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From homo-œconomicus to non-human primate: three case studies on the cognitive micro-foundations of economics

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Aurélien Nioche. From homo-œconomicus to non-human primate: three case studies on the cognitive micro-foundations of economics. Economics and Finance. Sorbonne Université, 2018. English. NNT : 2018SORUS361 . tel-02865426v1

HAL Id: tel-02865426

<https://theses.hal.science/tel-02865426v1>

Submitted on 11 Jun 2020 (v1), last revised 11 Jun 2020 (v2)

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From homo-*o*economicus to non-human primate:
Three case studies on the cognitive
micro-foundations of economics

THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY OF

SORBONNE UNIVERSITÉ
ECOLE DOCTORALE CERVEAU COGNITION COMPORTEMENT

BY AURÉLIEN NIOCHE

THE 31TH OCTOBER 2018

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From homo-*o*economicus to non-human primate: Three case studies on the cognitive micro-foundations of economics

ABSTRACT

Through three studies, this thesis aims to explore the cognitive micro-foundations of economics.

In a first study, I investigate the role of the information for coordination on a unique medium of exchange, that is to say money emergence. Relying on the search theoretical models (Kiyotaki & Wright, 1989, and Iwai, 1996), the goal of this study is to challenge the assumption that an exhaustive information is a necessary condition for money emergence. The results obtained by simulation show that artificial agents learning by a simple reinforcement mechanism are able to develop a monetary exchange system, even if their access to information is strongly restricted. However, the results obtained during our experiments with human subjects go against the results obtained by simulation, raising the question of the possibility of such a coordination phenomenon in humans when access to information is extremely restricted.

In a second study, I tackle the role of the information in duopoly competition. Using a model *a-la*-Hotelling (1929), we test the hypothesis that varying the amount of information available by consumers substantially impacts market's dynamics. Computational results indicate that firms could relax competition by establishing local monopolies when information is low, and *a contrario*, face an intense competition when consumers are well-informed. The results obtained in human subjects point in the same direction as simulations, showing also how the equilibrium of the observed system may depend on heuristics deployed by the individuals.

In a third study, I focus on decision-making under risk in rhesus monkeys, with the specific goal of examining how well rhesus behavior hews to aspects of prospect theory (Kahneman & Tversky, 1989, 1992). In line with observations made in humans, I report results indicating an asymmetric treatment of gains and losses (i.e. the reflection effect), with some evidence for probability distortion.

De l'homo-œconomicus au primate non-humain : Trois études de cas sur les micro-fondations cognitives de l'économie

RÉSUMÉ

Comment expliquer un macro-phénomène économique tel que l'émergence d'une institution par des micro-phénomènes tels que la prise de décision individuelle? Telle est la question qui fait l'enjeu d'une démarche micro-fondationnelle : micro-fonder l'économie n'est rien d'autre que fonder la macro-économie sur des modèles de rationalité individuelle.

Un projet de microfondation *cognitive* requiert en outre de substituer aux agents rationnels disposant d'une information complète classiquement employés dans les modèles économiques, des agents aux capacités de calcul limitées et disposant d'une information imparfaite. Dans les études qui font le corps de cette thèse, le premier candidat qui a été retenu pour un tel remplacement est l'agent artificiel dont les capacités de calcul et d'accès à l'information ont été bridées. Dans le but de formuler des conclusions sur la base de résultats empiriques, le deuxième candidat qui s'est imposé est l'être humain. Voulant faire un pas de plus dans notre démarche d'utilisation d'agents cognitivement limités, un troisième candidat a également été retenu : le primate non-humain.

L'objectif d'offrir des micro-fondations cognitives à l'économie est ambitieux et il est bien évidemment impossible de pouvoir réaliser dans le temps d'une thèse l'entièreté de ce projet. C'est ainsi que trois études pouvant être considérées de manière relativement indépendante constituent le corps de cette thèse.

Dans une première étude, je m'intéresse au rôle de l'information dans le processus d'émergence d'une monnaie, compris comme une coordination sur un moyen d'échange unique. Au cours des dernières décennies, l'économie monétaire est passée d'une compréhension purement macroéconomique de la monnaie à une analyse de ses fondements microéconomiques, tant dans sa dimension théorique que dans sa dimension comportementale. Plusieurs modèles de prospection monétaire, tels que ceux de Kiyotaki & Wright (1989) et Iwai (1996) ont été proposés afin d'identifier les conditions d'émergence d'une monnaie. Ces modèles appartiennent à la classe des modèles macroéconomiques microfondés avec attentes rationnelles. Ils cherchent à expliquer un phénomène macroéconomique — l'émergence d'une monnaie — à partir de décisions individuelles, fournissant ainsi une micro-fondation

pour leurs modèles. Cependant, les décisions individuelles émanent dans ces modèles d'agents qui sont extrêmement bien informés de l'état global de l'économie et qui font preuve de capacités de calcul exemplaires. L'approche adoptée ici a pour but de remettre en question l'hypothèse selon laquelle un accès exhaustif à l'information est une condition nécessaire à l'émergence d'une monnaie. Nous montrons ainsi que des agents artificiels apprenant par un simple mécanisme de renforcement sont capables de développer un système d'échange monétaire : un accès extrêmement restreint à l'information tels que les agents n'obtiennent des informations que sur leurs tentatives d'échange personnelles permet un phénomène de synchronisation à grande échelle — ici, l'adoption d'une monnaie commune. Nous avons mis en place un protocole visant à savoir s'il était possible d'obtenir les mêmes résultats chez des sujets humains. Les résultats obtenus lors de nos expériences vont toutefois à l'encontre des résultats obtenus par simulation, laissant ouverte la question de savoir sous quelles conditions un tel phénomène de coordination est effectivement possible chez des sujets humains lorsque l'accès à l'information est drastiquement restreint.

Dans une deuxième étude, j'étudie le rôle de l'information dans un contexte de concurrence en situation de duopole. Prenant appui sur un modèle dérivé du modèle séminal d'Hotelling (1929), nous testons l'hypothèse selon laquelle la variation de la quantité d'information disponible par les consommateurs aurait un impact substantiel sur la dynamique du marché. Les résultats obtenus au moyen de systèmes multi-agents indiquent que les entreprises peuvent échapper à un phénomène de concurrence en établissant des monopoles locaux lorsque l'information est faible, et *a contrario*, se trouvent en situation de forte concurrence lorsque les consommateurs sont bien informés. Au moyen d'un jeu en ligne multijoueur, nous avons ensuite testé expérimentalement la robustesse de nos prédictions théoriques. Les résultats obtenus chez l'homme vont dans le même sens que les résultats obtenus par simulation. De plus, ils montrent que les situations d'équilibre observées dépendent également des caractéristiques psychologiques des individus incarnant les firmes, de par les heuristiques qu'ils sont amenés à déployer.

La troisième étude, quant à elle, porte sur la prise de décision dans le risque chez le macaque rhésus. Son but est d'examiner à quel point le comportement des macaques rhésus est conforme aux prédictions que l'on peut faire suite à la théorie des perspectives (Kahneman & Tversky, 1989, 1992), à savoir que le choix des individus serait l'expression d'une certaine aversion au risque pour les gains mais de recherche du risque pour les pertes, et que ce choix se ferait sur la base d'une perception des probabilités déformée (les probabilités faibles seraient sur-évaluées et les fortes probabilités seraient sous-évaluées). Nous avons entraîné des macaques rhésus à choisir entre des loteries pour obtenir de l'eau, avec des représentations symboliques des probabilités et des conséquences — ces conséquences impliquant des gains et des pertes potentiels. Nous avons mis en évidence un traitement asymétrique des gains et des pertes, ainsi qu'un phénomène de distorsion de probabilité. Établir du point de vue de la

théorie des perspectives à quel point la prise de décision des macaques rhésus est semblable à celle de l'homme constitue un travail préparatoire nécessaire à l'étude électrophysiologique des circuits sous-jacents et contribue en cela aux fondations micro-cognitives de l'économie.

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Acknowledgments

I thank Sacha and Thomas for coming up with the idea of this thesis project at the interface of two worlds which mix so little, for having put their trust in me and giving me the necessary support to make it a reality. I thank Nicolas for taking part in this project and for his generosity in helping me out. I thank Françoise, for encounter with her was decisive in making the choice to do this PhD. I thank all the people I have collaborated with over the past years, including Mathieu, Germain, Paul and Florian. I thank Bhargav for proofreading several parts of this document. Whether in the laboratory or at home, I thank all the people with whom I shared my daily life—and who also supported me on a daily basis—being in the front row of this epic! I also thank my family, and especially my parents without whom nothing would have been possible. Finally, I thank Basile for a list of reasons so long, that I will spare the reader.

1

Introduction

I.I COGNITIVELY MICROFOUNDING ECONOMICS: WHAT DOES IT MEAN?

GENERAL INTRODUCTION. The objective of offering cognitive microfoundations to economics is ambitious. It is obviously impossible to carry out the entire project in the time frame of a thesis. Thus, three studies that can be considered relatively independently will constitute the body of this document. The objective of this introduction is to explain how each of them contributes to the realization of this project. The issues concerning each of these studies are twofold. Each study aims to show *which* cognitive microfoundations can be brought to economics in a specific context, but this is impossible without solving a set of methodological problems. It is indeed necessary to show *how* it is possible to bring such

microfoundations.

This introduction will give the key guidelines of such a cognitive microfoundational approach and briefly introduce each of the three studies. Following the three studies, their limits and the prospects they offer to strengthen and develop the cognitive microfoundations of economics will be considered.

BETWEEN MACRO AND MICROECONOMICS, PERFECT AND IMPERFECT INFORMATION. How can an economic macro-phenomenon such as the emergence of an institution be explained by micro-phenomena such as individual decision-making? This is the question that is at stake in a microfoundational approach. Essentially, microfounding economics is nothing more than basing macroeconomics on models of individual rationality.

So, let us consider a set of individuals evolving in a specific stylized environment. Let us call them agents. Let us say that these agents are perfectly rational in the sense that they maximize their expected utility, i.e. they take the options that are deemed the best, both from their point of view and from that of the observer. Let us suppose that macro-phenomena emerge from the interaction of these agents. These macro-phenomena will be called micro-founded, because they will be based solely on the rationality of these agents. The question that may then arise is whether the macroeconomic phenomena resulting from the interaction of these agents would be the same as those observed in cognitively limited agents making their decisions on the basis of imperfect information. The hypothesis of an affirmative answer to this question is what is commonly called the “as if” hypothesis, the authorship of this formula having been entrusted to Milton Friedman who defended its use. This hypothesis can be summarized as follows: the aggregate behavior of cognitively limited

individuals making their decisions on imperfect information is similar to the aggregate behavior of perfectly rational individuals.

One of the constraints posed during this thesis is not to consider this hypothesis as true *a priori* and to work on the establishment of cognitive microfoundations. By cognitive, we mean that they must take account of the limitations of the agents involved in real economies, namely humans. These limitations are of two kinds: (i) computing ability, (ii) access to information. The first study attempts to show how access to very limited information and simple trial and error learning is sufficient for the emergence of a large-scale coordination phenomenon, namely the emergence of money. Focusing on the competition in a duopoly situation, the objective of the second study is to show that taking the agent information into account has an impact on the structure of the market.

FROM HOMO ÆCONOMICUS TO NON-HUMAN PRIMATE: BETWEEN THEORY, EXPERIENCE *IN SILICO* AND EXPERIENCE *IN VIVO*. A project of cognitive microfoundation requires substituting rational agents that have complete information conventionally used in economic models with those that have limited computing capacities and imperfect information. The first selected candidate for such a replacement is the artificial agent whose computing capabilities and access to information have been restricted. In order to ground conclusions on empirical results, the second candidate that was chosen for two of the three studies presented here is the human being. As third candidate and in order to take a further step in the direction of the use of cognitively limited agents, the non-human primate has also been selected.

One of the roles of experimental economics is to systematically identify deviations in the

actual behavior of embodied agents—understand human beings—from the predictions of a pre-existing economic theory. A difficulty that such a project faces, after demonstrating limits of a formal theory, is to be able to contribute to its improvement. The use of numerical models is an interesting possibility to avoid the pitfall of a simple deconstruction of initial theories and to propose an intermediary between axiomatic models and experience.

The methodology of two of the three studies is thus similar. Each of these studies is based on results that are generally obtained on the basis of axiomatic systems. However, we first reconstruct a numerically testable model taking the limitations of individuals into account. Indeed, during numerical simulations, we use cognitively limited agents. They do not make their decisions rationally by maximizing their expected utility but either learn by trial and error, the options that are preferable to them, or use heuristics based on a simplified model of the situation. Unlike purely rational agents, these agents do not need perfect information to decide and need only a few computational capabilities, making them more similar to living beings than a canonical homo-*o*economicus. These simulations then have theoretical value: as we designed the environment as well as the algorithm used by agents to make their decisions, they allow us to identify the conditions under which a given macro phenomenon can be observed. These conditions then pave the road for fine predictions about what should be observed in living beings.

While the two first studies use artificial agents and humans, the third study included in this document considers rhesus macaques as subjects. In addition to the further step in the direction of the use of cognitively limited agents, such a study is a mean to address a phylogenetic question, which is to what extent, displaying economic behaviors could be seen as a human specificity. On the other hand, since the macaque is a model in electrophysiology, if

we succeed in inducing economic behavior in this species that matches the one displayed by human agents, it opens the possibility of investigating the underlying neuronal mechanisms of these behaviors. While micro-founded models offer the possibility of building a bridge between individual decision-making and macro phenomena, decision-making processes specific to economic contexts need to be studied separately. Such a study would not be complete without a description of the electrophysiological mechanisms at work in living beings. If this study does not include electrophysiology, it is nevertheless intended to constitute a necessary preparatory work for such an approach.

1.2 THREE STUDIES: BETWEEN SIMILARITY AND DISSEMBLANCE

THE EMERGENCE OF AN INSTITUTION UNDER INFORMATIONAL CONSTRAINTS AND LIMITED COGNITIVE CAPACITIES. The first study of this thesis bears on the emergence of money. Its objective is to show how limited access to information for agents in an economy that is characterized by production specialization, does not prevent large-scale coordination.

Several microfounded macro-economic models with rational expectations, dubbed *search theoretical models*, address the issue of the emergence of money^{47,23,55,45}. However, what these models have in common is the use of agents that have perfect (or almost perfect) information on the overall state of the economy and that demonstrate quite important computational capabilities (i.e. they make predictions on their utility on an infinite horizon based on inferences over the other players beliefs).

The hypothesis this study seeks to test is that a common medium of exchange may also emerge in economies where agents have limited computing capabilities and do not have access

to information on the overall state of the market. Like the study on spatial competition, this one combines the use of numerical models and experimentation with human subjects. In addition, to test under which conditions an agreement on a single means of exchange may appear, the aim is to highlight the interaction effects between the cognitive characteristics and the economic structure.

THE INFLUENCE OF INFORMATION AVAILABILITY ON MARKET STRUCTURE. The second study of this thesis focuses on competition in a situation of duopoly. Its objective is to show how limited access to information for consumers can influence the positioning strategies developed by firms, and thus the structure of the market.

Several models have been developed to describe these duopoly situations in which two independent sellers compete for market share. Since the Hotelling's princeps model⁴⁰ in the 1920s, a prolific literature has been developed^{20,76,21,28,44}. Although classified as micro-economic models, spatial competition models can also be considered as connecting points between micro and macroeconomics. While they use traditional micro-economic objects such as consumers and firms, in doing so, these models give rise to a macro-economic object from the interaction of individuals, namely the market structure.

However, in a similar way to search theoretical models underlying the first study, most models assume that consumers have unlimited access to information. We consider here a situation where consumers have limited access to information and we explore how this factor influences the behavior of competing firms.

To do this, we first characterized three decision-making processes followed by individual

firms: (i) maximizing profits; (ii) maximizing difference between its profits and that of the competitor; and (iii) tacit collusion. We then simulated a number of savings by manipulating the amount of information to which each consumer had access. We then tested this model with human subjects embodying companies. We characterized their behaviors according to their proximity to the decision-making processes used by the simulated firms.

The major challenge of this study is to underline the importance of taking into account the information structure and cognitive characteristics of agents in the microfoundation of an economic system, by showing how the emerging structure of these interactions—corresponding here to the distribution on the market of companies—is dependent on them.

THE USE OF THE NON-HUMAN PRIMATE AS AN ANIMAL MODEL OF ECONOMIC BEHAVIOR: ASSESSMENT OF ATTITUDE TOWARD RISK IN RHESUS MONKEY. To conduct an electrophysiological study of the neuronal substrates underlying decision-making processes leading to economic behavior, it seems necessary to first verify that it is possible to induce economic behavior in non-human primates. The situations of choice between two lotteries, a classic paradigm since Von Neumann & Morgenstern⁸⁸, seemed to be a relevant task within the framework of an approach of microfoundation of economics. If one is able to find a system of representation of lotteries understandable by the non-human primate allowing it to make bets, then it would be possible to induce several other economic contexts specific behaviors. One can thus think about speculating: it would be sufficient to create circumstances allowing the realization of bets whose consequences are situated in short or long term, contrary to a situation of classic bet where the consequences are with immediate effect.

One of the objectives is to verify similarity of decision-making at risk in the rhesus macaque with that of human regarding specific features. We know that decision-making in human is subject to several biases. For example, when facing bets, humans show some asymmetry in their preference for the riskiest option depending on whether the stakes involve potential gains or potential losses^{49,86}. They are indeed reluctant to take risks for the bets involving gains, but seek to take risks for the bets involving losses.

Risk attitudes have been studied in many other species, ranging from insects to mammals, including fish, birds¹⁴ and peas²². Most of these studies report a risk aversion for gains, with the notable exception of monkeys^{63,68,73,80,34}. This exception raises questions about the validity of the macaque as an animal model of economic behavior.

The objective of this study is to assess whether the asymmetry in treatment between gains and losses observed in humans can also be demonstrated in non-human primates and, if it can be, to provide a detailed description by characterizing it according to three aspects: (i) risk aversion, (ii) probability distortion, (iii) stochasticity of choice.

To do so, two female macaques were placed before choice situations where they had to choose between two lotteries involving either winnings or potential losses. The behavioral data thus obtained were fitted to a decision-making model based on the prospect theory^{49,86}, to contrast the treatment of losses and the treatment of gains.

2

Impact of limited information on money emergence: Insights from a computational and experimental approach^{*}

ABSTRACT. Several micro-founded macroeconomic models with rational expectations address the issue of money emergence. These models have in common the use of agents who dispose of perfect or near-perfect information on the global state of the economy and who display full-fledged computational abilities. We assume that a commodity money can also

*. The content of this chapter is an independent research article submitted. Its has been simply formatted for the sake of graphical consistency. The co-authors of this article are Basile Garcia, Germain Lefebvre, Thomas Boraud, Nicolas Rougier & Sacha Bourgeois-Gironde.

emerge in economies where agents endowed with limited computational abilities don't have access to information about the global state of the economy. Through multi-agent simulations, our findings show that a commodity money can indeed emerge under such restrictions and highlight interaction effects that can be involved between cognitive features and economic structure. However, under the same kind of informational constraints, human subjects encounter more difficulties than artificial agents to coordinate on a unique medium of exchange. The reasons of such a departure between computational and experimental results are discussed.

2.1 INTRODUCTION

Following the intuitions of Karl Menger⁶⁵ and starting with the Jones' model in the mid-1970's⁴⁷, several *search-theoretical* models have been proposed in order to identify the conditions for money emergence^{23,54,55,67,1,56,78,45,50,93,60}. These models belong to the class of micro-founded macroeconomic models with rational expectations. They provide an explanation of a macroeconomic phenomenon—money emergence—from individual decisions. An interesting feature of these models is that they offer an explanation for money emergence that does not require the economies to be centralized (i.e. no authority is necessary in order for the agents to coordinate). Indeed, focusing on the function of medium of exchange, these models highlight the key role that the money can play in facilitating exchange processes (i.e. limiting the friction due to the difficulty to find an exchange partner).

However, in these models, agents dispose of complete information about the global state of the economy, and are endowed with efficient computational abilities that allow them to draw inferences by means of nested reasoning. Therefore, a question that may

arise is whether this is a necessary condition, or whether money emergence is also possible in an economy populated by agents with restricted abilities and having a limited access to information. More precisely, we could wonder whether a coordination over a unique medium of exchange is possible by agents proceeding by trial and error in a context where they dispose only of a local information.

A partial answer has been brought to this question, by means of simulations with artificial agents using a reinforcement learning procedure^{62,25,53} in a Kiyotaki-and-Wright's environment^{55,56}. Here, reinforcement learning agents have by construction limited computational abilities, and their informational inputs are only constituted by the success and failures of each exchange attempt. In contrast with Kiyotaki-and-Wright's theoretical agents, they are completely blind to the global state of the economy, and the construction of their preferences does not rely on the latter. Yet, results report achievement of monetary equilibria.

The Kiyotaki's and Wright's model^{55,56} has also been experimentally tested. Results show that a monetary equilibrium can be reached with human subjects evolving in a search-theoretical environment^{9,26,25}. Interestingly, Duffy and Ochs²⁶ show that a reinforcement model fits well their experimental data obtained in a Kiyotaki-and-Wright's environment^{55,56}, suggesting that although more sophisticated behavior rules were available, subjects tended to favour immediate past feedback. However, in contrast with virtual agents learning by reinforcement, subjects had still access to extended information about the global state of the economy.

