish as possible and each collected fish led to a monetary payoff. In every trial, participants decided between three possible net sizes for fishing: one, two or three (Martinez-Saito et al., 2022). Depletion of the resource (fishing out the lake) was caused by their own behavior and the behavior of two other anonymous players present in the room (see Figure 2 for the stages comprised in one trial).

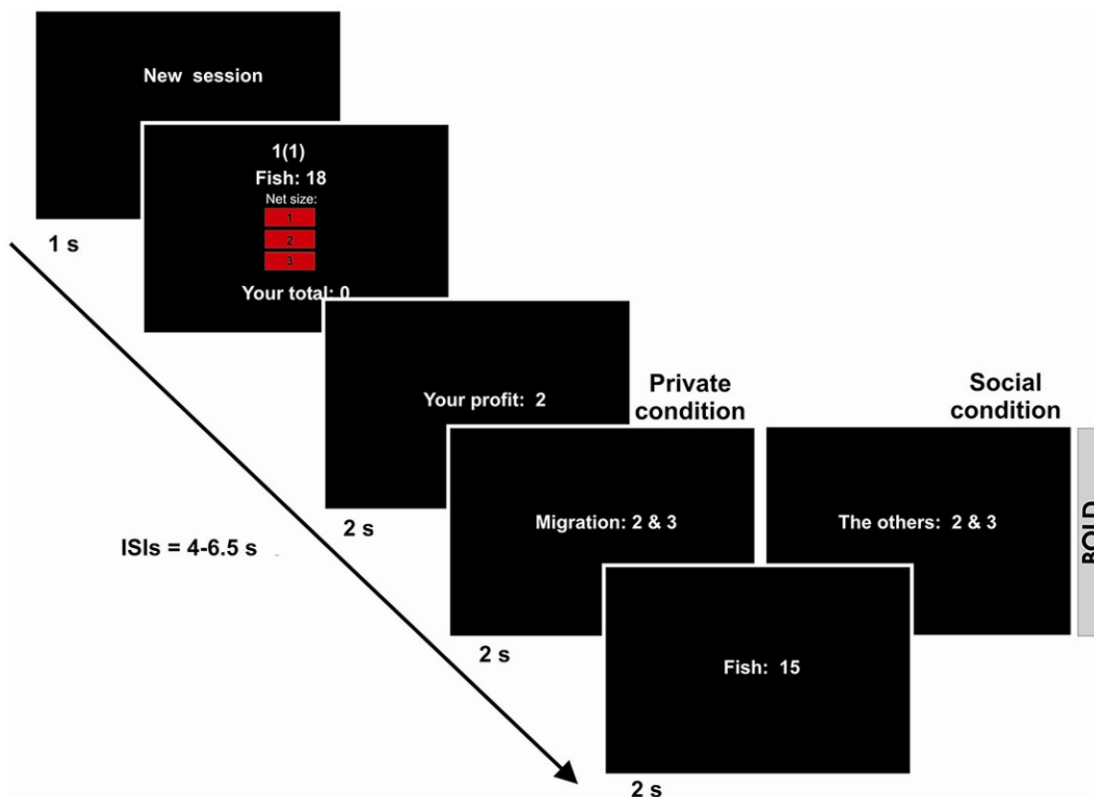


Figure 2 | Neural correlates of pseudo-RPE and DS signals based on the best-fitting DL algorithm in anterior putamen and nucleus accumbens area and posterior putamen during the outcome of the game. Correlated activity in the anterior ($y = 16$) and posterior ($y = -10$) putamen was stronger for pseudo-RPE and DS, respectively, during feedback. Here a pseudo-RPE signal is a RPE where the expected value is assumed to be the currently preferred bid (adapted from Martinez-Saito et al., 2019). From left to right columns: pseudo-RPE ($p < 0.05$, FWER), DS ($p < 0.05$, FWER), pseudo-RPE orthogonalized with respect to DS ($p < 0.001$, unc) and DS orthogonalized with respect to pseudo-RPE ($p < 0.001$, unc). From Martinez-Saito et al. (2022).

Image analysis was performed with SPM12 and in the same manner as in Study I.