The purpose of this study is to know whether economies populated with human subjects can still reach a monetary state with drastic restrictions on information access. In other

words, the question is to know whether results obtained with virtual agents combining a restriction on computational abilities and on informational input can be generalized to economies populated with humans. In addition, we decided to use a search-theoretical structure that presents more generality than Kiyotaki and Wright's one, based on the Iwai's model⁴⁵. One criticism that we can address to the aforementioned studies, is that although they succeeded in demonstrating achievements of a monetary equilibrium, they were mainly considering the fundamental equilibrium of Kiyotaki and Wright. The latter relies on the use as medium of exchange of the good that is less costly to store than the other goods in circulation, this feature explaining why it is preferred. Results concerning the achievement of the speculative equilibrium—the equilibrium that requires to incur at first supplementary costs (i.e. to speculate)—were scarcer. That is why we decided to adopt an environment with indistinguishable goods, in a way to avoid that money emergence bears on intrinsic features of goods. Secondly, to our knowledge, the previous computational and experimental studies are based on search-theoretical models involving three goods. In this case, only one type of agent use the monetary good genuinely as a medium of exchange. The question remains to know if their conclusions can hold if there is more than three goods in circulation. Therefore, to assess their reliability and to broaden our conclusions, we decided to include an additional good.

We conducted a series of simulation, where we borrowed certain elements from the previous search-theoretical models to define the structure of our virtual economies, such as the production-consumption specialization and the absence of double coincidence of needs. In the economies we simulated, agents were producing a certain good and looking to obtain another one through exchanges, had little knowledge about the environment in which they operate—they only knew if their attempt of exchange was a success or a failure. They were

learning on the basis of a basic reinforcement learning mechanism, associating a value to each choice option available to them and updating by trial-and-error the efficiency of each type of exchange. We used the results of these simulations to identify the relevant experimental conditions. We then observed the behaviors of human subjects under similar informational constraints. We compare thereafter the results obtained by simulation and by experiment, and discuss the possibility of a macroeconomic phenomenon—money emergence—under minimal information.

2.2 RESULTS

COMPUTATIONAL. In order to test our hypothesis regarding the possibility of emergence under constraint of minimal information, we ran 2,700 simulations of economies with 3 goods in circulation ($G = 3$), and 2,700 simulations with 4 goods ($G = 4$).

Each economy is composed by different types of agents. A type of agent is defined by what agents of this type produce and consume. The goal of each agent is to obtain his consumption good. Agents proceed to exchanges between them to achieve this goal. Agents have a feedback only about their own exchange attempt and learn by reinforcement the efficiency of each type of exchange.

We vary across simulations the distribution of agents among the existing types.

By construction, if a good m becomes money, an agent that produces it or consumes it should try to exchange directly his production good against his consumption good. Otherwise, the agent is supposed to use it as a medium of exchange (i.e. to exchange his

production good against m , and then m against his consumption good). This defines what we called a *monetary behavior*. For each simulation, we measured the proportions of monetary behavior with each good in circulation.

To investigate the influence of the distribution of agents among types on money emergence, we fixed the agent type x_1 in economies with 3 goods, while we fixed the agent types x_1 and x_2 in economies with 4 goods. We drew a 2-dimensional phase diagram representing the average monetary behavior for each good (see Fig. 2.1). We set the constant to 50 and varied the other values between 10 and 190. All goods being identical, we arbitrarily chose the good 1 as the ‘target’, that is to say the good that we wanted to see emerge.

When $G = 3$, the higher frequency of monetary behavior with good 1 observed is when the value of x_2 is equal to that of x_1 and when the value of x_3 is at least twice that of x_1 (see Fig. 2.1). One may notice that the use of a uniform distribution of agent types ($x_1 = 50$, $x_2 = 50$, $x_3 = 50$) results in a low monetary behavior frequency. This led us to set the value of x_2 equal to that of x_1 and set the value of x_3 twice that of x_1 for the simulations under experimental conditions with $G = 3$ where our goal was to promote money emergence (see Fig. 2.2).

When $G = 4$, the higher frequency of monetary behavior with good 1 observed is when the value x_3 as well the value of x_4 is nearly twice that of x_1 and x_2 (see Fig. 2.1). As for when $G = 3$, the use of a uniform distribution of agent types ($x_1 = 50$, $x_2 = 50$, $x_3 = 50$, $x_4 = 50$) results in a low monetary behavior frequency. This led us to set the value of x_2 equal to that of x_1 and to set the value of x_3 and x_4 twice that of x_1 for the simulations under experimental conditions with $G = 4$ where our goal was to promote money emergence (see Fig. 2.3).

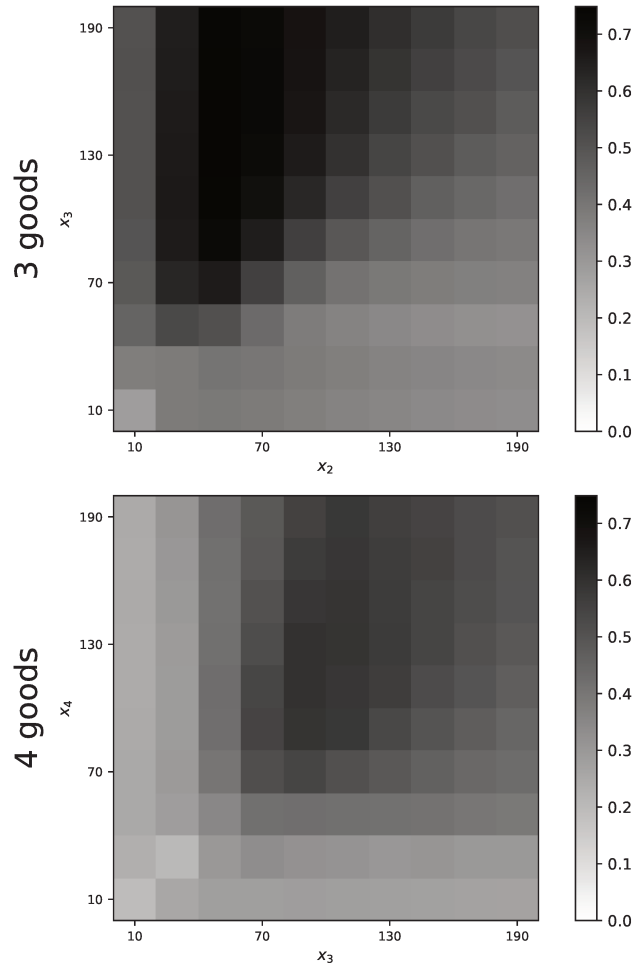


Figure 2.1 – Computational results: Influence of agents distribution on monetary behavior. The phase diagram on top panel summarizes the results of 2,700 simulations with 3 goods. The number of type-31 agents is set to 50 while the number of agents of type 12 and 23 varies between 10 and 190 (corresponding respectively to the values on the x -axis and y -axis). The darker the color, the higher the frequency of use of the good 1 as a medium of exchange. Similarly, the phase diagram on bottom panel summarizes the results of 2,700 simulations with 4 goods. The number of agent of types 41 and 12 is set at 50 while the the number of agents of type 23 and 34 varies between 10 and 190 (corresponding respectively to the values on the x -axis and y -axis). When $G = 3$, the higher frequency of monetary behavior with good 1 observed is when the value of x_2 is equal to that of x_1 and when the value of x_3 is at least twice that of x_1 . When $G = 4$, the higher frequency of monetary behavior with good 1 observed is when the value x_2 as well the value of x_3 is nearly twice that of x_0 and x_1 .

These results led us to formulate the following operational hypotheses regarding our experiments: (i) setting the number of agents of a type involving either the production or the consumption of the particular good half of the number of agents of another type promotes the emergence of this good as money; (ii) setting the number of agents of each type equal precludes the emergence of a medium of exchange.

To make predictions about the experiments with human subjects, we ran 80 additional simulations, distributed over groups corresponding to the four experimental conditions. For two of the groups, we promoted the use of good 1 as money, and for the two other groups, we use a configuration where it is expected that no good emerges as money. Note that as all the goods are identical, the choice to promote good 1 is arbitrary.

The economies simulated were therefore economies with:

1. 3 goods in circulation and a Non-Uniform distribution promoting the use of good 1 as Money (NUPM-distribution), that is a distribution such as the number of agents of a type involving either the production or the consumption of the monetized good being half the number of agents of another type;
2. 3 goods in circulation and a Uniform distribution (U-distribution), that is a distribution such as there is an equal number of agents of each type;
3. 4 goods in circulation with a NUPM-distribution;
4. 4 goods in circulation with a U-distribution.

For each condition, we measured the proportion of monetary behavior over time for each

good, as well as the number of use of each good as a medium of exchange over time (see Fig. 2.2 and 2.3).

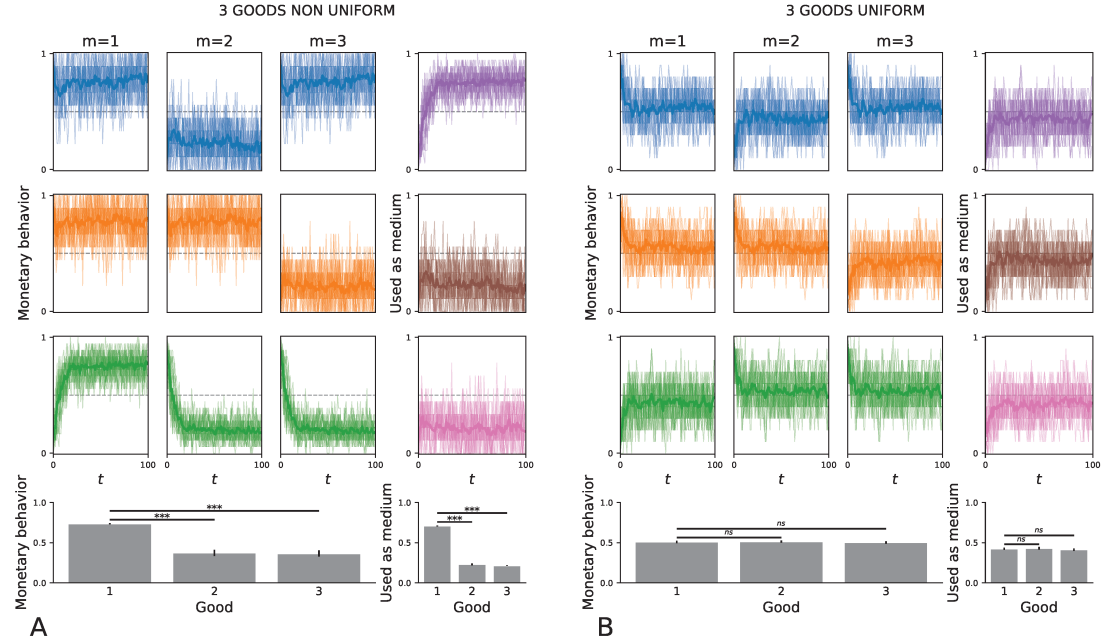


Figure 2.2 – Computational results: Experimental conditions with 3 goods in circulation. The computational results allowed us to settle for a non-uniform distribution promoting the use of 1 as money. Experimental results for such agents distribution are depicted in panels A. We put in contrast the results for a uniform distribution in panel B. The first three columns indicate the proportion of monetary behaviors over time. Each column corresponds to a specific good (respectively 1, 2 and 3). Each row corresponds to a type of agent (respectively from top to bottom type 31, 12 and 23). The gray dotted lines report the chance level (0.5). The last column indicates for each good, the proportion of agent using this good as a medium of exchange (respectively from top to bottom row, good 1, 2, and 3). The gray dotted lines indicate 0.5. On each panel, the left-side bar plot represents the proportions of monetary behaviors averaged over individuals. The right-side bar plot represents the proportions of use of a medium of exchange averaged over individuals. Error-bars correspond to standard errors. The number of stars indicates the level of significance of Mann-Whitney U-test (1, 2 and 3 stars correspond respectively to $p < 0.05$, $p < 0.01$ and $p < 0.001$). We observe that in the non-uniform condition (panel A), the proportion of monetary behaviors for good 1 and the proportion of agents using it as a medium of exchange are significantly greater than the corresponding proportions for good 2 and 3, while in the uniform condition (panel B), we observe no significant difference.

With $G = 3$ and a NUPM-distribution (see Fig. 2.2A), we observe that the proportion of agents displaying monetary behaviors with good 1 is high (above the chance level) and significantly greater than the corresponding proportions of agents for good 2 and 3 (respectively

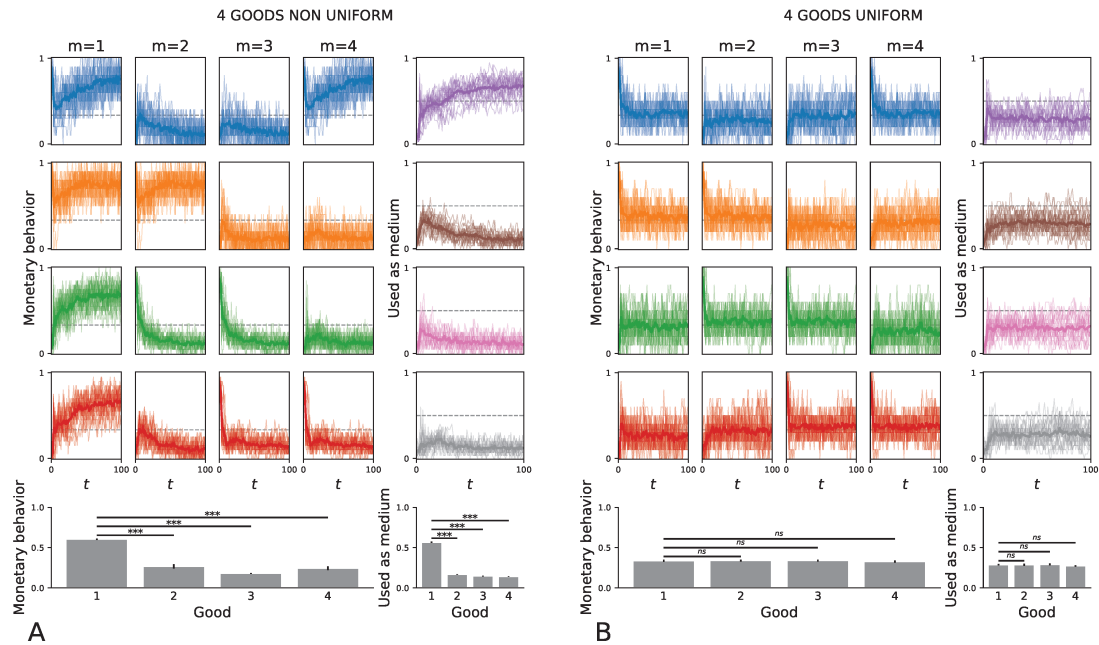


Figure 2.3 – Computational results: Experimental conditions with 4 goods in circulation. The computational results allowed us to settle for a non-uniform distribution promoting the use of good 1 as money. Experimental results for such agents distribution are depicted in panels A. We put in contrast the results for a uniform distribution in panel B. The first three columns indicate the proportion of monetary behaviors over time. Each column corresponds to a specific good (respectively 1, 2, 3 and 4). Each row corresponds to a type of agent (respectively from top to bottom type 1, 2, 3 and 4). The gray dotted lines report the chance level (0.33). The last column indicates for each good, the proportion of agent using this good as a medium of exchange (respectively from top to bottom row, good 1, 2, 3 and 4). The gray dotted lines indicate 0.5. On each panel, the left-side bar plot represents the proportions of monetary behaviors averaged over individuals. The right-side bar plot represents the proportions of use of a medium of exchange averaged over individuals. Error-bars correspond to standard errors. The number of stars indicates the level of significance of Mann-Whitney U-test (1, 2 and 3 stars correspond respectively to $p < 0.05$, $p < 0.01$ and $p < 0.001$). In the non-uniform condition (panel A), the proportion of monetary behaviors for good 1 and the proportion of agents using it as a medium of exchange are significantly greater than the corresponding proportions for good 2, 3 and 4, while in the uniform condition (panel B), we observe no significant difference.

$u = 256.5, p < 0.001$ and $u = 206.5, p < 0.001$). Regarding the number of use of each good as a medium of exchange, the proportion of agents using the good 1 as a medium of exchange is greater than the corresponding proportions for good 2 and 3 (respectively $u = 0, p < 0.001$ and $u = 0, p < 0.001$). This means that agents that neither produce the good 1 nor consume it try to obtain it when they have their production good in hand, and, once in hand, try to obtain their consumption good using it as an intermediary good.

On the contrary, with a U-distribution (see Fig. 2.2B), the proportion of monetary behavior for each good oscillates around chance level, meaning that we have obtained the same results with agents playing randomly. The proportion of monetary behavior for good 1 is not significantly different from the corresponding proportions for good 2 and 3 (respectively $u = 444, p = 0.935$ and $u = 427.5, p = 0.745$). Similarly, in the U-distribution, each good is equally used as a medium of exchange. Therefore, the proportion of agents using good 1 as a medium of exchange is not significantly different from corresponding proportions for good 2 and 3 (respectively $u = 48, p = 0.91$ and $u = 40.5, p = 0.496$).

When $G = 4$, we observe similar patterns (see Fig. 2.3A). (i) With a NUPM-distribution, the proportion of agents displaying monetary behaviors with good 1 is high (above the chance level) and significantly greater than the corresponding proportions of agents for good 2, 3 and 4 (respectively $u = 549, p < 0.001, u = 0, p < 0.001$ and $u = 425, p < 0.001$). (ii) The proportion of agents using the good 1 as a medium of exchange is greater than the corresponding proportions for good 2, 3 and 4 (respectively $u = 0, p < 0.001, u = 0, p < 0.001$ and $u = 0, p < 0.001$). (iii) On the opposite, with a U-distribution (see Fig. 2.3B), the proportions of monetary behavior for good 1, 2, 3 and 4 oscillate around chance level and the proportion of agents displaying monetary behaviors with good 1 was *not* significantly different from the

corresponding proportions for good 2, 3 and 4 (respectively $u = 741, p = 0.860, u = 761.5, p = 1.000$ and $u = 724.5, p = 0.706$). (iv) The proportion of agents using the good 1 as a medium of exchange is *not* significantly different from the corresponding proportions for good 2, 3 and 4 (respectively $u = 195, p = 1.000, u = 195, p = 1.000$ and $u = 158, p = 0.392$).

EXPERIMENTAL. Results for experiments are depicted in Fig. 2.4 and Fig. 2.5.

For the condition with $G = 3$ and a NUPM-distribution that brought together 36 subjects (see Fig. 2.4A), we expected the use of the good 1 as money to be promoted. But contrary to what has been observed in the artificial agents, the good 1 is not used as money: the proportion of agents displaying monetary behaviors with good 1 is *not* significantly different from the corresponding proportions for good 2 and 3 (respectively $u = 596.5, p = .565$ and $u = 564.5, p = .350$). Similarly, the proportion of agents using the good 1 as a medium of exchange is *not* significantly different from the corresponding proportions for good 2 and 3 (respectively $u = 80, p = 0.979$ and $u = 63.5, p = 0.381$).

For the condition with $G = 3$ and a U-distribution that brought together 30 subjects (see Fig. 2.4B), we expected no good to emerge as a money. However, the good 2 has emerged as a preferred medium of exchange. Indeed, if the proportion of agents displaying monetary behaviors with good 1 is *not* significantly different from the corresponding proportion for good 3 ($u = 414.5, p = .605$), it is significantly lower than the corresponding proportion for good 2 ($u = 273, p = .009$). Similarly, if the proportion of agents using the good 1 as a medium of exchange is *not* significantly different from the corresponding proportion for good 3 ($u = 41.5, p = 0.545$), it is significantly lower than the corresponding proportion for good 2 ($u = 20, p = .026$).

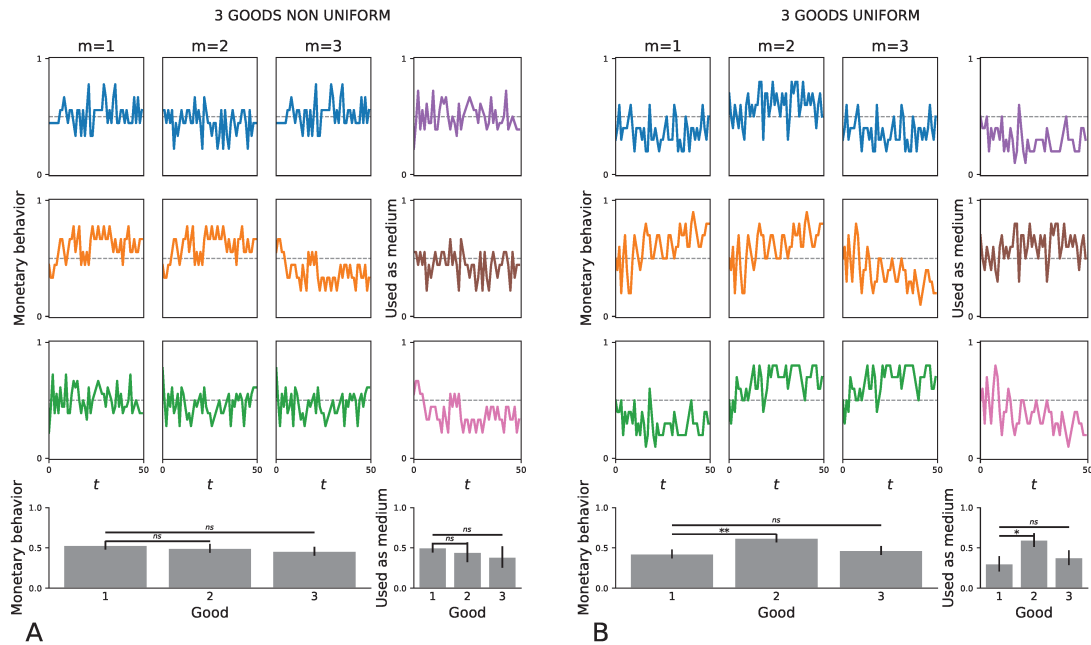


Figure 2.4 – Experimental results: 3 goods in circulation. The computational results allowed us to settle for a non-uniform distribution promoting the use of good 1 as money. Experimental results for such agents distribution are depicted in panels **A**. We put in contrast the results for a uniform distribution in panel **B**. The first three columns indicate the proportion of monetary behaviors over time. Each column corresponds to a specific good (respectively 1, 2 and 3). Each row corresponds to a type of agent (respectively from top to bottom type 31, 12 and 23). The gray dotted lines report the chance level (0.5). The last column indicates for each good, the proportion of agent using this good as a medium of exchange (respectively from top to bottom row, good 1, 2, and 3). The gray dotted lines indicate 0.5. On each panel, the left-side bar plot represents the proportions of monetary behaviors averaged over individuals. The right-side bar plot represents the proportions of use of a medium of exchange averaged over individuals. Error-bars correspond to standard errors. The number of stars indicates the level of significance of Mann-Whitney U-test (1, 2 and 3 stars correspond respectively to $p < 0.05$, $p < 0.01$ and $p < 0.001$). In the non-uniform condition (panel **A**), contrary to expectations related to the computational results, we observe no significant difference. In the uniform condition (panel **B**), the proportion of monetary behaviors for good 1 and the proportion of agents using it as a medium of exchange are significantly lower than the corresponding proportions for good 2, while we expected no significant difference.

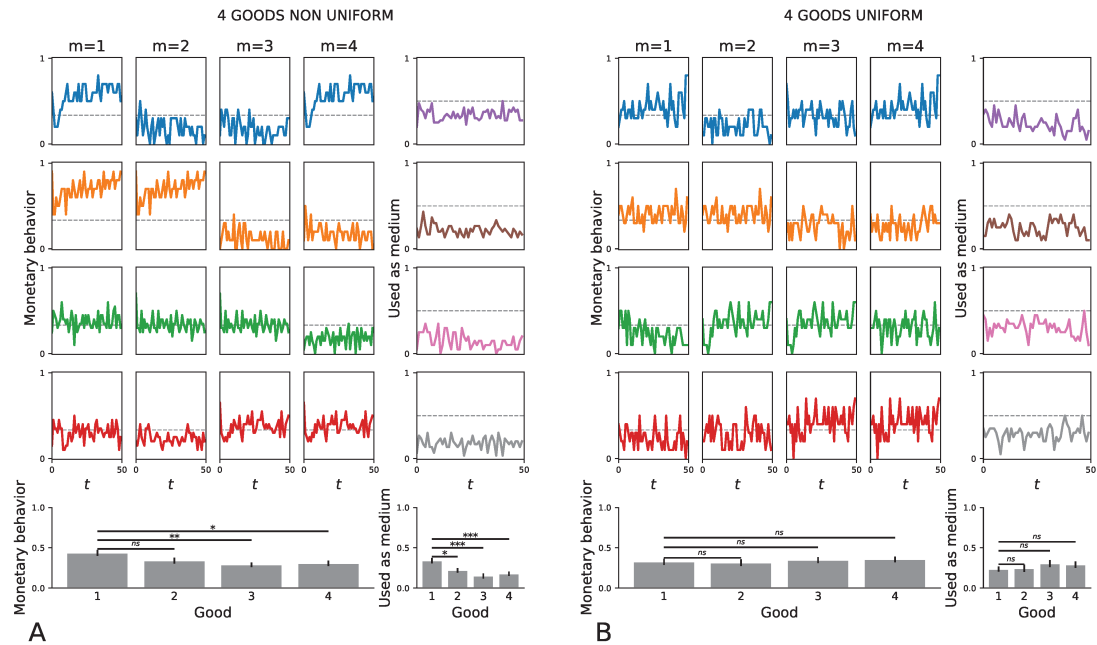


Figure 2.5 – Experimental results: 4 goods in circulation. The computational results allowed us to settle for a non-uniform distribution promoting the use of good 1 as money. Experimental results for such agents distribution are depicted in panels A. We put in contrast the results for a uniform distribution in panel B. The first three columns indicate the proportion of monetary behaviors over time. Each column corresponds to a specific good (respectively 1, 2, 3 and 4). Each row corresponds to a type of agent (respectively from top to bottom type 41, 12, 23 and 34). The gray dotted lines report the chance level (0.33). The last column indicates for each good, the proportion of agent using this good as a medium of exchange (respectively from top to bottom row, good 1, 2, 3 and 4). The gray dotted lines indicate 0.5. On each panel, the left-side bar plot represents the proportions of monetary behaviors averaged over individuals. The right-side bar plot represents the proportions of use of a medium of exchange averaged over individuals. Error-bars correspond to standard errors. The number of stars indicates the level of significance of Mann-Whitney U-test (1, 2 and 3 stars correspond respectively to $p < 0.05$, $p < 0.01$ and $p < 0.001$). In the non-uniform condition (panel A), the proportion of monetary behaviors for good 1 and the proportion of agents using it as a medium of exchange are significantly greater than the corresponding proportions for good 3 and 4, but only the proportion of agents using at a medium of exchange is significantly greater for good 2. In the uniform condition (panel B), as expected, we observe no significant difference.

For the condition with $G = 4$ and a NUPM-distribution that brought together 60 subjects (see Fig. 2.5A), we expected the use of the good 1 as money to be promoted (as for $G = 3$). However, and contrary to what has been observed in artificial agents, it did not emerge as a money. It is only slightly preferred. Indeed, the proportion of agents displaying monetary behaviors with good 1 is significantly greater than the corresponding proportions for good 3 and 4 (respectively $u = 1270.5, p = 0.008$, and $u = 1313, p = 0.016$) but not significantly different from the proportion for good 2 ($u = 1424, p = 0.073$). Nonetheless, and in line with what has been observed in the artificial agents, results show that the good 1 is indeed preferred as a medium of exchange: the proportion of agents using the good 1 as a medium of exchange is significantly greater than the corresponding proportions for good 2, 3 and 4 (respectively $u = 400, p < 0.027$, $u = 176.5, p = 0.001$ and $u = 309, p = 0.001$).

For the condition with $G = 4$ and a U-distribution that brought together 40 subjects (see Fig. 2.5B), we expected no good to emerge as a money and no money indeed emerged. The proportion of agents displaying monetary behaviors with good 1 is *not* significantly different from the corresponding proportions of agents for good 2, 3 and 4 (respectively $u = 754.5, p = 0.997$, $u = 747.5, p = 0.925$ and $u = 728, p = 0.736$). Similarly, the proportion of agents using the good 1 as a medium of exchange is *not* significantly different from the corresponding proportions for good 2, 3 and 4 (respectively $u = 188.5, p = 1.000$, $u = 153.5, p = 0.318$ and $u = 166, p = 0.546$).

2.3 DISCUSSION

The results obtained by means of simulations are in line with our initial assumption, that is to say that the emergence of a commodity money is possible in a decentralized economy with agents having very poor information on the global state of the economy and endowed with limited computational abilities. However, results obtained in humans did not follow our expectations: under the same conditions, human subjects did not reach a consensus in the use of a unique medium of exchange.

The results with artificial agents show that they do not need to have any expertise concerning the economic system in which they evolve to allow this system to acquire certain remarkable macroeconomic properties—such as the existence of a unique medium of exchange. Said differently, these agents do not need to know the macroeconomic properties of the system to be able to influence them. These results extend precedent work^{62,25,53} using a Kiyotaki-and-Wright’s environment^{55,56}. In particular, it shows that in an Iwai-like environment⁴⁵, monetary coordination does not even require agents to have an extended knowledge of other players’ preferences, or to construct a sophisticated belief system: a trial and error approach—comprised in our case as a reinforcement learning mechanism—is sufficient. Of course, this coordination between agents over a unique medium of exchange is not systematic: our results in artificial agents suggest that structural constraints are necessary, as a non-equal distribution of agents over types in our environment. The need for such structural constraints can be interpreted as an interaction between economic structure and agents’ cognition, as a particular endowment-need distribution can render sensitive the benefits of coordinating on a unique medium of exchange.

However, by placing human subjects under the same conditions as our artificial agents, we expected to be able to replicate the results obtained in artificial agents, that is to say to establish a clear contrast between situations where money emergence was promoted, and situations where subjects did not succeed to coordinate. Indeed with three goods in circulation, no money emerged in the situation (non-uniform distribution of agents) where one specific good was theoretically promoted to be used as money, while a good emerged as a preferred medium in the situation (uniform distribution of agents) where it was not expected to. When four goods are in circulation, the experimental results are more in line with the simulation results, in the sense that a good is indeed preferred as a medium of exchange in the situation where it was promoted to be used as a money, and no money emerged in the situation where it was not expected to. However, in the first situation, the specific good that we expected to emerge as money is only *preferred* and not the unique medium of exchange.

This failure to reproduce results obtained with artificial agents may carry several interpretations. (i) We possess data from almost two hundred subjects, but this corresponds to data for only four economies and we expected convergence for only both of them. We can not reject the possibility that the lack of convergence over a medium of exchange for both concerned economies is specific to our sample. (ii) Although several studies point out the fact that reinforcement learning model fits well the behavior of human subjects in economic contexts^{74,30,32}, and specifically in a Kiyotaki & Wright environment^{26,25,53}, it is ineffective in producing accurate predictions in our case. This could be due to the fact that the artificial agents from a same economy were having homogeneous cognitive features—they were learning using the same algorithm and the same of parameters—whereas we can suppose a certain heterogeneity among the human subjects that could make the coordination

more difficult. (iii) In a Kiyotaki & Wright environment^{55,56}, in the specific case where a speculative equilibrium is expected—that is to say when the monetary good has a higher storage cost than the other good—, it has been noted that a non-negligible part of subjects had difficulties to endorse the primary cost implied by the use of the monetary good as a medium of exchange (i.e. to speculate)^{26,53}. It means that some subjects that neither produce or consume the monetary good were reluctant to engage in indirect exchange strategies. Similarly, our experimental results show that part of the subjects that were supposed to proceed to indirect exchanges and suffer from a primary temporal cost, did not adopt such strategies, although most of the subjects that were supposed to use direct exchanges did so (see for instance the results for the condition with a non-uniform distribution promoting the good 1 with four goods depicted in the Fig.2.5A). As in our protocol, subjects do not play against artificial agents that use a deterministic algorithm but against other human subjects, it is nonetheless difficult to tell whether subjects playing (almost) always a direct exchange strategy did it because of the behavior of other subjects, or because they were initially strongly biased toward this option.

If these interpretations are right, one solution could be to scale the experiments in two ways: increasing the number of economies that are tested, while also increasing the number of individuals inside of each economy. Scaling up the number of economies tested would solve *de facto* the problem raised by the first interpretation. Scaling up the number of subjects inside an economy would probably solve the problem raised by the second and third interpretations. Indeed, it will lower the impact that a single subject has on the overall behavior of the economy. By doing so, it will also lower the impact of the few subjects that are strongly biased toward the direct exchange strategy. As a consequence, we can assume that it will affect the accuracy of predictions yield by multi-agent systems using a reinforcement learning

model. However, such a solution would be difficult to put into practice: it would require to be able to recruit a huge number of subjects and at the same time to organize experimental sessions with many subjects playing together. Even if applying such solution is theoretically possible, it highlights the difficulties raised by bringing macro-economics into the laboratory.

As the results obtained by simulation and with human subjects are not completely in line, it is difficult to draw strong inferences about the possibility of money emergence under informational constraints. Reinforcement learning, although effective, is far from being the most sophisticated learning model. It is unlikely that human subjects have failed to coordinate on a single medium of exchange due to more limited cognitive abilities than agents learning by reinforcement. Since the level of information for artificial agents was strictly identical to that of humans, it is probably for other reasons than because of a lack of information. For instance, as we highlighted it, this could be due to a strong inter-individual heterogeneity coupled with too few participants. If this assumption is right, it can offer an explanation of why some societies did not have developed a monetary systems: heterogeneity inside small groups could have been the cause that precludes the emergence of stable coordination phenomenon—money emergence.

2.4 MATERIALS & METHODS

MODEL

PRODUCTION-CONSUMPTION SPECIALIZATION. We consider an economy with G goods in circulation, with $G \geq 3$. We denote these goods $1, 2, \dots, G$. Each agent is specialized in production and consumption. A type- ij agent produces good i and consumes good j (with $j \neq i$). We suppose a non double coincidence of needs: if there exists a type- ij agent, then

there doesn't exist a type- ji agent. We use a *minimally connected endowment-need distribution*⁴⁵, such that existing agent types are: $(G, 1), (1, 2), \dots, (G-1, G)$. The number of agents for each type is exogenously set. We designate by x_1 the number of agent of type $(G, 1)$, x_2 the number of agent of type $(1, 2)$, ... , x_G the number of agent of type $(G-1, G)$. Each agent enters the economy with a unit of his production good. Each time an agent gets his consumption good, he consumes it and immediately after, produces a new unit of his production good (each agent possess a single storage unit).

EXCHANGE TECHNOLOGY. The exchange technology relies on a trading-post mechanism⁴⁵. At each time step, each agent chooses the type of exchange he wants to perform, depending on the good he has in hand. This choice determines to which exchange area he goes. There is an equal number of markets and goods in circulation. We note m_{ij} , the market where it is possible to exchange i against j , and j against i . Our trading technology works synchronously, that is to say that all exchanges occur simultaneously. Thus, in each m_{ij} , we randomly associates each i seller – j buyer to a j seller – i buyer, if there is a sufficient number of j sellers – i buyers. Therefore, in each market m_{ij} , the probability of successfully exchanging a good i against a good j depends on the respective number of i sellers – j buyers and j sellers – i buyers.

LIMITED ACCESS TO INFORMATION. An agent has no knowledge of the probabilities of success of each exchange: the only information he has access to is whether or not he succeeded in the desired exchange.

STRATEGIES. The goal of each agent is to obtain as quickly as possible his consumption good. A strategy is a *tuple* of choices. Each of these tuples contains an alternative of choice for every type of decision an agent can face, giving an action policy to follow. The cardinality

of this tuple is equal to the number of types of decisions an agent can face.

We will specifically consider:

- The *direct exchange strategy*. For a type- ij agent with i in hand (his production good), it consists in trying an exchange against j (his consumption good). An agent applying this action policy would always have i in hand; action policies for other goods can then be ignored. Therefore, with $G = 3$, it is equivalent to the strategies (ij, ki) and (ij, kj) .
- The *indirect exchange strategy* with k as medium of exchange. For a type- ij agent with i in hand (his production good), it consists in trying an exchange against the good k (with $k \neq i, j$). With k in hand, it consists in trying an exchange against j (his consumption good). As this agent would never have anything else than i or k in hand, action policies for other goods can be ignored. Therefore, with $G = 3$, it is equivalent to the strategy (ik, kj) .

MONETARY BEHAVIOR. An economy is in a (pure) *monetary state* if there is a good k^* such as all agents for whom it is their production or their consumption good use a *direct exchange strategy*, and all agents for whom it is neither production good nor consumption good, use an *indirect exchange strategy* using the good k^* as a medium of exchange. If all agents apply this policy, then the markets where the money does not circulate are empty. By extension, we will designate by *monetary behaviors* choices that conform to the use of good k^* as money.

For instance, in an economy with $G = 3$, if the good 1 emerges as money, then type-23 agents use an indirect exchange strategy (using the good 1 as a medium of exchange) while agents of type 31 and 12 use a direct exchange strategy. Table 2.1 in supplementary material illustrate distribution of agents among markets in such a case.

SIMULATIONS

DECISION-MAKING PROCESS. Each agent learns to estimate the success rate of each type of exchange. This allows him to estimate the time needed to get his consumption good depending on the choice he made.

Success rates estimates for each exchange type are based on a reinforcement learning process. At each time step t , an agent attempts to exchange i against j and he updates the estimation associated to this type of exchange, noted e_{ij} , in the following manner:

$$e_{ij}^{t+1} = e_{ij}^t + \alpha \cdot (s - e_{ij}^t)$$

with $\alpha \in [0, 1]$ being the learning rate and s a binary variable such as $s = 1$ if the agent succeeded in his exchange, 0 otherwise. α is a free parameter which defines to which extent an agent takes into account his latest attempted exchange. If $\alpha = 1$, the agent considers only his latest attempted exchange. If $\alpha = 0$, the agent does not take into account the new observations of failure or success of the last attempted exchange.

When making a decision, each agent considers the expected temporal interval between the time of choice and the time he gets his consumption good. It is assumed that the longer the time interval, the lower the value for the agent. Let $v(ij)$ be the value associated to the choice ij (i.e. exchange i against j) and Δ_{ij} the estimation by the agent of the time that will be spent before consumption if he chooses ij :

$$v(ij) = 1/(1 + \beta)^{\Delta_{ij}}$$

with $\beta > 0$, a discount factor parameter. The closer to 0, the more subjective values are discounted with time.

Since it takes at least one unit of time for the agent to get his consumption good, the value function v is bounded between 0 and 1.

We assume that for each type- ij exchange, the agent has an estimation of the success rate associated to this type of exchange (e_{ij}). The higher the estimated success rate, the lower the estimated time to succeed in this exchange. Let δ_{ij} be the estimated time to achieve a type- ij exchange:

$$\delta_{ij} = 1/e_{ij}$$

For a type- ij agent, $\Delta_{ij} = \delta_{ij}$. If a type- ik agent (with $k \neq j$), the value of Δ_{ij} depends on the action policy chosen by the agent, as Δ_{ij} would be equal in this case to the sum of the δ -values for each intermediary exchange planned by the agent. For instance, for a type- ik agent following an indirect exchange strategy with good j , $\Delta_{ij} = \delta_{ik} + \delta_{kj}$. An exhaustive description of valuation functions for the specific case where $G = 3$ is given in the supplementary section.

In order to be able to learn, the agents use a probabilistic decision-making rule. As the use of a standard softmax function to introduce stochasticity in choice could induce unintended side effects when using utility functions with discount rate parameters³, the rule implemented is a simple ε -rule⁸³. Let $v(ij)$ be the value associated with choice ij , $p(ij)$, the prob-

ability to choose to exchange i against j , $p(ij)$, is computed as follows:

$$p(ij) = \begin{cases} 1 - \varepsilon & \text{if } \forall k : v(ij) > v(ik), \\ \varepsilon / (G - 1) & \text{otherwise.} \end{cases}$$

with $\varepsilon \in [0, 1]$ being the exploitation-exploration rate. The lower the ε -value, the more prone the agent will be to choose the option with the highest subjective value among the other available options. On the contrary, the higher the ε -value, the more the agent will be prone to choose an another option.

PROTOCOL & PARAMETRIZATION. We ran 2,700 simulations with $G = 3$. x_1 was set to 50 while x_2 and x_3 were varied between 10 and 190. We ran another 2,700 simulations with $G = 4$. x_1 and x_2 were set to 50 (following results from simulations with $G = 3$) while x_3 and x_4 were varied between 10 and 190. Each simulation lasted 100 time-steps. The exploration parameter (ε) was varied between 0.10 and 0.15. The learning rate (α) was varied 0.10 and 0.25. The discount factor (β) was varied between 0.80 and 1.20. The initial values of success rate estimates for all types of exchanges and for all agents were set to 1. The fact that the initial values were set to 1 precluded the presence of a bias in preferences, such as the appearance of a commodity money was more likely. With these values, the value associated with exchanging his production good against his consumption good was indeed higher than the value of any other exchange for all agents, implying that all agents were preferring the direct exchange strategy at the first time-step. We ran 80 additional simulations using the same distribution of agents as for experiments (see below).

CODE AVAILABILITY. Simulations have been implemented using Python and the scientific stack^{87,46,42}. The code is available at <https://github.com/AurelienNioche/MoneyAnalysis>.

EXPERIMENTS

SUBJECTS. 166 subjects have been recruited by the Maison des Sciences Économiques (106–112, boulevard de l’Hôpital, 75013 Paris, France). We noticed a gender parity (women represented 49.4% and men 50.6%). The average age is 29.15 ± 12.83 .

TASK. A subject embodies a producer of a good i and consumer of a good j , in an economy comprising between 29 and 59 other agents, embodied by other participants. During 50 time steps, he has to choose which type of exchange he wants to try. The only information he gets is whether he succeeded or not in the exchange. Further details are provided in the supplementary section.

EXPERIMENTAL CONDITIONS. Each subject went through only one of the four conditions. The conditions differ by the number of goods in circulation and the distribution mode of agents among types. The number of goods was either 3 or 4. Following the simulation results, we contrasted two modes of distributions, either promoting the money emergence or precluding it:

- *Uniform (U)*. There is an equal number of agents of each type.
- *Non-uniform and promoting money emergence (NUPM)*. The number of agents for a specific type depends on whether this type involves producing or consuming a specific good, that we arbitrarily chose to be the good 1. The number of agent for a type meeting this condition is half the number of agents of a type not meeting this condition.

Combining the variation of the number of good and the type of distribution, the four conditions were the following:

1. $G = 3$ and U-distribution. x_1, x_2 and x_3 were set to 10.
2. $G = 3$ and NUPM-distribution. x_1 and x_2 were equal to 9 but the value of x_3 was doubled (18)—the choice of setting x_1 and x_2 to 9 instead of 10 and x_3 to 18 instead of 20 is due to the absence of some subjects the day the experiment took place.
3. $G = 4$ and U-distribution. x_1, x_2, x_3 and x_4 were set to 10.
4. $G = 4$ and NUPM-distribution. x_1 and x_2 were still equal to 10 but the values of x_3 and x_4 were doubled (20).