We focused on the ventral striatum and the ventromedial prefrontal cortex because they belong to the brain's valuation system through their essential role in valuation and reward-based learning (Levy and Glimcher, 2012; Bartra et al., 2013). Similarly to (Bartra et al., 2013), I built ventromedial prefrontal cortex (vmPFC) and striatum regions of interest (ROI) with labels from the 1 mm anatomic atlas parcellation resolution of (Rolls et al., 2015) by taking the bilateral union of gyrus rectus, medial orbitofrontal, anterior orbitofrontal and posterior orbitofrontal regions for vmPFC.

A sharp decrease of common and private resources was associated with deactivation of the ventral striatum, a brain region involved in the valuation of outcomes (Martinez-Saito et al., 2022). Across individuals, when facing a common resource, ventral striatal activity is anticorrelated with resource preservation (less harvesting), whereas with private resources the opposite pattern is observed (Martinez-Saito et al., 2022). The goodness of fit of computational models suggested that on average participants learned less in the nonsocial condition, which is in agreement with the stronger modulation of ventral striatum activity in response to perceived decreases of common resources, in the

social condition than in the nonsocial condition (Figure 3). Thus, the social model predicts the enhanced selfish behavior of humans under a scarcity of resources (Martinez-Saito et al., 2022). Our fMRI results indicate that the striatum is involved in social comparisons and generates a negative prediction error when a person receives less than the competitors and a positive prediction error when she receives more than the competitors (Martinez-Saito et al., 2022). Thus, ventral striatum activity not only monitors outcomes (resource depletion) but also integrates outcomes into the specific social context.

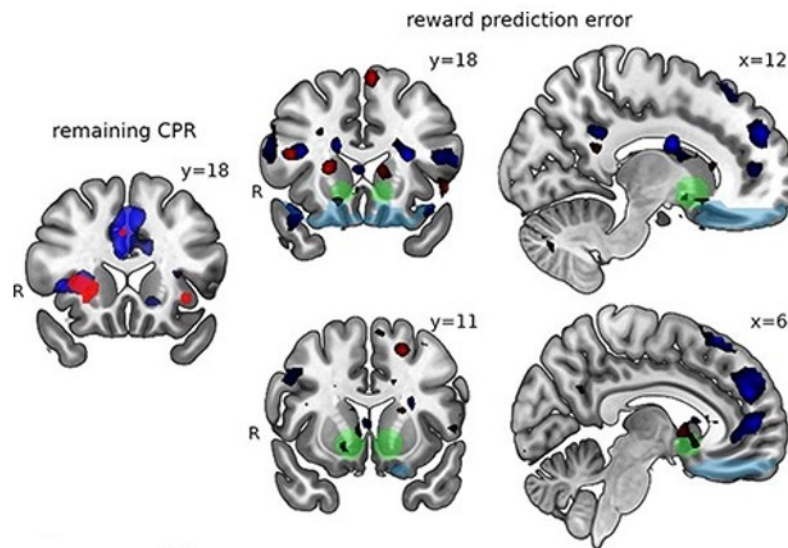


Figure 3 | Neural activity involved in monitoring and managing CPR exploitation. Left: neural deactivations associated with the size of the remaining CPR, indicating that activity was parametrically modulated by the change of the CPR size trial-by-trial in social (red) and nonsocial (blue) groups. Right: activity associated with learning signals: social (red) and nonsocial (blue) reward prediction errors; ventral striatum ROI (translucent green) and vmPFC ROI (translucent light blue) (adapted from Martinez-Saito et al., 2022).

In summary, neural value signals distinctly modulated behavior in response to the depletion of common vs private resources and computational modeling suggested that overharvesting of common resources was facilitated by the modulatory effect of social comparison on value signals (Martinez-Saito et al., 2022). We can also conclude, that when exploiting a scarce resource, the functional role of the striatum—a prominent subcortical region involved in learning—is modulated by the social implications of the learning context, i.e. by whether the resource is public or private.