ANALYSIS. We measured (i) at each time step, for each good, the proportion of agents (subjects) demonstrating a monetary behavior, (ii) at each time step, for each good, the proportion of agents (subjects) using it as a medium of exchange. For statistical analysis of each measure realized during the experiment-like simulations, we compared for each good a set comprising the mean over time of all the agents number 1 of each economy (20 economies simulated by condition), the mean over time of all the agents number 2 of each economy, ..., the mean over time of the agents number n of each economy. For statistical analysis of each measure realized during the experiment, we compared for each good a set comprising the mean over time for the individual number 1, the mean over time for the individual number 2, ... , the mean over time for the individual number n . As we did not expect a normal distribution of data due to clustering effects at the boundaries of our scale, assessment of statistic relevancy of our observations has been made with Mann-Whitney's U ranking test⁶¹, applying Bonferroni's corrections for multiple comparisons inside a same economy. We set the significance threshold at 5%.

CODE AVAILABILITY. The software we used was based on a client/server architecture. The client part has been developed using Unity game engine. The appli-

cation ran on 7" Android tablets. The assets of the application are available at <https://github.com/AurelienNioche/MoneyApp>. The experiment server was hosted on a local server and has been developed in Python. The code of the server part is available at <https://github.com/AurelienNioche/MoneyServer>. The analysis program is available at <https://github.com/AurelienNioche/MoneyAnalysis>.

DATA AVAILABILITY. The data are available at the same address than the analysis program: <https://github.com/AurelienNioche/MoneyAnalysis>.

2.5 SUPPLEMENTARY MATERIAL

EXPERIMENTS

USER INTERFACE. Following the assumption that a visually appealing serious-game would increase subject's engagement^{90,17} and induce naturalistic decision-making³⁷, we chose to design a game-inspired interface (see Fig. 2.6) instead of a textual interface.

Whatever the good really produced or consumed, a subject is represented in the interface as a producer of wood and a consumer of wheat, having at his disposal stone as a medium of exchange. This choice was motivated by an attempt to limit 'cheating' between subjects: no agent can infer the macroeconomic state by looking at the screens of the other participants.

TRAINING. Each subject went through an interactive tutorial, teaching him the rules and controls for the experiment. He then played a game with random-playing artificial players in order to get comfortable with the interface for 20 time-steps.

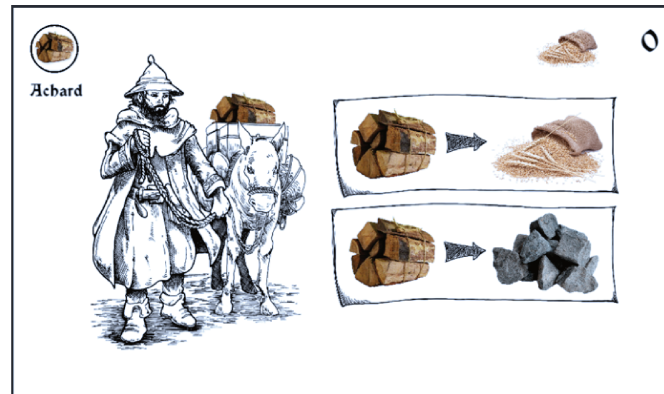


Figure 2.6 – Screen-shot of the user interface during the decision-making phase.

MODEL

MARKETS ATTENDANCE FOR A MONETARY ECONOMY. Table 2.1 provides expected markets attendance when good k^* has emerged as money in an economy with $G = 3$.

m_{ij}	m_{jk^*}	m_{k^*i}
(Nobody)	n_{jk^*}	n_{k^*i}
(Nobody)	$(1 - \lambda) \cdot n_{ij}$	$\lambda \cdot n_{ij}$

Table 2.1 – Markets attendance for a monetary economy with good k^* as a unique medium of exchange and $G = 3$. If k^* is the monetized good in an economy with no double coincidence of needs, then the type- k^*j and type- ik^* agents (that is to say all the agents that are either producers or consumers of k^*) use a direct exchange strategy and type- ij agents use an indirect exchange strategy—a proportion of them (λ) is seeking k^* in exchange for their production good, while the rest of them ($1 - \lambda$) is seeking his consumption good in exchange of k^* .

VALUATION FUNCTIONS FOR $G = 3$. We provide here the equations for the value function for each of the options associated with the two types of decisions that an agent can face when $G = 3$ (the process can be easily generated for any value of G).

Let i be the production good, j , the consumption good and k , the medium of exchange for

the agent under consideration, we have:

$$v(ij) = 1/(1 + \beta)^{\Delta_{ij}} = 1/(1 + \beta)^{\delta_{ij}} = 1/(1 + \beta)^{1/e_{ij}}$$

$$v(ik) = 1/(1 + \beta)^{\Delta_{ik}} = 1/(1 + \beta)^{\delta_{ik} + \delta_{kj}} = 1/(1 + \beta)^{(e_{ik} + e_{kj})/(e_{ik} \cdot e_{kj})}$$

$$v(kj) = 1/(1 + \beta)^{\Delta_{kj}} = 1/(1 + \beta)^{\delta_{kj}} = 1/(1 + \beta)^{1/e_{kj}}$$

$$v(ki) = 1/(1 + \beta)^{\Delta_{ki}} = 1/(1 + \beta)^{\delta_{ki} + \delta_{ij}} = 1/(1 + \beta)^{(e_{ki} + e_{ij})/(e_{ki} \cdot e_{ij})}$$

3

Induction of a non-competitive behavior in a duopoly^{*}

ABSTRACT. Duopolies describe situations where two independent sellers compete for capturing market shares. Such duopolies do exist in the world economy (e.g. Boeing / Airbus, Samsung / Apple, Visa / MasterCard) and have been extensively studied in the literature using theoretical models. Among these models, the spatial model of Hotelling (1929) is certainly the most prolific and has generated a subsequent literature, each work introducing some variation leading to different conclusions. However, most models assume consumers to have an

*. The content of this chapter is an independent research article under review. It has been simply formatted for the sake of graphical consistency. The co-authors of this article are Basile Garcia (equal contribution), Thomas Boraud, Nicolas Rougier & Sacha Bourgeois-Gironde.

unlimited access to information (perfect information hypothesis) and to be rational. Here we consider a situation where consumers have a limited access to information and explore how this factor influences the behavior of the competing firms. We first characterized three decision-making processes followed by individual firms (maximizing one's profit, maximizing one's relative profit with respect to the competitor; or tacit collusion) using a simulated model, varying the level of information of consumers. These manipulations alternatively lead the firms to minimally or maximally differentiate their relative position. We then tested the model with human participants in the role of firms and characterized their behavior according to the model. Our results demonstrate that a limited access to information by consumers can actually induce a mutually beneficial non-competitive behavior of firms, which is not traceable to explicit collusive strategies. Imperfect information on the part of consumers can therefore be exploited by firms through basic and blind heuristics.

3.1 INTRODUCTION

Hotelling⁴⁰ introduced in 1929 a formal turn-based model aimed at describing competition in a duopoly. This model considers a pool of consumers that are uniformly spread over a one-dimensional segment. Two firms selling the same product have to decide where to locate on this segment and what price to offer for their product, knowing that each consumer will choose a firm according to its relative distance (linear transportation costs) and the price of the product. The original study holds that in such conditions, firms have a tendency to aggregate and compete near the center of the segment (minimal differentiation principle) due to the effort of the firms to capture the largest number of consumers. However, subsequent research^{20,28,18,7,29} demonstrated the existence of an antagonist principle of maximal differentiation, using either quadratic transportation costs, a higher number of

competitors or a higher number of dimensions on which firms can differentiate themselves. In the end, both minimal and maximal differentiation can be incentivized and observed^{21,44}. Here we show how the level of information of consumers may induce different behavior for the two firms, depending on their strategies.

Several experimental studies have already attempted to characterize the various factors influencing differentiation. For instance, Kruse & Schenk⁵⁸ allowed for communication between participants in the role of firms and showed that they tend to group in the center when communication is limited, but on the contrary, to differentiate themselves if communication is unlimited (cooperation). Similarly, Kephart & Friedman⁵¹ set up a protocol contrasting continuous and discrete time and demonstrated that continuous time could trigger a maximal differentiation strategy, as it allows some form of communication, and as a consequence, some form of cooperation. These two findings brought together suggest that quick and/or full information transmission can help to reach a cooperative equilibrium in a typical Hotelling's model. Several other studies brought up arguments supporting the robustness of the minimal differentiation phenomenon such as, for example, the four-player version of the game by Huck et al.⁴¹ or in Barreda et al.⁵, where subjects tended to group in the center under several experimental conditions. Although there is a treatment in Barreda et al.⁵ with human subjects as consumers, what is common to all these works is their shared assumption of the fact that firms are competing to capture rational and fully informed consumers—even when they document spatial behavior that departs from Nash equilibrium when it theoretically exists. The case when consumers have no full informational access to the firms' strategies and when firms must compete over this less than completely informed consumers have not been addressed, to our knowledge, in the experimental literature related to Hotelling. It has yet important implications

as it is a common fact that consumers are not fully aware of all options available on the markets they participate in and that firms know and anticipate this fact in their own strategies.

Stigler⁸¹ argued that the information question should be fully taken into account in such competition models, as it can deeply impact the nature of equilibria. This is particularly important as consumer choices are known to be subject to several biases and based on partial information^{84,48}. More precisely, the uncertainty resulting from the imperfect nature of information has been shown to provide an incentive for the firms to regroup and transparency of the market is thus a prominent factor for differentiation^{91,79}. In line with predictions from earlier studies^{27,10,24,77}, we postulate that in a duopoly context, the consumers' access to information is a critical factor for the differentiation of the two firms. We thus defined a formal turn-based model (based on the original Hotelling model) that allows us to explicitly manipulate the amount of information available to consumers while retaining their rational nature. Agents can act rationally under partial information and thereby induce observable organizational patterns in the market that differ from what is expected under perfect information. We therefore test the hypothesis that the amount of information accessible to consumers can variably drive the differentiation of the two firms: when this amount is low, firms will be maximally differentiated; when this amount is high, firms will be minimally differentiated. We test this hypothesis using a simulation where we consider three decision-making processes for the firms, namely (i) a maximization of short-term profits, (ii) a maximization of the difference of profits between the firm and its opponent, (iii) a maximization of the profits of the two firms. They constitute plausible behavioral responses on the part of firms in the light of partial information on the part of consumers. These heuristics helped us to characterize the behavior of human subjects for the experimental part of this work where subjects play the role of the firms under different informational conditions.

3.2 RESULTS

COMPUTATIONAL. In order to test our hypothesis regarding the influence of the information level of consumer (measured by his view radius) on the differentiation of the two firms, we ran 1000 simulations using a random view radius between 0.00 and 1.00 and tested three different heuristics for the firms, namely Profit Maximization (PM), Difference Maximization (DM) and Tacit Collusion (TC). For each of these simulations, we measured the mean distance between the two firms, which is the distance separating the two firms averaged over the last third on the 100 turns. We report on Figure 3.1 all these distances on the y axis and the corresponding view radius on the x -axis. Minimal differentiation corresponds to a mean distance of 0.00—firms being placed at the center of the linear city—while maximal differentiation corresponds to a mean distance of 0.50—one firm being placed on the first quarter of the linear city and the other one at the last quarter.

The high dispersion of the points when r is close to 0.00 or near 1.00 can be explained by the fact that the firm location has almost no impact on the firm profits. If the value of r is close to zero, the consumers are almost blind in the sense that their view radius is so narrow that except if the competitor is very close, each firm would sell its product to only a few consumers, regardless of its position. If r is close to 1.00, the visual field of the consumer is so broad that it will see both firms and these firms will always compete. For such extreme values of r , the mean distance observed is close to 0.33, which corresponds to the mean distance observed for random moves. Because each consumer sees only its own position or sees both firms, it is indeed expected that the firms randomly choose their location, which corresponds to a mean distance of 0.33.

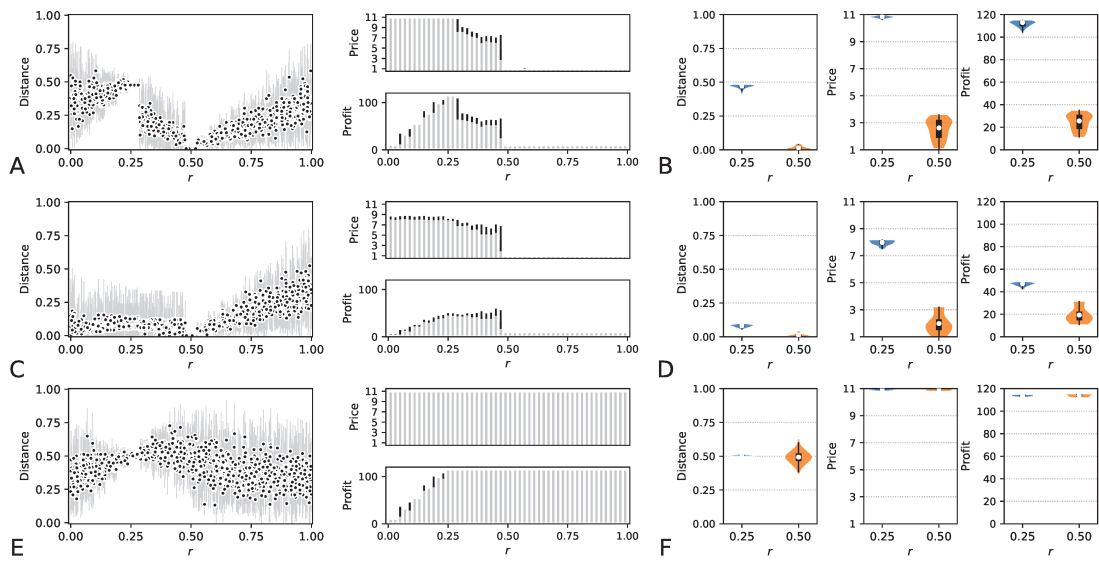


Figure 3.1 – Simulation results. For each of the three heuristics (Profit Maximization [PM], Difference maximization [DM], Tacit collusion [TC]), 1000 simulations were run with a random (uniform) view radius for the consumers. The distance between the two firms, the profit and the price as a function of the consumers' view radius is displayed on panels A (PM), C (DM) and D (TC). Each dot corresponds to the mean distance that has been observed between the two firms during a single simulation and vertical bars indicate the standard deviation. Mean prices and profits are reported on the right using gray bars and the standard deviation in black. For each of the three heuristics (PM, DM, TC) and for low and high view radius ($r = 0.25, r = 0.50$), 25 additional simulations were ran and observed distance, price and profit are displayed on the right (B, D, F) in order to compare them to the experimental results.

We can observe on figure 3.1A that for the PM heuristic, a view radius of 0.50 corresponds to the minimal differentiation principle where the two firms compete to occupy the central position because this is the unique position that gives access to all the consumers (all consumers are potential consumers for the firm positioned at the center). It thus makes sense for the two firms to compete around this position and to try to get a maximum number of consumers in order to maximize their profit. Because of this competition, the mean price for both firms is very low and leads to moderate profits. When the view radius is reduced to 0.25, the mean distance between the two firms is maximal (0.05). This specific radius corresponds to a case where there is a possibility of local markets as shown on Fig. 3.4. The two ends of the plateau when $r = 0.25$ represents a compromise between competition and a lesser number of consumers, but those consumers are captive for each firm. This allows both firms to set higher prices and to maximize their profits. When the DM heuristic is used (see Fig. 3.1C), there is no maximal differentiation anymore when $r = 0.25$. Firms tend to minimally differentiate, their respective position forcing them to reduce their prices and hence, greatly reducing their profits compared to what happens with firms using a PM heuristic. As one would expect, when firms try to optimize at the same time their profit and their opponent's profit (TC heuristic), prices become independent of the firm position and the principle of maximal differentiation only applies in the vicinity of $r = 0.25$ where the two firms can equally share the market (see Fig. 3.1E).

Focusing our attention on the specific cases where $r = 0.25$ or $r = 0.50$ (figures 3.1B, 3.1D and 3.1F), one can notice quite different situations in terms of distance, price and profits for the three policies respectively. For $r = 0.25$, the principle of maximal differentiation applies for PM and TC heuristics, leading to maximal prices and profits. This is not true for the DM heuristic where the principle of minimal differentiation seems to apply, leading

to moderate prices and profits. For $r = 0.50$, the situation is different and both the PM and DM heuristics lead to a minimal differentiation of the two firms with low prices and profits. Only the collusive heuristic (TC) allows for an implicit equal share of the market, with highest prices and profits. Together, these three heuristics allow to give account on minimum or maximum differentiation in the two specific cases of low and high level of information available to the consumers.

EXPERIMENTAL. When considering the effect of the view radius of consumers on the mean distances, prices and profits, experimental results are very similar to the results of simulations when the Profit Maximization (PM) heuristic is used, and this, independently of whether the opponent's profit is visible or not. More precisely, the median distance is greater when $r = 0.25$ than when $r = 0.50$ ($u = 81.5, p < 0.001$ when $s = 0$; $u = 33.0, p < 0.001$ when $s = 1$). The same applies for the prices ($u = 128.5, p < 0.001$ when $s = 0$; $u = 30.5, p < 0.001$ when $s = 1$) and for the profits ($u = 178.0, p < 0.001$ when $s = 0$; $u = 131.5, p < 0.001$ when $s = 1$). The display of the opponent's profit (condition $s = 1$) has a limited effect on the general shape of the data relatively to distance, price and profit. It only has an effect on distance when $r = 0.25$ ($u = 191.0, p = 0.007$). Although the general shape of data is close to what has been observed in is to be able simulations using the PM heuristic, the dispersion of results is much more spread out and we assume this scattering of the data can be attributed to inter-individual differences.

In order to study this inter-individual variability, we computed three individual scores for each subject, assessing the compatibility of their behavior for each time step of the experiment with the use of (i) a PM heuristic, (ii) a DM heuristic, (iii) a TC heuristic. Distribution by experimental condition of PM, DM and TC scores are shown in Fig. 3.2B.

A matrix correlation of the scores by experimental condition has also been computed (see Fig. 3.2C). Several observations regarding this individual scoring can be made. First, whether opponent profit is displayed ($s = 0$) or not ($s = 1$), the radius r has an impact on PM, DM and TC scores. The DM median score is higher when $r = 0.50$ compared to when $r = 0.25$ ($u = 488, p < 0.001$ when $s = 0$; $u = 460$ when $s = 1$) while PM median score is lower ($u = 1048, p = 0.001$ when $s = 0$; $u = 861, p = 0.009$ when $s = 1$), as is the TC median score ($u = 179, p < 0.001$ when $s = 0$; $u = 87, p < 0.001$ when $s = 1$). Second, the display of the opponent's profit has an effect on individual scoring. When $s = 1$, the DM median score is higher when $r = 0.25$ ($u = 733.0, p < 0.001$), and the TC median score is lower for both value of r ($u = 948.0, p = 0.002$ when $r = 0.25$; $u = 881.0, p < 0.001$ when $r = 0.50$). Third, similarly as results obtained in simulation, a radius value of 0.25 allows to discriminate the use of a PM heuristic from a TC heuristic, and a radius value of 0.50 allows to discriminate the use of a PM heuristic from a DM heuristic. This is especially noticeable when looking at the distribution of the scores (figure 3.2B) but also when looking at the correlation matrix (figure 3.2C). When $r = 0.25$, a subject who has a high score in PM would likely to have a high score in TC but a low score in DM, while when $r = 0.50$, a subject who has a high score in PM would likely have a high score in DM but a low score in TC.

If we now look more closely at individual behaviors, it is striking to see that when subjects competing together has been identified both as users of a specific heuristic (i.e. obtained a high score toward PM, DM or TC), the dynamics of his playing is very similar to the corresponding simulation. With $r = 0.25$, subjects using PM heuristic tend to position themselves at the first and third quarters of the segment and both set a high selling price (see Fig. 3.3A). However, when $r = 0.50$, subjects position themselves at the center and immediately lower their price (see figure 3.3B) even though they are less inclined to do so compared to simulated

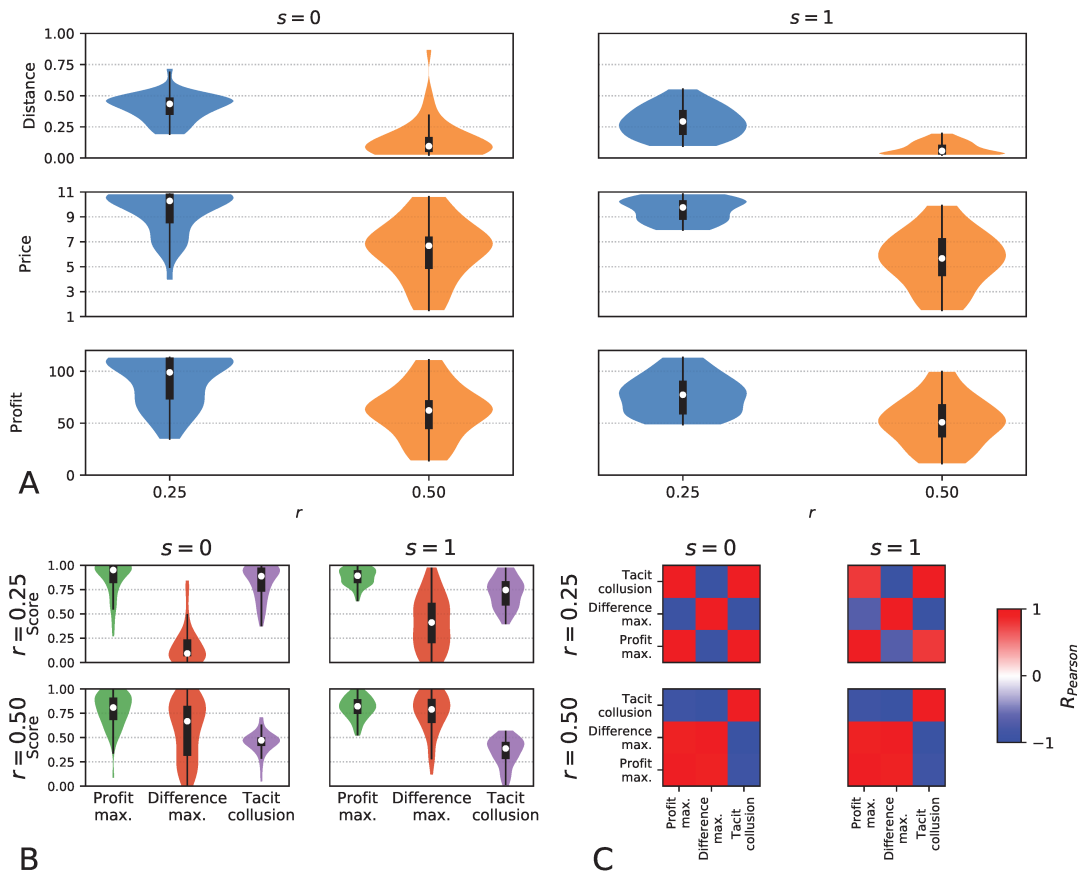


Figure 3.2 - Experimental results. **A.** Combined effect of the consumers' view radius and the display of the opponent's score on distance, price, and profit. The white dots indicate the median, the thick black bars indicate the IQR. The extrema of the thin bars indicate the lower and upper adjacent values. The colored areas give an indication of the shape of the data distribution. **B.** Mean scores of Profit Maximization (PM), Difference Maximization (DM) and Tacit Collusion (TC) by experimental condition. The white dots indicate the median, the thick black bars indicate the IQR. The extrema of the thin bars indicate the lower and upper adjacent values. The colored areas give an indication of the shape of the data distribution. **C.** Score correlation matrix. Blue color indicates a strong negative correlation and red color a strong positive correlation.

firms using the corresponding heuristic. They are actually trying to regularly increase their price. The situation is a bit different for subjects using a DM heuristic when $r = 0.25$ (see Fig. 3.3C). In that case, the positions of subjects oscillate around the center accompanied with an increase and decrease in prices, indicating a will to capture the market of their opponent. When $r = 0.50$, both simulated firms and human subjects using a TC heuristic set their prices at their maximum but the dynamics are not exactly the same (see Fig. 3.3D). Subjects positioned themselves further apart, and this increase of the distance can be assumed to be due to an intent from the subjects to communicate their goodwill to their opponent.

3.3 DISCUSSION

The principle of minimal differentiation as exposed in the seminal paper of Hotelling⁴⁰ did not reach consensus in the abundant subsequent literature. Once some restrictive assumptions of the initial model are relaxed (for instance, number of firms, spatial structure or cost structure), it has been shown that the principle of minimal differentiation can be invalidated and that the antagonistic principle of maximal differentiation could apply^{20,28,18,29,44}. Coincidentally, both simulations and experiments allowed us to demonstrate that the consumers' amount of information also affects the differentiation of firms with respect to their decision-making features. We isolated incentives supporting either a geographic concentration and a fierce price competition resulting in drastic reduction of profits, or a maximal differentiation inducing a softening of the price competition and thereby a large increase in firms' profits.

This means that the principle of maximal differentiation may be systemic and cannot be uniquely attributed to the deliberate use of a cooperative strategy on the part of firms,

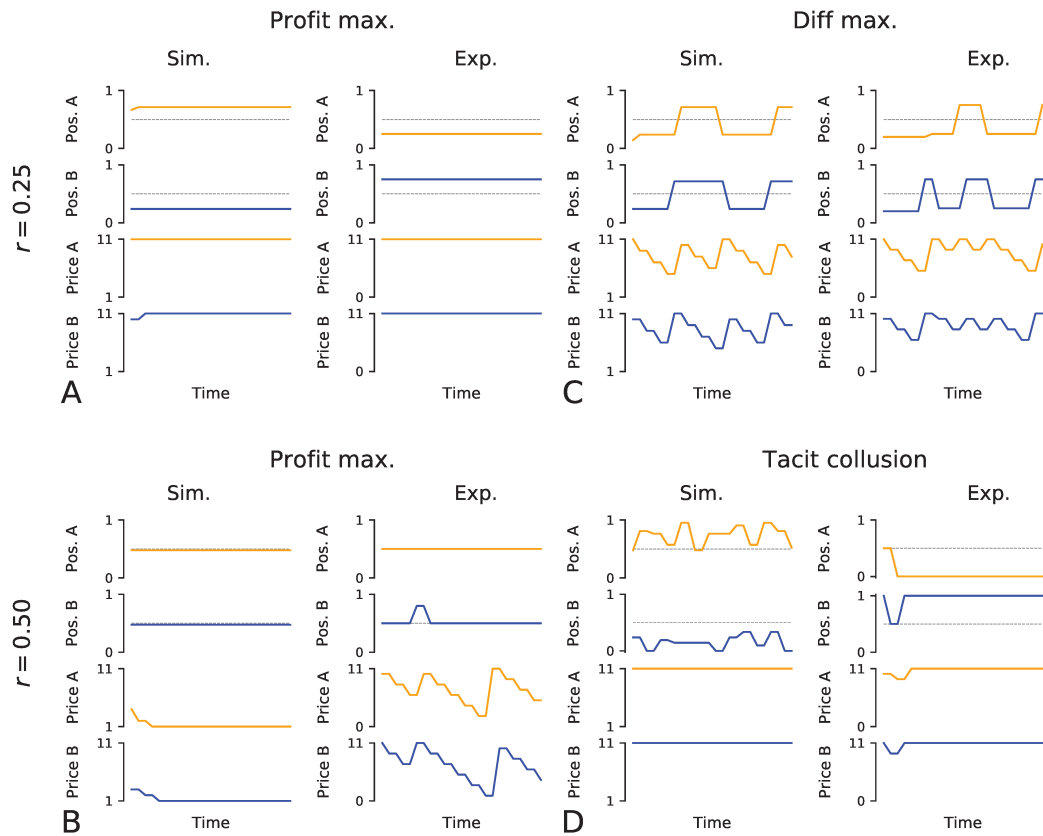


Figure 3.3 – Analysis of dynamics. Comparison of dynamics between artificial firms and human controlled firms. Each figure presents evolution of positions and prices of two firms in competition. **A.** Left: artificial firms using a profit maximization strategy; right: two participants with a high score in profit maximization; $r = 0.25$. **B.** Left: firms using a Profit Maximization (PM) heuristic; right: two participants with a high score in PM; $r = 0.50$. **C.** Left: two firms using a Difference Maximization (DM) heuristic; two participants with a high score in DM; $r = 0.25$. **D.** Left: two firms using a Tacit Collusion (TC) heuristic; right: two participants with a high score in TC; $r = 0.50$.

or to tacit collusion as in Kruse & Schenk⁵⁸ and Kephart & Friedman⁵¹. In our case, the use of a tacit collusion in the condition where high information is available, led a few participants in our experiment to maximally differentiate themselves from their competitor. However, when consumers have only access to a low level of information, the occurrence of maximal differentiation in experimental results can in turn be interpreted as an adaptation to these consumers' limited access to information. In that circumstance, firms using a profit maximization heuristic formed local monopolies without any willingness to cooperate with the other firm. This supports and provides a possible rationale to d'Aspremont et al.'s final open remark in their fundamental reexamination of Hotelling's model²⁰, according to which, contra Hotelling, one should intuitively expect differentiation to be a distinctive feature of oligopolistic competition. Oligopolists should indeed be better off by dividing the markets into submarkets over which they each exert quasi-monopolistic control. Our results actually demonstrate that a limited access to information, on the part of consumers, can be an underlying factor—and a prevailing one in actual competitive markets—that induces a non-competitive behavior from which firms, without prior explicit collusion, can take advantage of the situation and establish local monopolies which are detrimental to consumers. Our results show that only the use of a profit difference maximization heuristic precludes the formation of such local monopolies.

Besides, the use of these heuristics allowed us to emphasize heterogeneous behaviors. Thinking these various behaviors in terms of deviation from a rational behavior—understood as the maximization of a unique utility function—would have prevented us from making sense of this heterogeneity. In order to define our heuristics, we measured whether our subjects looked for maximizing their own profit, whether they aimed at maximizing the difference of profits with their opponents, or finally whether they tried to

create a tacit collusion. The profit maximization heuristic appears to be a good predictor of the firms' aggregated behavior, while the other heuristics offer an opportunity to account for less expected behaviors.

The use of a difference maximization heuristic indeed supported a fierce competition when informational structure opened the possibility of quasi-monopolies. The use of this heuristic could be explained by the presence of an underlying anchoring bias⁸⁵: as it is difficult to evaluate the success of a move *per se*, a move is considered efficient if it leads to better profits than its opponent. In other words, firms' strategy evaluation relies on comparisons to a given point instead of an evaluation in absolute terms. This could explain why this heuristic has been promoted by the display of the opponent score. The use of such heuristic could also be due to an underlying *zero-sum* bias^{64,75}: considering wrongfully that a greater profit for its opponent is necessarily a profit loss for itself, a firm could decide to make its choice only considering the profit difference.

While difference maximization heuristics precluded under certain conditions the formation of monopolies, the use of a tacit collusion heuristic allowed to relax price competition when information structure was promoting it. As a means to avoid the drawbacks of a competition situation leading to lower profits, the use of such heuristic could be explained by the search for a Pareto optimality⁷⁰—that is to say following the strategies that lead to a repartition of profits such as no firm could earn more, otherwise it would be at the expense of the other. It could also be interpreted as deliberate attempts to emit signals in order to relax competition in a situation where the communication technology needed to lead it rationally is lacking.

Another consideration that is raised by our study is that the consequences of using such heuristics can differ from Nash predictions applied to a basic Hotelling’s model under full information: for instance, the use of a tacit collusion heuristic under full information leads to maximally differentiate while minimal differentiation would be expected. However, it is now a well-trodden theme that heuristics can be interpreted in terms of their adaptive rationality³⁵. As long as a chosen heuristic improves the outcome of the game and corresponds to relatively stable observable spatial patterns, we can speak of a specific form of rationality arising under the imposed informational constraint. A work by Sutton⁸², applied to the Hotelling’s model, explores such an equilibrium notion and weak rationality requirement, based in his case on a single heuristic, which is to seize an opportunity when it presents itself. It would take a further study to understand how the heuristics highlighted here indeed constitute adaptive rational behaviors to informational constraints, either exerted on consumers—by means of their difficulty to have access to information—, or exerted on firms—by means of their disability to communicate.

3.4 MATERIALS & METHODS

SIMULATIONS. We consider a normalized unidimensional space with a linear city constituted by a normalized segment $[0, 1]$, two firms $\{F_i\}_{i \in [1, 2]}$ and a group of N consumers $\{C_i\}_{i \in [1, N]}$. Each consumer $C_i = (x_i, r_i)$ is characterized by a position x_i and a view radius r_i . Each firm $F_i = (x_i, p_i)$ is characterized by a position x_i and a price p_i . Consumers are uniformly spread over space such that $x_i = i^{-1}/N^{-1}$. View radius is defined on a per-experiment basis. Firm position is a free variable and must correspond to a consumer position such that there are only N different possible positions for a firm. Price p_i is a free variable and is discrete: there are P possible prices spread uniformly between a minimal price P_{min} and a max-

imal price P_{max} . Simulations are turn-based^{72,59}. We distinguish at each turn an active firm that is allowed to select a strategy and a passive firm that has to wait for the next turn to react and deploy its own strategy. More specifically, at turn t , Firm A (F_1 or F_2) chooses its location and its price, consumers choose a firm and profits are collected for both firms. At turn $t + 1$, Firm B (F_2 or F_1) chooses its location and its price (while firm A keeps location and price from previous turn t), consumers choose a firm and profits are collected for both firms. Let Π_i be the profit of the firm F_i for a single turn defined by $\Pi_i = p_i \cdot q_i$ with p_i the price at which F_i sells its product, and q_i the quantity F_i sold. Each consumer has a view radius that defines a segment centered on the consumer $[x_i - r_i, x_i + r_i]$. Only firms located inside this segment are considered by the consumer (see Fig. 3.4). Consequently, at each turn, some consumers will see only one firm and will be captive since they cannot choose what firm to buy from. Some consumers will see both firms and are named volatile because they can choose any of the two firms depending on their choice criterion. Some consumers won't see any firms and cannot buy, and thus are named ghost consumers. A view radius of 0 means the firm has to be at the same position to be seen while a radius of 1 means firms are always seen by the consumer. Reciprocally, and depending on the consumer view radius, firms have access only to a subset of all the consumers, they are named the potential consumers and represent the sum of captive and volatile consumers.

PARAMETERS. For all the simulations, we used the following parameters: N (number of consumers) = 21, P (number of prices) = 11, P_{min} (minimal price) = 1, P_{max} (maximal price) = 10, Number of turns = 100. The initial position and price for the passive firm (first turn) are randomly assigned. The view radius (r) is the same for all the consumers and is comprised between 0 and 1. For each of the three different decision-making processes, we ran (i) 1000 simulations with r randomly (uniformly) drawn between 0 and 1 for each simulation; (ii)

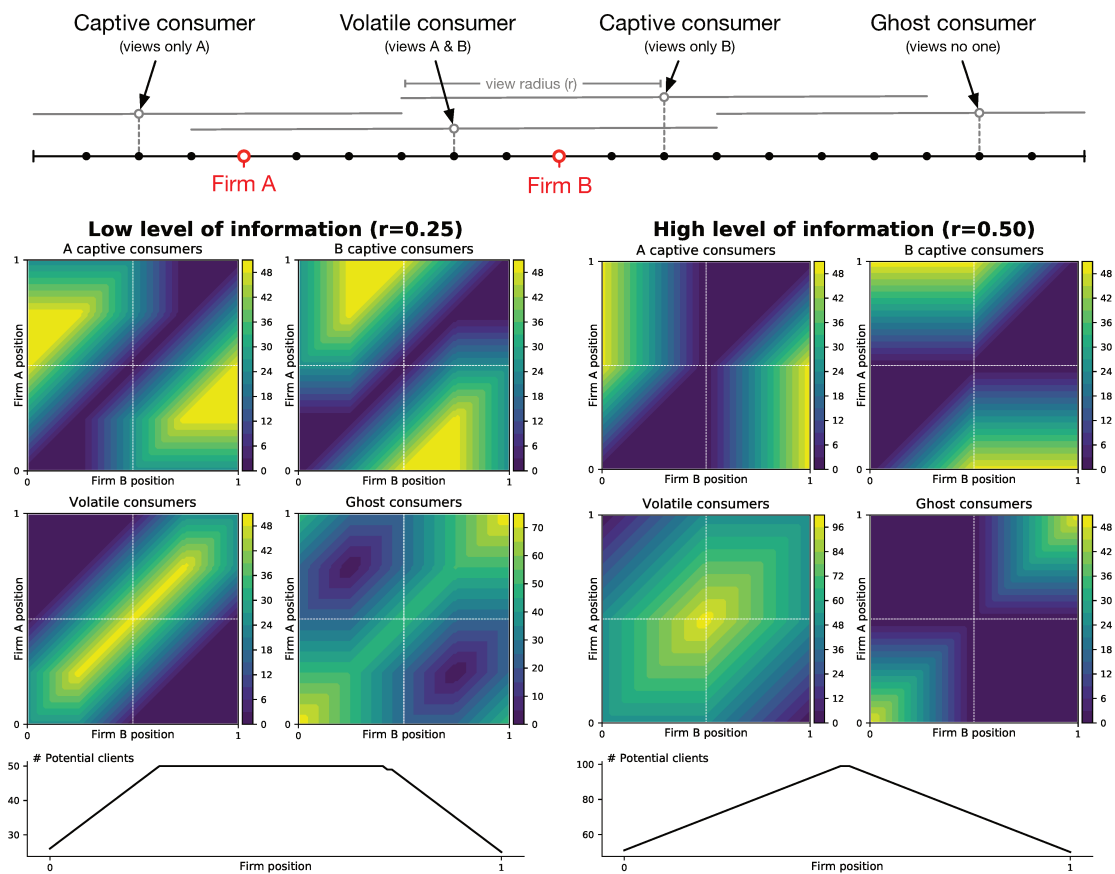


Figure 3.4 – Model. The model is represented by a one-dimensional line segment over which consumers (black dots) are spread uniformly. Firms (outlined red dots) are free to position themselves on any consumer position. Consumers view firms that fall within their view radius such that some consumers view only one firm (captive consumers), some consumers view both firms (volatile consumers) and some consumers view none (ghost consumers). The number of captive, volatile and ghost consumers for a firm depends on the size of the view radius of the consumers and the respective position of the two firms. The number of captive consumers increases as the view radius of consumers decreases. The number of potential consumers (captive + volatile) of a firm is a function of the position of the firm and the view radius of the consumers. When the level of information is high ($r = 0.50$), there is a unique position where all the consumers are potential consumers for a firm. When the level of information is low ($r = 0.25$), there is a whole segment where exactly half the consumers are potential consumers for a firm.

25 additional simulations with $r = 0.25$ and $r = 0.50$ respectively, in order to characterize experimental data.

DECISION-MAKING PROCESSES. Consumers do not choose the amount of information they dispose and may see zero, one or two firms. In the event that they do not see any firm, they are unable to buy and have to wait for the next turn. If they see a single firm, they have no means to compare prices and have to buy from this firm, independently of the price (each consumer has an unlimited budget). When they are able to see the two firms, they buy from the firm offering the lowest price. In the specific case where prices of both firms are equal, they choose randomly between the two. Firms have perfect knowledge of the environment: they know (i) the price and the position of the opponent, (ii) the location of each consumer x_i , (iii) the view radius r_i of each consumer and (iv) the decision-making method of consumers. Firms from two different simulations can differ in their decision-making process but two firms from the same simulation share the same decision-making process. Decision-making process of a firm is either one of the three following heuristics:

Profit Maximization (PM). Each time an active firm plays, it computes the potential profits for all the possible couples position-price regarding the current decision-making process of the passive firm, and chooses the couple position-price that maximizes profit (in the case where several couples position-price lead to the same best payoff, the firm chooses randomly between these moves);

Difference Maximization (DM). If Firm A is the active firm, the difference between its own profit and the profit of Firm B is computed for each possible move, and the move leading to the greatest difference is chosen (in case of multiple moves leading to the greatest difference, the move is randomly chosen between those moves);

Tacit Collusion (TC). The distance to the maximum profit for Firm A and the distance to the

maximum profit for Firm B are computed for each move the active firm can play, the chosen move is the one leading to the minimum sum of the distances.

EXPERIMENTS. Participants were recruited using the Amazon Mechanical Turk (AMT) platform. AMT is an online crowdsourcing service where anonymous online workers complete web-based tasks in exchange of a compensation. It was noted that responses from AMT participants were at least as reliable as those obtained in laboratory^{11,2}. In addition, AMT participants exhibit similar judgment and decision biases such as framing effects, conjunction fallacy, or outcome bias⁶⁹. The ethics approval for this project was provided by the Ecole Normale Supérieure as per the school's guidelines. In line with ethical guidelines, all participants provided informed consent before proceeding to the experiment. Participants also had to fill in a survey asking their age, nationality, and gender. A financial compensation of one dollar was offered to each participant, with a bonus proportional to their score. Participants were paired inside a dedicated virtual room and each pair went through one of the four treatments. The four treatments correspond to the combination of two factors: consumers' view radius (r) and the display of the opponent's profit (s). The consumers' view radius that was either low ($r = 0.25$) or high ($r = 0.50$) and the opponent's profit was either hidden ($s = 0$) or displayed ($s = 1$). For all the rounds, we used the same parameters as for simulations except that we maintained constant the initial locations of firms: one of the two firm was placed at one of the extrema of the segment, the other firm at the other extrema. Their initial price was set to 5. The subject playing first was randomly selected. The number of rooms for each condition and corresponding number of subjects which went through all the process is: ($r = 0.25, s = 1, n = 26$), ($r = 0.25, s = 0, n = 30$), ($r = 0.50, s = 1, n = 26$), ($r = 0.50, s = 0, n = 29$). Additional information is provided in the supplementary section.

ANALYSIS. Only data obtained from subjects that have fully completed the experimental procedure has been used for analysis. Among the 420 subjects that signed up to the platform, 216 subjects went through all the process. The reasons why a subject may not have completed the procedure are (i) the impossibility to match him with another subject, (ii) quit before the end, (iii) a technical problem (i.e. poor computer performances). The sample of subjects we used for analysis matches the demographic characteristics of AMT⁴³. Regarding the composition of the participants, we noticed a gender parity (women represented 54.1% and men 45.9%). The average age was 34.75 ± 9.54 . We counted a dozen nationalities, the most common being American (75.78%) with a large majority, and, to a lesser extent, Indian (11.71%).

We drew a three-dimension profile for each subject by assessing at which extent he maximized at time t (i) his profit—Profit Maximization (PM) score—, (ii) the difference of profit with the other subject—Difference Maximization (DM) score—, (iii) the profits of both him and his opponent—Tacit Collusion (TC) score. Let $v_H(c, t)$ be the value of the choice $c \in C$ of position-price couple given the use of an heuristic H at time $t \in [1, t_{\max}]$ (for instance, $v_{PM}(c, t)$ is equal to the profits at the end of t if the firm chooses c using heuristic PM). We compute the intermediate score for a subject i for heuristic H for each t :

$$f_H(i, t) = \begin{cases} \frac{v(c_i^t, t)}{\max_{c \in C} v(c, t)} & \text{if } \max_{c \in C} v(c, t) > 0, \\ 1 & \text{otherwise.} \end{cases}$$

with c_i^t the choice made by subject i at time t . We then compute the score for a subject i and

for a heuristic H in the following way:

$$s_H(i) = \frac{1}{t_{max}} \sum_t f_H(i, t)$$

For the analysis, we pooled the individual scores by experimental condition. As we did not expect a normal distribution of data due to clustering effects at the boundaries of our scales (i.e. price), assessment of statistic relevancy of our observations has been made with Mann-Whitney's U ranking test⁶¹, applying Bonferroni's corrections for multiple comparisons. We set the significance threshold at 1%.