2.3 Study III. Meta-analysis on learning under social versus nonsocial uncertainty

Understanding to what extent learning in social contexts is a specialized function is important to facilitate adaptation to different social contexts. In Study III, we further explored whether there are learning mechanisms specialized in resolving uncertainty of exclusively social origin. The real-life social contexts may dramatically modulate learning processes. We hypothesized that since the ventral striatum, not only continuously monitors our own outcomes, but also monitors the outcomes of others, ventral striatum activity might facilitate competitive behavior that may lead negative outcomes (Martinez-Saito & Gorina, 2022). We searched for studies through the websites PubMed and Web of Science, which aggregate multiple academic databases. The keywords used to filter results were: [“fmri” AND “learning” AND “social”]. We selected all accessible articles that satisfied the inclusion criteria. The selection consisted of two stages: identification, or abstract-based culling, and screening, where studies lain aside during identification are perused to checked all inclusion criteria (Figure 4). We also found studies by tracing citations of discovered articles and references in the bibliography of reviews. If whole-brain maps were not included in an article that satisfied the remaining requirements, we selected it in case we could retrieve

the maps by contacting the authors. When the statistical significance level reported in a study was unclear, we followed the recommendations of Albajes-Eizagirre et al. (2019).

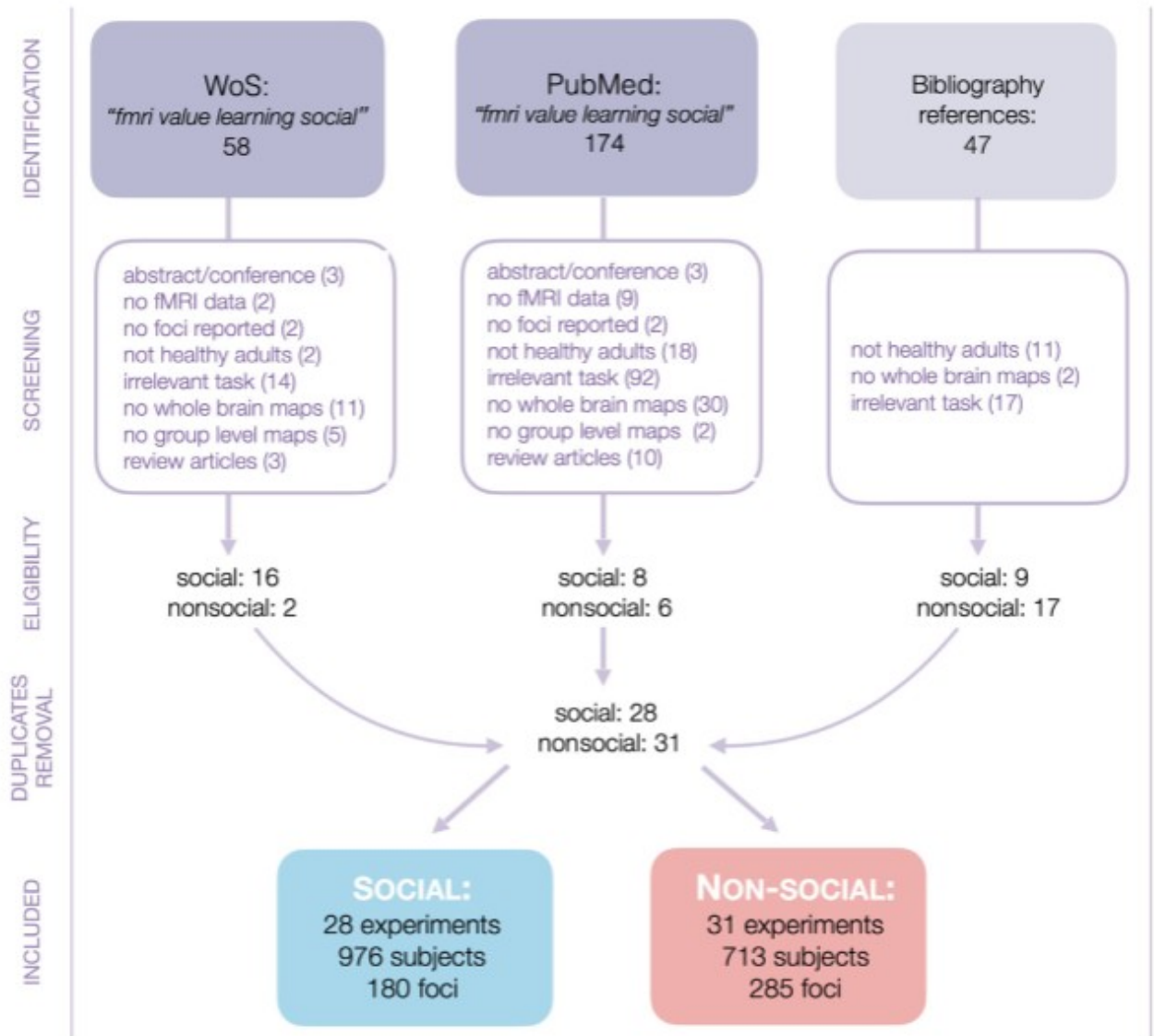


Figure 4 | Scheme of the process used to identify and cull articles that met the criteria of the two groups used in meta-analyses, in PRISMA flowchart format (Moher et al., 2009). Some studies count as both social and nonsocial (adapted from Martinez-Saito et al., 2022).

This investigation showed that most of the neural circuitry in value learning and representation regions was not segregated into distinct modules processing uncertainty (noise) of social versus nonsocial origin, which suggests that most behavioral adaptations to navigate social environments are reused from frontal and subcortical areas along the mesolimbic pathway processing generic value representation and learning (Figure 5). Although most of the brain activations associated with learning error signals were shared between social and non-social conditions, there was some evidence for functional segregation of error