CODE AVAILABILITY. Simulations were implemented using Python and the Python scientific stack^{46,87,42}. The code is available at <https://github.com/AurelienNioche/SpatialCompetition>. The software used for the experimental part is based on a client/server architecture. The client part was developed using the Unity game engine, hosted on a dedicated server and ran in the subjects' web browser using WebGL API. The code of the assets is available at <https://github.com/AurelienNioche/DuopolyAssets>. The experiment server was hosted on a dedicated server and developed using the Django framework. The code of the server part is available at <https://github.com/AurelienNioche/DuopolyDjango>. The analysis program is available at <https://github.com/AurelienNioche/DuopolyAnalysis>.

DATA AVAILABILITY. Figures 3 and 4 were produced using raw data that are available at <https://github.com/AurelienNioche/DuopolyAnalysis>.

3.5 SUPPLEMENTARY MATERIAL

USER INTERFACE. In most of the previous experimental studies on Hotelling, subjects were interacting using textual interfaces^{58,16,41,51}. However, it has been shown that Amazon Mechanical Turk's workers would complete the task more carefully if they find it enjoyable¹⁹. Following the assumption that a visual appealing serious-game would increase subject's engagement^{90,17} and induce naturalistic decision-making³⁷, we chose to design a game-inspired interface (see Fig. 3.5) instead of a textual interface.

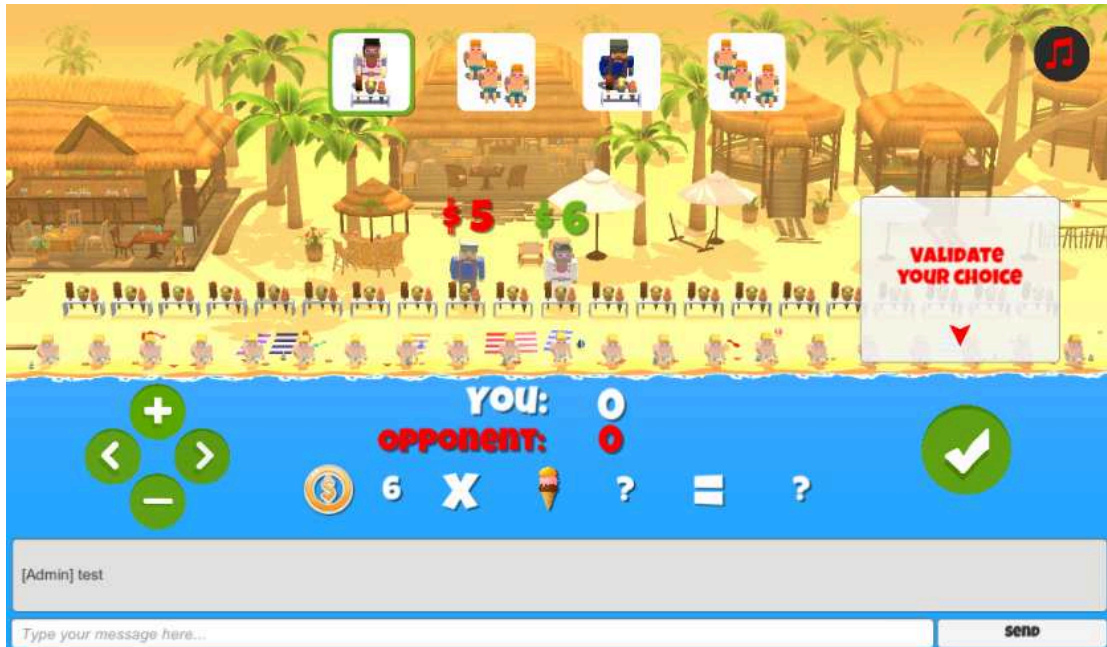


Figure 3.5 – User interface. The game was running in the subjects' web browser. The subjects may choose their location using left and right arrows on the left button pane and their price using the minus-plus button couple. The choice is submitted using the validation button located on the right side of the interface. They were able to contact the experimentalist using the chat tool (bottom of the screen).

MATCHMAKING. Participants were recruited using the *Amazon Mechanical Turk* platform. Once the task accepted, the subjects were asked to visit a dedicated website in order to

pass the experiment. Subjects matching relied on a room system comparable to the system used on online gaming platforms. Each room accepted two subjects. As they were four experimental conditions, they were four types of rooms (see 'Materials & Methods' section).

After logging in, subjects were assigned to a room. The room assigned was in priority a room where there was only one missing player. Otherwise, they were assigned to an empty room and were asked to wait for another subject. If no other subject joined within the next 10 minutes, a message was displayed alerting the subject that the experiment could not take place as no opponent could be found. Once two subjects joined a room, the room was considered 'complete' and the training started.

All along the process, if a subject closed the tab of his web browser for more than 6 minutes, he was considered disconnected and a message was displayed to his opponent informing him that the experiment had to stop as his opponent has quit unexpectedly.

TRAINING. Each subject went through an interactive tutorial, teaching him the rules and controls for the experiment. He then confronted an artificially intelligent firm using a profit maximization heuristic (see 'Materials & Methods' section).

As in simulations, both firms (subject and simulated firm) competed in terms of location and prices, on a turn-by-turn basis, during 25 time steps (same duration as the game). Consequently, the subject had to select every two turn a location on the map, as well as a price using the interface shown in Fig. 3.5.

Once both subjects that have been paired together completed their round against the sim-

ulated firm, they were playing a second round, this time playing against each other.

4

When rhesus monkeys play lotteries: An asymmetry of treatment between gain and loss^{*}

ABSTRACT. One interesting characteristic of decision-making under risk in humans is the asymmetry of the attitude toward risk depending on whether the decision-maker faces potential gains or potential losses. Indeed, humans are generally risk averse for bets involving gains, but risk seeking for bets involving losses. They also exhibit a distorted perception of probabilities. It is not clear whether non-human primates exhibit the same decision-making irrationalities. Two rhesus monkeys were allowed to make choices between lotteries involv-

*. The content of this chapter is an independent research article (submitted). Its has been simply formatted for the sake of graphical consistency. The co-authors of this article are Sacha Bourgeois-Gironde & Thomas Boraud.

ing either gains or losses, in order to assess the presence of such an asymmetry. This revealed an asymmetry in the treatment of gains and losses comparable with that of humans.

4.1 INTRODUCTION

Attitudes toward risk include different behavioral features that can be studied independently: risk-aversion, loss aversion, and the distortion of probabilistic information (see Fig. 4.1). The connection between risk aversion and the utility of an action for an individual was established early in the history of decision-theory^{6,88}. Loss aversion and distortion of probabilities have been identified much more recently when expectations of gains and losses were studied from the current reference point of the decision maker^{49,86}. Indeed, the seminal studies from Tversky and Kahneman show that humans (i) are generally risk averse for bets involving gains but risk seeking for bets involving losses, (ii) exhibit loss aversion, and (iii) their perception of probabilities is distorted in the sense that small probabilities are over-weighted and high probabilities are under-weighted. These works led to the formulation of the cumulative prospect theory—a common denomination of the second version of the model of Kahneman and Tversky⁸⁹—that made the psychological insights compatible with the maximization of a utility function⁸⁶.

In view of the phylogenetic proximity between monkeys and apes (that include human), it seems of interest to study attitude toward risk in the former in order to extend the descriptive validity beyond the realm of human decision making. Oddly enough, several studies in rhesus monkeys (*Macaca mulatta*) report preferences for the riskier option over the safer one when the expected values are equivalent^{63,68,73,80,34}. However, this has been contradicted by other studies that report risk aversion for gains⁵². In order to explain these discrepancies,

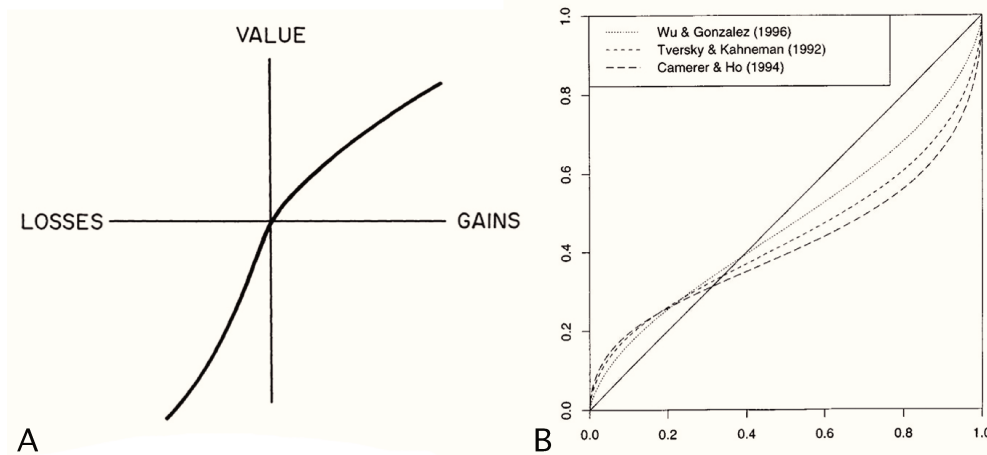


Figure 4.1 - Attitude toward risk: gain-loss asymmetry and probability distortion. **A.** A typical utility function for a human subject. The concavity of the curve for gains indicates risk aversion, while the convexity of the curve for losses indicates risk seeking. Loss aversion is indicated by a steeper curve for losses than for gains (figure reproduced from Tversky & Kahneman⁸⁶). **B.** The function of distortion probabilities as they have been described by Tversky & Kahneman⁸⁶, Camerer & Ho¹² and Wu & Gonzalez⁹⁴. All these functions have in common that small probabilities are over-weighted while high probabilities are under-weighted (figure reproduced from Gonzalez & Wu³⁶).

some authors have advanced the idea that confounding factors could skew the data in the studies reporting risk seeking^{95,38}. The amount of reward is generally low (the stake for a bet is generally under 100 μ L of water) and this could create an incentive to prefer risky options (called *peanuts effect*). Another factor is that a similar bet is proposed several times in a same session. This could lead to a bias toward the risky options driven by a meta-preference for behavioral diversification. It is also noticeable that most of these studies focus on the attitude toward risk for gains only.

The objective of the present study is to evaluate whether the asymmetry of treatment between gains and losses seen in humans can also be evidenced in non-human primates, and if so, provide a fine description of this asymmetry by characterizing it toward (i) risk-aversion, (ii), probability distortion, (iii) stochasticity in choice. For this purpose, we designed an experimental paradigm in which rhesus monkeys had to choose between choices involving

either gains or losses. We then fitted their behavioral data to a cumulative-prospect-theory based decision model to assess the contrast between the treatments of losses and gains.

4.2 RESULTS

TASK. We trained two monkeys, Monkey H and Monkey G, to perform choices when facing a pair of lotteries. At each trial, the monkey had to touch one of two circular targets on a touchscreen, each of them associated to the choice of a lottery. Each lottery had two outcomes, a positive or negative amount x and o . The amount x is the actual outcome of the lottery with probability p , and o is the actual outcome with probability $1 - p$. Amounts were represented by texture (different line orientations) and probabilities by the slice taken by the corresponding outcome on the target (see Fig. 4.2). For implementing losses, the monkey was rewarded at the end of trial with an amount of water proportional to the level of gauge filled with tokens. Starting each trial with 3 tokens, the monkey could win or loss up to 3 tokens (see Fig. 4.9).

We distinguished two sets of lottery pairs. The first set comprises lottery pairs where there was a very dominant option. The second set comprises lottery pairs that allow to assess attitude toward risk: for such pairs, the choice is between a risky lottery leading to a greater gain (greater loss) but with a smaller probability, and a safer lottery leading to a smaller gain (smaller loss) but with a higher probability. For commodity purpose, we will name thereafter lottery pairs with potential gains LPG, and lottery pairs with potential losses LPL.

CERTAINTY-RISK TRADE-OFF. In this first section, we report results for the case similar to that proposed by Kahneman and Tversky⁴⁹. The two monkeys were faced with two lottery pairs. In the first, they had the choice between a lottery giving one token with certainty and

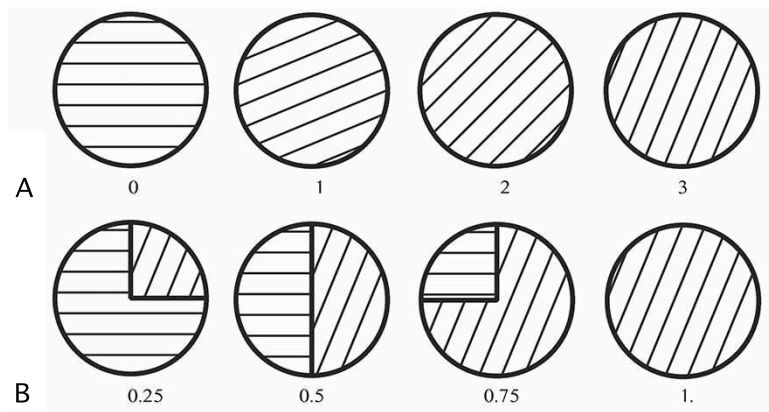


Figure 4.2 – Representation of outcomes and probabilities. **A.** Quantity of token earned (lost) is encoded by the pattern. From left to right: 0, 1, 2 and 3 tokens (rotation of the horizontal lines in the other direction would indicate a negative amount). **B.** Each lottery with non-degenerate probability is represented by a pie chart composed of two slices. The arc length of each slice represents the probability associated to the amount corresponding to the pattern of this slice. From left to right: 3 token gain with probability 0.25, 0.5, 0.75 and 1.

one giving two tokens half of the time. The second pair was similar to the first, except that the amounts were negative.

Fig. 4.3 shows the results for these two lottery pairs (Monkey H: 251 trials, Monkey G: 236). The monkeys behaved similarly to the behavior reported in humans in similar trade-offs⁴⁹: the monkeys preferred the safest option if the lottery offered a gain and the riskiest option if the lottery offered a loss (Monkey H: $dll = 1$, $\chi^2 = 301.39$, $p < 0.01$; Monkey G: $dll = 1$, $\chi^2 = 89.37$, $p < 0.01$).

STOCHASTIC DOMINANCE. In order to assess the understanding of the task by the two monkeys, we consider separately the lottery pairs where there was a strictly dominant lottery. The results of the 96 lottery pairs meeting this condition are summarized in Fig. 4.4 (Monkey H: 19,594 trials; Monkey G: 16,938 trials).

For Monkey H, the median success rate was 0.98 (IQR = 0.95 – 1.00) for lottery

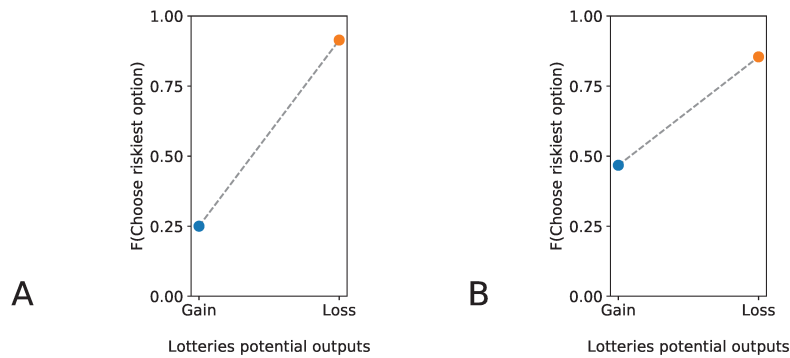


Figure 4.3 – Certainty-risk trade-off. Each dot corresponds to the frequency with which the riskiest lottery was chosen, when the choice was between two lotteries with equal expected values but one of the both having a certain outcome. Blue: potential gains only; orange: potential losses only. **A.** Monkey H. **B.** Monkey G.

pairs containing one lottery with potential losses and on lottery with potential gains; 0.85 (IQR = 0.68 – 0.91) for LPG differentiating only by the x values; 0.62 (IQR = 0.57 – 0.71) for LPL differentiating only by the x values; 0.86 (IQR = 0.80 – 0.94) for LPG differentiating only by the p values; 0.87 (IQR = 0.67 – 0.93) for LPL differentiating only by p values.

For Monkey G, the median success rates was 0.96 (IQR = 0.89 – 0.99) for lottery pairs containing a lottery with potential losses and a lottery with potential gains; 0.76 (IQR = 0.70 – 0.85) for LPG differentiating only by the x values; 0.61 (IQR = 0.55 – 0.70) for LPL differentiating only by the x values; 0.78 (IQR = 0.72 – 0.85) for LPG differentiating only by the p values; 0.80 (IQR = 0.61 – 0.94) for LPL differentiating only by the p values.

All interquartile range are above 0.5, which is the chance level, as the task design includes only two choice options for each trial. It shows that the animals understand the significance of the stimuli. However, both monkeys performed worst in the condition where they had to choose between two lotteries that had two different potential losses with the same probability.

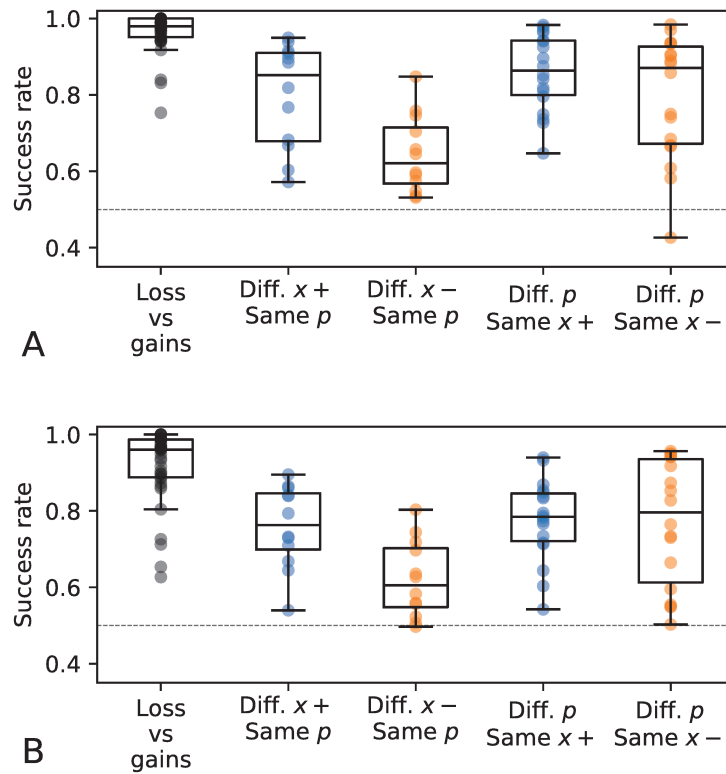


Figure 4.4 – Performance during control trials. Each dot represents the frequency with which the best option was chosen for a particular pair of lotteries. Blue: lottery pairs with potential gains only; orange: lottery pairs with potential losses only. Each box plot extends from the lower to upper quartile of frequencies observed, with the central line at the median. The whiskers represent the value of 1.5 IQR. **A.** Monkey H. **B.** Monkey G.

This could be interpreted as bad discrimination of losses, but not as a bad understanding of what a loss is in general because their performance was good for the case in which there was a choice between a lottery with a potential loss and a lottery with a potential gain, and the case where there was a choice between two lotteries with the same potential loss but with different probabilities depending on the lottery.

PERFORMANCE APPRAISAL FOR TRIALS WITH NO STOCHASTIC DOMINANCE. For lottery pairs where it is possible to distinguish a safer option and a riskier option, we checked that the frequency with which the riskiest option was chosen was dependent on the difference between the expected values of the safest option and the riskiest option. To assess this relationship we used an ordinary sigmoid function to fit the data obtained on 18 different lottery pairs involving only gains and 18 different lottery pairs involving losses (Monkey H: 4,952 trials, Monkey G: 4,435 trials). Results are shown in Fig. 4.5.

The slope of the curve of the sigmoid function in Fig. 4.5A on the left side (in blue) is steep and the points are close to the curve, indicating that Monkey H had a good understanding of incongruent lotteries with potential gains. However, the slope of the curve of Fig. 4.5A on the right side (in orange) is smooth and the points are further from the curve than for gains, indicating a less accurate understanding of lotteries with potential losses, even if the function fitting these points is still monotonically increasing.

The same is also true of Monkey G. The slope of the curve of Fig. 4.5B on the left side (blue color) is steep and the points are close to the curve, indicating a good understanding of lotteries with potential gains. The fact that the slope is steeper and the points closer to the curve than for Monkey H indicates a better understanding. As was shown for Monkey H,

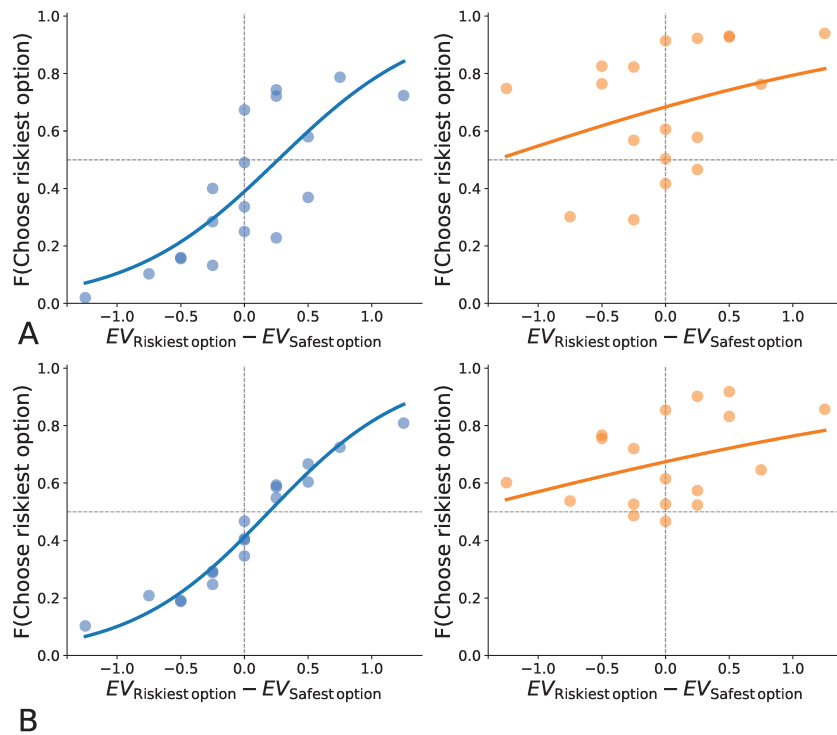


Figure 4.5 – Monotonicity of risky choice frequency over expected value differences. Each dot represents the frequency with which the riskiest option is chosen for a particular pair of lotteries. The function fitting these points increases monotonically: the more the difference between expected values favors the riskiest option, the more the monkey is expected to choose this option. **A.** Monkey H. Left: pairs of incongruent lotteries involving gains (blue). Right: pairs of incongruent lotteries involving losses (orange). **B.** Monkey G. Left: pairs of incongruent lotteries involving gains (blue). Right: pairs of incongruent lotteries involving losses (orange).

the slope of the curve of Fig. 4.5B on the right side (orange color) is smooth and the points are further from the curve than for gains, indicating a poor understanding of lotteries with potential losses, even if the function fitting these points is still monotonically increasing.

ATTITUDE TOWARD RISK IN NON-HUMAN PRIMATE. To better identify how the macaques behaves in relation to risk, we fitted a decision-making model including six free parameters:

- ω_G and ω_L that describe to which extent the monkey is risk-averse for lottery pairs involving respectively gains and losses;
- α_G and α_L that describe to which extent the monkey has a distorted perception of probabilities for lottery pairs involving respectively gains and losses;
- λ_G and λ_L that describe to which extent the decision-making process is stochastic for lottery pairs involving respectively gains and losses.

We optimized these free parameters on monkeys preferences over 18 different lottery pairs involving only gains and 18 different lottery pairs involving losses (Monkey H: 4,952 trials, Monkey G: 4,435 trials). It allows us to describe to which extent the two monkeys present an asymmetry of treatment between gain and loss. The results of this optimization are summarized in Table 4.1. We provide a visual representation for the functions for which these parameters are used: Figure 4.6 shows the utility functions, Figure 4.7 shows the probability distortion functions and Figure 4.8 shows the stochasticity functions using the average best free parameter values for each monkey separately.

For Monkey H, the average best value is a little above 0 for ω_G (0.26) and very low for ω_L (−0.73). for Monkey G, the average best value is a little above 0 for ω_G (0.14) and very low

	ω_G, ω_L	α_G, α_L	λ_G, λ_L
Range	$[-0.99, 0.99]$	$[0.01, 1.00]$	$[0.00, 5.00]$
Monkey H	$0.26 (\pm 0.09); -0.73 (\pm 0.11)$	$0.60 (\pm 0.07); 0.21 (\pm 0.09)$	$2.25 (\pm 0.40); 1.66 (\pm 0.27)$
Monkey G	$0.14 (\pm 0.10); -0.91 (\pm 0.12)$	$0.95 (\pm 0.06); 0.25 (\pm 0.10)$	$1.23 (\pm 0.29); 1.02 (\pm 0.30)$

Table 4.1 – Average best parameter values fitting monkeys' behavior. The first row of this table indicates the range for the free parameters. The second and third rows give the average best values found for fitting behavioral data (\pm SD), respectively for Monkey H and Monkey G. Average log-likelihood sums are respectively $68.89 (\pm 5.03$ SD) and $67.83 (\pm 4.95$ SD) for Monkey H and Monkey G.

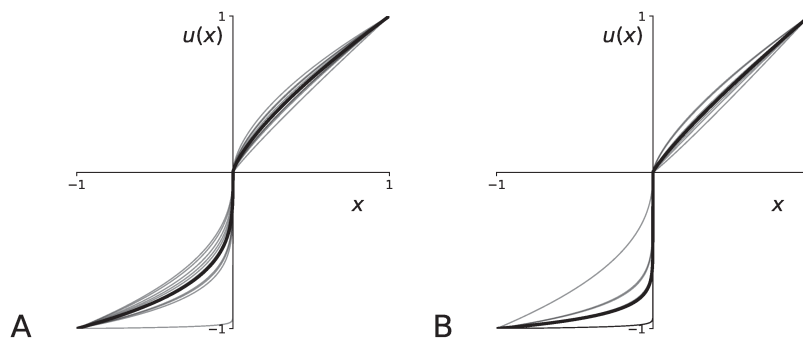


Figure 4.6 – Utility functions. Built upon data fitting, they are characterized by the optimization of two parameters: ω_G , describing to which extent the monkey is risk averse for gains, ω_L describing to which extent the monkey is risk averse for losses. **A.** Monkey H. Data fitting reveals a slight risk aversion for gains ($\omega_G = 0.26$) and a strong risk aversion for losses ($\omega_L = -0.73$). **B.** Monkey G. Data fitting reveals a quasi risk neutrality for gains ($\omega_G = 0.14$) and a strong risk aversion for losses ($\omega_L = -0.91$).

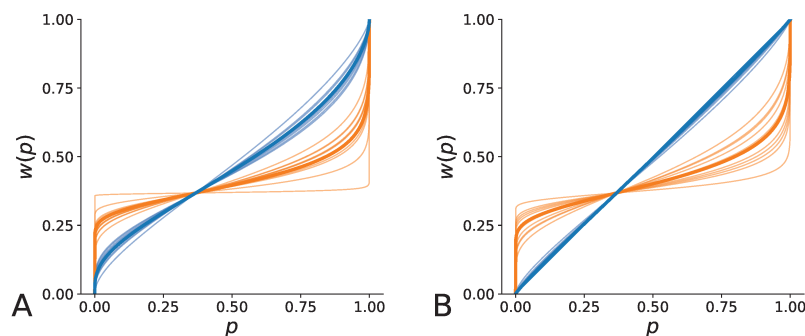


Figure 4.7 – Probability distortion functions. For each monkey, two probability distortion functions are drawn: one for lottery pairs involving gains (in blue), one for lottery pairs involving losses (in orange). Based on data fitting, each of these functions is characterized by the optimization of one parameter, respectively α_G and α_L . These parameters describe the extent to which the probabilities are distorted. **A.** Monkey H. Data fitting reveals a slight probability distortion for gains ($\alpha_G = 0.60$) and a strong probability distortion for losses ($\alpha_L = 0.21$). **B.** Monkey G. Data fitting reveals a quasi linear distortion of probabilities for gains ($\alpha_G = 0.95$) and a strong probability distortion for losses ($\alpha_L = 0.25$).

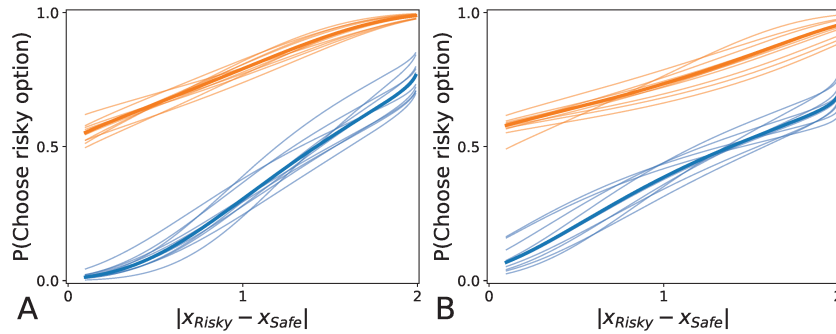


Figure 4.8 – Stochasticity functions. For each monkey, two stochasticity functions are drawn: one for lottery pairs involving gains (in blue), one for lottery pairs involving losses (in orange). Based on data fitting, each of these functions is characterized by the optimization of one parameter, respectively λ_G and λ_L . These parameters describe the extent to which the decision-making is stochastic (the closer λ is to zero, the more the decision-making process is stochastic). In blue is depicted how the probability of choosing a risky lottery that gives 3.00 with probability 0.25 increases as the amount with certainty of a second lottery decreases progressively from 2.99 to 0.10. In orange is depicted how the probability of choosing a risky lottery that results in a loss of -1.00 with probability 0.25 increases as the loss with certainty resulting from a second lottery increases progressively from -0.10 to 2.99. The smoother the slope, the more the choice is stochastic. **A.** Monkey H. Data fitting reveals a stronger stochasticity of choice for losses than for gains ($\lambda_G = 2.25, \lambda_L = 1.66$). **B.** Monkey G. Data fitting reveals a stronger stochasticity of choice for losses than for gains ($\lambda_G = 1.23, \lambda_L = 1.02$).

$\omega_L (-0.91)$. For both monkeys, this indicates a slight risk-aversion for gains and a strong risk-seeking for losses. These optimized values (ω_G and ω_L) allow to reconstruct the utility functions of the two monkeys, as shown in Fig. 4.6.

For Monkey H, the average best value of α_G is a little lower than 1 (0.60) while that of α_L is very lower lower than 1 (0.21). This indicates a slight distortion of probabilities for gains and a strong one for losses (see Fig. 4.7A).

For Monkey G, the average best value of α_G is close to 1 (0.95) while that of α_L is very low (0.10). This indicates a quasi-linear perception of probabilities for gains and a strong probability distortion for losses (see Fig. 4.7B).

For Monkey H as for Money G, the average best values of λ_G are higher than those of λ_L

(respectively 2.25 and 1.23 versus 1.55 and 1.02). This indicates a greater stochasticity in choice for losses than for gains for both monkeys (see Fig. 4.8).

4.3 DISCUSSION

This study has developed a new paradigm assessing attitude toward risk in macaque monkeys facing lotteries that comprised either potential gains or losses. Both macaques investigated displayed an asymmetric behavior toward gain and losses. They were slightly risk averse or risk neutral for gains but strongly risk seeking for losses. They also exhibited either a slight probability distortion or a linear perception of probabilities for gains but a strong probability distortion for losses. Such an asymmetry of treatment between lotteries involving gains and losses is congruent with the predictions of the prospect theory and is similar to what has been observed in humans^{49,86}.

UNDERSTANDING OF THE TASK & STOCHASTICITY IN CHOICE. Despite the large number of different lottery pairs, both monkeys generally showed a good understanding of the task. The large number of choice situations rules out the possibility that the monkeys would have been able to memorize the best choice in each case, without decoding the stimuli (the protocol included 126 different pairs of lotteries, with stimuli rotated randomly from one trial to another).

However, if the animals seem to understand well both magnitude and probability concerning gains (see Fig. 4.4), they seem to be less accurate for losses. Indeed, if in the control condition where both the lotteries contain potential losses of similar magnitudes but the probabilities vary, the monkeys had good performances (i.e. they selected the lottery

with the smallest probability of loss more than 80% of the time), it is not the case for lotteries where probabilities were fixed and magnitudes varied (see Fig. 4.4).

Also, there is a greater stochasticity in choice for losses than for gains, as captured by the precision parameter in our data fitting (for both monkeys, λ_G was superior to λ_L). We can assume that it is the consequence of the asymmetry of understanding of gains and losses revealed by the control trials.

ASYMMETRIC ATTITUDE TOWARD RISK. In this study, we observed a strong asymmetry in attitude toward risk between gains and losses for both monkeys. Monkey H exhibited a slight risk aversion for gains (positive value of the parameter ω_G) while Monkey G was nearly risk neutral for gains. However, both exhibited strong risk seeking behavior for losses (very negative value of the parameter ω_H).

If our results fulfill the predictions of the prospect theory^{49,86} to that respect, they do not replicate the previous results in rhesus monkeys that report a tendency to seek risk for gains^{63,73,34,31}. This discrepancy can have at least four reasons. (i) Strong individual differences have been noted in humans and can also be expected to occur in rhesus monkeys—that is why the behavior of the two monkeys has been analyzed separately. (ii) In our task, at the start of each trial the monkeys had an initial amount of water, to which their gains (losses) were added (subtracted). This makes the stake for a single trial larger and maybe allows the *peanuts effect* to be avoided—risky behavior is promoted with small rewards⁹². (iii) The number of different pairs of lottery in previous studies was much lower. It is therefore possible that the results of previous trials were too strongly influenced by findings from rather specific lottery pairs. (iv) In a recent study that implement also losses³¹, the

introduction of a small amount of water for each successful trial is maybe the cause of the report of risk seeking for gains: the certainty for the monkeys to have a small reward may induce an incentive to choose the riskiest option.

Concerning the attitude toward losses, our data are consistent with the two studies that addressed specifically the question and revealed risk seeking behavior for losses in capuchins¹⁵, or rhesus monkeys³¹. The latter proposed an experimental paradigm that mixes losses and gains and found risk seeking behavior both for gain (see above) and losses. However, no separate assessment of the understanding of losses was performed. Therefore, the very flat utility function in losses—function drawn upon data fitting—could be an indicator of a poor understanding of the losses similar to the one we observed in our data (see Fig. 4.4).

Capuchins and rhesus monkeys come from two different parvorders of primates (respectively Platyrrhini and Catarrhini, the latter including also the apes). It suggests that attitude toward risk in losses is pretty well conserved across all Simiiformes species (i.e. monkeys and apes).

PROBABILITY DISTORTION. Strong probability distortion has been observed in humans³⁶ and rhesus monkeys⁸⁰ for lotteries involving gains and was therefore expected in this study. In our study, we observe only a moderate one in lotteries involving gains. However, we observed a strong probability distortion for lotteries involving losses. Monkeys seemed to seek risk when dealing with potential losses, but this behavior is combined with difficulty to evaluate the quantity of loss (see Fig. 4.4). It is thus hard to discriminate if the animals do seek for risk or just try to avoid losses whatever the magnitude. This could be pointing to an adaptive

behavior in the sense that, if an individual cannot correctly evaluate the amount of a loss, one solution could be to avoid all loss as far as possible, leading to adopt a seemingly risky behavior. This could explain why our two monkeys are far more risk-seeking when facing potential losses than they are risk-averse when facing potential gains. Unfortunately, to the extent of our knowledge, the previous studies on probability distortion either did not mixed losses and gains or did not use a different parametrization for both. Therefore, even if such an asymmetry of probability is not predicted by the prospect theory^{49,86}, it would be interesting to know if distortion is depending of the composition of lotteries and can be generalized to other species, including humans.

INSIGHT ON THE ENCODING OF UTILITY IN THE BRAIN. Our behavioral data may help to solve an old paradox concerning the encoding of utility by the primate brain. It has been proposed that, in a choice decision situation, dopaminergic (DA) neurons encode the expected value of the chosen option⁶⁶. Expected reward is proposed to be encoded by the magnitude of the increase in the firing rate of DA neurons, while negative outcome is encoded by a decrease^{33,66,13}. However, the baseline firing rate of DA neurons is quite low (about 2 spikes per seconds). This does not allow the system to encode negative outcomes as accurately as positive ones and precludes the possibility of a linear representation of the magnitude of loss. The definition of negative outcome is not clear from the literature. It has been associated with punishment (such as air puff in the face or electric shock) as well as loss or absence of reward. These different forms of negative outcome could well represent different categories and be encoded differently in the brain. Alternative theories proposed alternative pathways to encode negative value⁸ or that different DA neurons populations encode positive and negative expected values⁴. However, the behavior of the monkeys in this study suggests an alternative hypothesis. The animals were not able to distinguish a

large loss from a small one precisely because the encoding of expected losses is inaccurate. We therefore don't need to find an alternative pathway to encode losses (but punishment can still be encoded differently). To test this elegant alternative hypothesis, it would be necessary to record DA-neurons (and their striatal target) during the task used in this study.

The present study has demonstrated that the attitude toward risk of rhesus monkeys is similar to that reported in humans and followed quite closely the predictions of the cumulative prospect theory. This validates the use of the macaque model for the study of decision making under risk and investigating the underlying mechanisms.

4.4 MATERIALS & METHODS

BEHAVIORAL PROTOCOL

ANIMALS. The study was performed on two female rhesus monkeys, Monkey H born in 2012 and Monkey G born in 2011. The monkeys were housed in the animal facility of the Institute of Neurodegenerative Diseases (UMR CNRS 5293, Bordeaux, France) under standard conditions (a 12h light/dark cycle with light on from 7.00 am to 7.00 pm; humidity at 60%, temperature $22^{\circ}\text{C} \pm 2^{\circ}\text{C}$). Experimental procedures were performed in accordance with the Council Directive of 2010 (2010/63/EU) of the European Community and the National Institute of Health Guide for the Care and Use of Laboratory Animals. The protocol received agreement from Ethical Committee for Animal Research CE50 (agreement number: C33063268). Data using for analysis were collected over 151 days (Monkey H: 195.07 ± 102.42 SD trials per day; Monkey G: 171.76 ± 97.30 SD trials per day).

CODE AVAILABILITY. The code for monitoring the task and for data analysis has been written in Python, using the Python scientific stack^{46,87,42}. It ran under macOS Sierra. The code for the task is available at <https://github.com/AurelienNioche/MonkeyProject>. The code for the analysis is available at <https://github.com/AurelienNioche/MonkeyAnalysis>.

DATA AVAILABILITY. The data are available at the same address than the analysis program: <https://github.com/AurelienNioche/MonkeyAnalysis>.

COMPOSITION OF LOTTERIES. At each trial, the monkey had to choose between two lotteries. Each lottery L_i with $i \in \{1, 2\}$ had two outcomes, x_i and 0. x_i is the outcome of the lottery i with probability p_i while 0 is the output of the lottery with probability $[1 - p_i]$, with $p_i \in \{0.25, 0.50, 0.75, 1.00\}$. For all lottery i , x_i is a non-zero integer in the interval $[-3, 3]$.

Because of the large number of possible lottery pairs, several cases were distinguished and grouped in two sets.

The first set is composed of lottery pairs that were used to evaluate the animal's understanding of the task. Pairs belonging to this set are those in which there was a very dominant option whatever the attitude towards risk of the subject: L_1 dominates L_2 so the monkey is expected to choose L_1 if it understands the task. The following cases were extracted:

- $x_1 > 0$ and $x_2 < 0$ while $p_1 = p_2$; assess the discrimination of *losses from the gains* (this is the only case included in the design mixing potential gains and potential losses in a single trial); 36 different lottery pairs.
- $p_1 = p_2$ and $x_1 > x_2$, with $x_{i \in \{1,2\}} > 0$; assess the discrimination of *positive quantities*; 12 different lottery pairs.

- $p_1 = p_2$ and $x_1 < x_2$, with $x_{i \in \{1,2\}} < 0$; assess the discrimination of *negative quantities*; 12 different lottery pairs.
- $p_1 > p_2$ and $x_1 = x_2$, with $x_{i \in \{1,2\}} > 0$; assess the discrimination of *probabilities* associated to *positive* quantities; 12 different lottery pairs.
- $p_1 < p_2$ and $x_1 = x_2$, with $x_{i \in \{1,2\}} < 0$; assess the discrimination of *probabilities* associated to *negative* quantities; 18 different lottery pairs.

The second set is composed of lottery pairs that allowed the attitude toward risk of the subjects to be evaluated. Quantities and probabilities differ at the same time in an incongruent way: a trade-off has to be found and a choice made between L_1 , which is the riskiest option, and L_2 which is the safest option. If the subject is risk-seeking, he will be biased toward choosing L_1 . The following cases were extracted:

- $p_1 < p_2$ and $x_1 > x_2$, with $x_{i \in \{1,2\}} > 0$; 18 different lottery pairs.
- $p_1 < p_2$ and $x_1 < x_2$, with $x_{i \in \{1,2\}} < 0$; 18 different lottery pairs.

We will name thereafter lottery pairs with potential gains LPG ($x_{i \in \{1,2\}} > 0$), and lottery pairs with potential losses LPL ($x_{i \in \{1,2\}} < 0$).

IMPLEMENTATION OF LOTTERIES, GAINS AND LOSSES. During experimental sessions, the monkeys have restricted access to water five days per week. This motivates them to perform the task. Hence, the potential gain from each lottery was water in place of the monetary gains customarily used in human experiments.

Each trial, the monkey had to choose between two lotteries. A single lottery is represented by a pie chart (see Fig. 4.2), as proposed by Stauffer et al.⁸⁰. Each pie chart is composed of

two slices. Starting from a reference point at the top of the circle, the first pie segment is shifted by a random angle between 0 and 359° . Each slice encodes one possible outcome of the lottery (x_i or 0). The arc length of each slice represents the probability of this outcome (p or $[1 - p]$). The pattern of each slice represents the number of tokens earned or lost. The orientation of the parallel lines constituting the pattern indicates a quantity (see Fig. 4.2). Hence, horizontal lines represent 0. A rotation of these horizontal lines *clockwise* by one, two, three quarters of 45° respectively represent a loss of -1, -2, -3 tokens. A rotation of these horizontal lines counter-clockwise by one, two, three quarters of 45° represent a gain of 1, 2, 3 tokens.