signals of exclusively social origin during learning in limited regions of ventrolateral prefrontal cortex and insula (Martinez-Saito & Gorina, 2022). This has implications for social, developmental, and evolutionary neuroscience, because it suggests that the mesolimbic pathway could have been reused and deployed, with little modification, to serve the mounting computational needs of human ancestors' brains in an increasingly complex social environment. Overall, our results suggest, that the neural circuitry involved in learning is at least partially generic, such that social-specialized frontal modules may tweak and modulate the generic learning scheme (Martinez-Saito & Gorina, 2022).

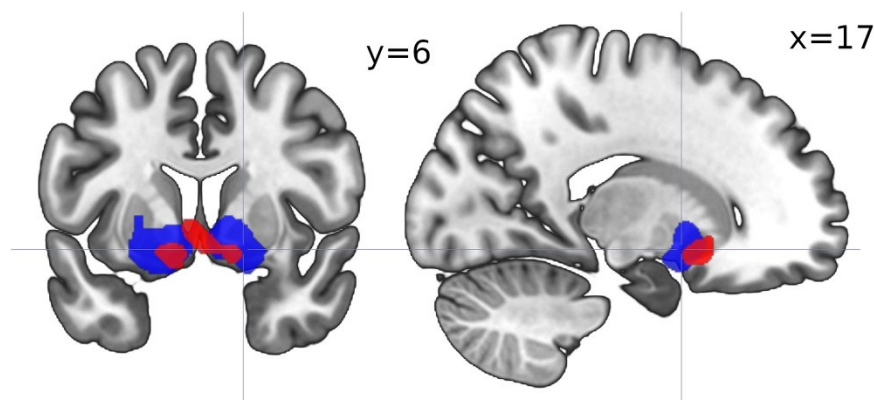


Figure 5 | Results for the metanalysis for social (red) and nonsocial (blue) error signal studies. Activation likelihood estimation maps were thresholded at $p < .05$ (adapted from Martinez-Saito & Gorina., 2022).

3. Conclusion

The three studies' joint results portray a fuzzy yet suggestive account where evolutionarily old, subcortical brain structures, in particular the striatum, are involved in learning processes are recruited independently of the context, but modulated from brain regions elsewhere.

In Study I, neural correlates of learning signals were elicited in the striatum, whereas the posterior parietal cortex represented the continuous action space of the task, and the frontopolar prefrontal cortex distinguished among conditions of social competition (Martinez-Saito et al., 2019). This hints at a scheme where the joint effects from frontopolar cortex (which determines context), and parietal cortex (which executes numerical computations) modulated learning signals in striatum. In Study II, computational modeling suggested that competitive decisions – over-harvesting of common resources – were facilitated by the modulatory effect of social comparison (presumably from prefrontal regions) on value signals. These results furnish an explanation of people's tendency to over-exploit unregulated common natural resources (Martinez-Saito et al., 2022). Finally and congruously, the results of meta-analysis of Study III suggested that most behavioral adaptations to navigate social environments are reused from frontal and subcortical areas processing generic value representation and learning, but that a specialized circuitry might have evolved in the prefrontal cortex to deal with social context representation (Martinez-Saito & Gorina, 2019).

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