In each trial the monkey could gain between -3 and +3 tokens. At the end of the trial the monkey would be rewarded with water proportional to the tokens gained. Because it is not possible to give negative water, the monkey started each trial with 3 tokens, visible on the screen. The monkey would therefore have between 0 and 6 tokens at the end of the trial. For each token the water tank valve would be opened for 150ms. This duration of opening gave approximately $100 \mu\text{L}$ of water. So, at the end of each trial the monkey would receive between 0 and $600 \mu\text{L}$ of water.

EXPERIMENTAL PARADIGM. The monkey sat in a primate chair positioned 20 cm from a touch screen. The experimental session was composed of a series of trials. Each trial consisted of several steps (see Fig. 4.9). At the beginning of the trial, a gauge with 3 tokens was displayed. The monkey had to grasp a grip for a short duration that varied randomly in a range from trial to trial ($150 \sim 300$ ms) to ensure that the monkey could not anticipate the stimuli display.

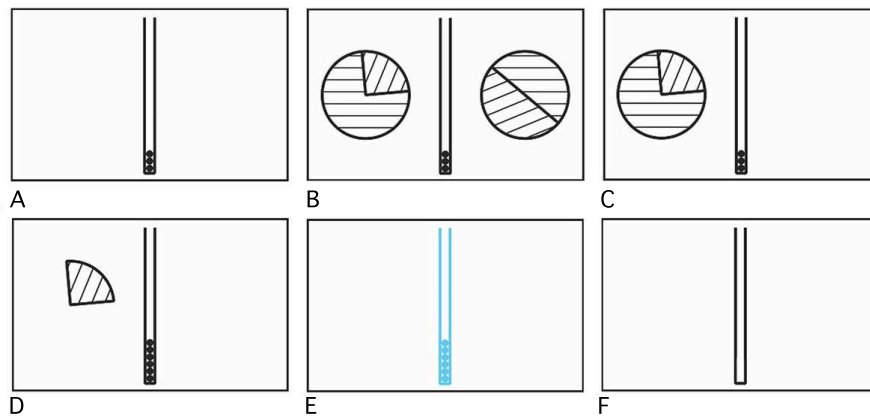


Figure 4.9 - Experimental paradigm. A. The monkey has to grasp a grip (50 ~ 300 ms). B. Stimuli appear. In this example, on the left side: 3 tokens with probability 0.25 (0 otherwise); on the right side: 1 token with probability 0.5 (0 otherwise). C. Once the choice is made, only the lottery chosen remains. D. After returning the hand to the grip, displaying of the outcome and addition (removing) of the tokens from the gauge. E. End of the trial: gauge draining and admission of the reward. F. Inter-trial.

If the monkey did not hold the grip long enough, the trial was considered as failed and an error was raised. Error trials were concluded with the display of a black screen, and the monkey had to wait 2000ms for the beginning of the next trial.

After the monkey had held the grip for the required amount of time (150 ~ 300 ms), stimuli appeared. The stimuli presented were two circles representing two lotteries. The monkey had 2000 ms to decide which lottery to choose. If the monkey did not choose within the allotted decision time, an error was signaled.

After making a choice by touching one of the two circles the other circle disappeared. The monkey then had 5000ms to return its hand to the grip (otherwise, an error was raised). Once the monkey had returned its hand to the grip the outcome was determined based on the probabilities shown in the two slices of the chosen circle. The amount of reward (loss) was indicated to the animal by the disappearance of the non-selected slice. The gauge filled

(emptied) by the amount earned (forfeited), one token at the time. The time of the filling animation was kept constant at 1500ms. At the end of the trial, the gauge emptied itself and the monkey received one drop of water (100 μ L) for each token in the gauge. The time of the emptying animation was kept constant at 1500ms.

The inter-trial interval varied randomly between 150 and 300ms.

MODELING

LOTTERIES, OUTCOMES AND PROBABILITIES. Based on prospect theory^{49,86}, we constructed a simple decision-making model designed to evaluate the attitudes to risk of the two monkeys. In our task, a lottery L has two possible outcomes x a non zero integer in the interval $[-3, 3]$ with probability p and 0 with probability $[1 - p]$. The formula given below supposed the use of a normalized value of x such as $x \in [0, 1]$.

UTILITY FUNCTIONS. We define a function U that represents the utility — or the subjective expected value — of a lottery L :

$$U(L_i) = w(p_i) \cdot u(x_i)$$

with w being the probability distortion function and u the utility function of an amount $x_i \in [0, 1]$. w is defined over the interval $[0, 1]$ and is continuous, with $w(0) = 0$ and $w(1) = 1$. u is defined over the interval $[-1, 1]$ and is continuous, with $u(0) = 0$ and $\forall x_i : -1 \leq u(x) \leq 1$.

Let us define a utility function u such as:

$$u(x) = \begin{cases} u^{1-\omega_G} & \text{if } x > 0, \\ -|u|^{1+\omega_L} & \text{if } x < 0, \\ 0 & \text{otherwise.} \end{cases}$$

with $\omega_G \in [-1, 1]$, the parameter of risk aversion for gains, and $\omega_L \in [-1, 1]$, the parameter of risk aversion for losses. Thus, if r is positive, $u'(x)$ is positive for $\forall x > 0$, meaning an aversion towards risk for gains – this method of modeling attitude towards risk is very common³⁹. In the case where x is negative and b is positive, $u'(x)$ is positive $\forall x < 0$, meaning an aversion towards risk in losses.

PROBABILITY DISTORTION FUNCTION. We assume that probabilities are perceived in a distorted manner. Following Prelec⁷¹, we defined a probability distortion function, w , in the following manner:

$$w(p) = \exp(-[-\ln(p)]^\alpha)$$

with $\alpha = \alpha_G$ if $x > 0$ and $\alpha = \alpha_L$ if $x < 0$. Both α -values are drawn from interval $(0, 1]$ and describe the extent at which the probabilities are distorted (the closer the α -value is close to zero, the more the probabilities are distorted).

STOCHASTICITY FUNCTION. We also assume that action selection is probabilistic: the option that is subjectively seen as the best option is chosen only with a greater probability than the other options (and not always). As a classic *softmax* function⁸³ to introduce stochasticity can induce non-monotonicity concerning the effect of risk parameter on probability to choose the riskiest option for a given lottery (i.e. monotonicity is not guarantee for an arbitrary couple of two lotteries), we used the alternative proposed by Apesteguia &

Ballester³.

Let L_1 be a lottery riskier than L_2 , that is to say such as $p_1 < p_2$ and $x_1 > x_2$. Let $p(L_1)$ be the probability of choosing L_1 :

$$p(L_1) = \frac{\exp(\lambda f(L_1, L_2))}{\exp(\lambda f(L_1, L_2)) + \exp(\lambda \omega)}$$

with $\omega = \omega_G$ if x_1 and x_2 are positive and $\omega = \omega_L$ if x_1 and x_2 are negative, $\lambda \in (0, \infty)$ a free parameter describing to to which extent decision-making is stochastic, and f a function that gives the ω -value for which the decision-maker would be indifferent between the both lotteries. The lower the λ -value is, the more the decision-making is stochastic.

ANALYSIS

CERTAINTY-RISK TRADE-OFF. We treated separately a singular case similar to one proposed by Kahneman & Tversky's seminal paper⁴⁹: (i) "In addition to whatever you own, you have been given \$1,000. You are now asked to choose between: (A) \$1,000 with probability .50, and (B) \$500 for sure." and (ii) "In addition to whatever you own, you have been given \$2,000. You are now asked to choose between: (C) \$ -1,000 with probability .50, and (D) \$-500 for sure".

Although we did not vary the initial wealth as Kahneman and Tversky had, we offered a very similar proposition to the monkeys. At the beginning of the trial they had three tokens and they had the choice between one lottery giving one token (or removing one) for certain, and a second lottery giving two tokens (or removing two) half of the time.

To assess the extent to which the behavior of the monkeys was impacted by the fact that the lottery pair dealt with gains or losses, we used a *chi – squared test*. The null hypothesis was that animals would make an equal number of risky choices in lotteries involving gains and lotteries involving losses. We set the significance threshold at $p = 0.01$.

For Monkey H, we collected 88 trials for the pair of lotteries involving gains, 163 trials for the pair involving losses. For Monkey G, we collected 92 trials for the pair of lotteries involving gains, 144 trials for the pair involving losses.

LOTTERY PAIRS WITH STOCHASTIC DOMINANCE. To check that both monkeys had understood the task, we analyzed separately cases where one lottery was clearly superior to the other (i.e. the lottery pairs described as belonging to the first set in the methods section). Because we did not expect the distribution to be uniform, we computed the median and interquartile range (IQR) of success rate for each pair of lotteries such that $p_1 \geq p_2$ and $x_1 \geq x_2$.

For 36 lottery pairs containing one lottery with potential losses and one lottery with potential gains, we collected the results of 3,204 trials (89.00 ± 10.73 SD per pair) for Monkey H and 2,862 trials (79.50 ± 9.49 SD per pair) for Monkey G.

For the 12 LPG for which the only difference was the x values, we collected the results of 3,290 trials (274.17 ± 8.36 SD per pair) for Monkey H and 2,956 trials (246.33 ± 11.14 SD per pair) for Monkey G.

For the 12 LPL for which the only difference was the x values, we collected the results of

6,040 trials (503.33 ± 17.16 SD per pair) for Monkey H and 4,969 trials (414.08 ± 69.72 SD per pair) for Monkey G.

For the 18 LPG for which the only difference was the p values, we collected 3,074 trials (170.78 ± 14.74 SD per pair) for Monkey H and 2,678 trials (148.78 ± 14.51 SD per pair) for Monkey G.

Finally, for the 18 LPL for which the only difference was the p values, we collected 3,986 trials (221.44 ± 13.54 SD per pair) for Monkey H and 3,473 trials (192.94 ± 21.70 SD per pair) for Monkey G.

LOTTERY PAIRS WITH NO STOCHASTIC DOMINANCE. Lottery pairs for which it is possible to distinguish a safest and a riskiest option were used to verify that the frequency with which the riskiest option was chosen was dependent on the difference between the expected values of the safest option and of the riskiest option. To assess this relation, we used an ordinary sigmoid function f to fit the monkeys' behavior such as $f(x) = 1/(1 + \exp(-\beta(x - \gamma)))$ with γ and β being two free parameters optimized to fit the data points using a Levenberg-Marquardt algorithm (SciPy library).

For Monkey H, the number of trials was 1,947 for the 18 LPG (108.17 ± 12.16 SD per pair) and 3,005 for the 18 LPL (166.94 ± 14.94 SD per pair) with no stochastic dominance.

For Monkey G, the number of trials was 1,794 for the 18 LPG (99.67 ± 12.12 SD per pair) and 2,641 for the 18 LPL (146.72 ± 15.29 SD per pair) with no stochastic dominance.

FITTING OF BEHAVIOR. To identify how the macaques behaved in relation to risk, we decided to optimize the free parameters of our model — $\omega_G, \omega_L, \alpha_G, \alpha_L, \lambda_G, \lambda_L$ — for each monkey separately, using a SLSQP optimization algorithm⁵⁷ (Scipy Library). The optimization was based on minimization of the inverse of log likelihood for a given set of parameters. Such a log likelihood is computed as follows:

$$\ln \mathcal{L}(\vartheta; c_1, \dots, c_{n_{\mathbb{P}}}) = \sum_i^{n_{\mathbb{P}}} \ln f(c_i | \vartheta)$$

with ϑ being a particular set of values of our five free parameters; $n_{\mathbb{P}} = 168$ being the total number of different lottery pairs a monkey encountered; c_i being a set of binary values for the pair of lotteries $i \in [1, n_{\mathbb{P}}]$, each of these binary values indicating if the monkey chose the lottery L_1 when facing the pair of lotteries i in a particular trial (the size of this set can vary among the lottery pairs depending on the number of trials the pair i appears), and f being the density function that gives the probability of this observation given the set ϑ of parameters. As each set of choices for a pair of lotteries i is composed of binary values (i.e. choosing L_1 or not), let f be:

$$f(c_i | \vartheta) = Pr(k_i, n_i, p_i | \vartheta)$$

with n_i being the number of trials in which the monkey encounters this pair of lotteries i , k_i the number of times the monkey chooses L_1 when it encounters the pair of lotteries i , and p_i , the (theoretical) probability of choosing the lottery L_1 when facing the pair of lotteries i given the set of parameters ϑ (naming the output of our model given ϑ). In other words, the value of f value depends only on k_i, n_i and p_i given ϑ . Knowing that, we can define f as the

following binomial mass function:

$$f(c_i|\mathcal{D}) = \binom{n_i}{k_i} [p_i|\mathcal{D}]^{k_i} (1 - [p_i|\mathcal{D}])^{n_i - k_i}$$

The trials used for this fit were the same than those for assessing the frequency with which the riskiest option was chosen was dependent on the difference between the expected values of the safest option and of the riskiest option.

To assess the stability of the fit, we used a cross validation process by binning the trials in 10 chunks for each monkey and computing the average best value over these 10 chunks.

5

Conclusion

5.1 RESULTS SUMMARY

INFORMATION RESTRICTION AND EMERGENCE OF AN INSTITUTION. The first study questioned the possibility of a large-scale coordination phenomenon—a macroeconomic variable—based on fairly strong constraints on access to information—a microeconomic variable. More specifically, we tested two hypotheses, the first being of a structural nature, since it concerns the type of environment in which agents evolve, and the second being of a cognitive nature. The first, common to all other search-theoretical models, is that money emergence is possible in a decentralized economy. The second is that such an emergence is possible in an economy in which agents have very little information on the overall state of

the economy and demonstrate limited computing abilities.

The results obtained through simulations in artificial agents are consistent with our initial hypotheses: money emergence is possible in a decentralized economy with agents with limited computing capabilities and very poor information on the overall state of the economy. This emergence implies a favorable economic structure, which in the case of our model corresponds to a certain ratio between the numbers of producers and consumers of each type of good.

However, results of experiments with human subjects were not in line with the results obtained with artificial agents. Indeed, even under conditions where we expected them to coordinate on a unique medium of exchange according to the simulations, they failed to do so. A certain heterogeneity among the human subjects is maybe one of the factors that made the coordination more difficult, but a scaling up of data—both of the number of economies and of the number of subjects inside an economy—would be required before drawing inferences with reasonable assurance. This highlights the difficulties related to the study of macroeconomic phenomena in a laboratory: as the consequences of an action from a single agent may depend on the actions of all other agents—and except if we do not dispose on a very large amount of subjects (several thousands)—the data can easily be skewed. A possible workaround is to make play subjects against artificial agents whose behavior is under control of the experimenter. However, if this approach allows to isolate the behavior of each subject, it does not offer the possibility to capture the genuine phenomenon, that emerges from interactions between decision-makers for which payoffs are interdependent.

INFLUENCE OF CONSUMER'S COGNITION ON FIRM STRATEGIES. The second study asked the question of the influence of consumer access to information—a microeconomic variable—on the distribution of firms in the market—a macroeconomic variable. To do this, we built a model a-la Hotelling⁴⁰, and tested by simulation with artificial agents and by experiment on human subjects how varying the level of information actually affected the firms' location strategies.

The results show that if the quantity of information available to consumers is relatively high, firms tend to locate very close to their opponent at the centre of the market, putting themselves in a situation of strong competition. *A contrario*, if the quantity of information available to consumers is relatively low, firms tend to put themselves in a quasi-monopoly situation, thus adopting a non-competitive behavior, behavior that is not attributed solely to an explicit collusion strategy. We have also shown that this effect can be modulated according to the decision-making process used by firms. Thus, a company seeking above all to achieve better profits than its adversary finds itself in a situation of strong competition, and this even in the case of relatively limited access to information for consumers, while a company striving to establish tacit collusion manages to avoid competition even in the opposite case where consumers have access to a relatively important quantity of information.

ATTITUDE TOWARDS RISK IN RHESUS MONKEYS. The third study put under question the relevance of using the rhesus macaque as an animal model of economic behavior by assessing its attitude toward risk. More specifically, the aim of this study was to evaluate whether rhesus macaque, like humans, presented an asymmetric treatment of gain and loss. To do this, a new paradigm of risk attitude assessment has been developed, allowing macaques to deal with lotteries that included either potential gains or potential losses.

Both monkeys studied were either risk averse or risk neutral for gains but highly risk seeker for losses. Besides, the two macaques had a slight distortion of probability or a linear perception of probabilities for gains, but a strong distortion of probability for losses. The presence of such asymmetric treatment of lotteries involving gains and losses follows some of the prospect theory's predictions^{49,86} and is similar in this respect to what has been observed in humans.

This opens two perspectives. The first is to study the neural mechanisms involved in betting. The question thus arises to what extent the presence of such an asymmetric treatment of gain and loss with regard to risk attitude can be explained by characteristics at the neuronal level (i.e. for instance, one could assume that this is partly due to the very low basal discharge level of the striatal dopaminergic neurons involved in the value assessment). Ultimately, such an undertaking would strengthen the microfoundations of economics, offering detailed explanations on the neural implementation of economic decision-making processes. The second perspective is to succeed in inducing behaviors specifically economic in non-human primates. While there was some asymmetry in the understanding of gains and losses (the loss magnitude is less well understood than gain magnitude), the stimuli used in the task were generally well understood by the monkeys. This opens the way for the design of more complex decision-making tasks. One way of complexifying these tasks might be to include a time dimension, with effects of decision-making over both short and long-term. As a consequence, it would offer the possibility to approach a certain form of speculation in monkey, making it a valuable model of economic behavior.

5.2 GENERAL DISCUSSION

TAKING COGNITIVE CHARACTERISTICS INTO ACCOUNT IN A MICROFOUNDATIONAL APPROACH. The results of the study on the emergence of money in artificial agents show that agents may not possess an extended knowledge about the economic system in which they operate to allow this system to acquire certain remarkable macroeconomic properties. In particular, it shows that coordination on the use of a single medium of exchange—money—does not require agents to have a broad knowledge of the preferences of other actors, or to build a sophisticated belief system. These results obtained by the means of simulation show that poorly informed agents learning by trial and error can, under certain conditions, behave as if they were well informed and capable of formulating rational expectations. This is thus an argument in favor of the “as if” hypothesis here, even though intuition might have led us to believe the opposite. This brings the idea that coordination over a unique medium of exchange under drastic restriction of information could be not as easy as with agents learning purely by reinforcement and that further constraints could apply.

However, if the “as if” hypothesis was partially validated looking at the results in artificial agents in the first study, the same does not apply to the results in humans in this same study, or to the results in both artificial agents and humans in the study on competition in a duopoly situation. Indeed, in the first study, when placing human subjects under the same informational conditions as the artificial agents, we could not replicate the results obtained in the latter, while in the second study, by modulating the cognitive capacities of some of the agents involved (consumers), we modify the structure of the market. Reducing or increasing the amount of information available to consumers leads companies to form either monopolies or a cluster. With regards to the consumers, presuming the “as if” hypothesis

to be true would have somewhat masked one of the two phenomena. The results also show that the effect of the amount of information available to consumers is modulated by the type of heuristics used by firms. Regarding firms, taking the “as if” hypothesis as true would no doubt have indicated a trend but would not have been able to reflect the diversity we observed in our human subjects.

These results considered together demonstrate the interest that lies in taking the individual cognitive capacities into account, when it comes to microfound economic phenomena. While the “as if” hypothesis seems to hold in some instances (see the results with artificial agents in the first study), data can falsify it in some others (see the results in humans for the first study, or the results in humans and artificial agents in the second study). The independence of macroeconomic results from micro-economic assumptions about how agents make their decisions is therefore relative: considered together, the results highlight the fact that such independence must be ensured on a case-by-case basis through the establishment of microfoundations for each case separately.

COULD THE NON-HUMAN PRIMATE BE AN ECONOMIC MODEL? One might wonder to what extent it might be relevant to use a non-human primate as an economic model. The results of the third study demonstrate a striking similarity between the attitude towards risk in macaques and that of humans. However, one can still argue that unlike humans, they did not develop any economic system *stricto sensu*. For instance, if we assume that such a similarity in terms of economic behavioral features could be generalized, why non-human primates, for which we defend the use as an economic model, did not know the development of money?

A possible answer to this question would lie in the following alternative. If money is the

prerogative of human, it is possible to either assume: (i) non-human primates, although exhibiting some similarities in terms of economic behavior in laboratory, do not have the necessary cognitive resources, or (ii) it is more because of the environmental or structural constraints are not being fulfilled than because non-human primates do not have the necessary cognitive resources *per se*.

The results in artificial agents of the first study on the emergence of money highlighted the fact that minimal cognitive capacities could be sufficient to make the emergence of money possible: a simple learning by trial and error is sufficient to obtain coordination on a single medium of exchange. Therefore, these results bring an argument in favor of the second possibility: non-human primates are perfectly able to learn by trial and error, and the reason for the non-development of an economic system should lie in the absence of some environmental structural features.

One of the founding hypotheses of monetary prospecting models is a specialization between production and consumption of agents. This assumption seems credible if we consider human activity: there is indeed a specialization in production (if we consider agriculture, we can observe that the exploitation of wheat is more important in certain regions than in others where, for example, farmers will focus their production on cattle breeding, etc.). However, this hypothesis is not very credible with respect to animal activity. Certain monkey species demonstrate forms of social organization but we have never seen such a level of specialization as some animals take care of fetching wood while the others pick fruit. Yet, this hypothesis of specialization in production only serves to guarantee the need for exchanges between agents. We therefore think that if no money has emerged in the non-human primates, it is surely because there are no environmental constraints that prompt

individuals to specialize in terms of production. Indeed if there are no such constraints, then there is no need for a sophisticated exchange system between individuals, and if there is no such need, then it is useless for these individuals to agree on a single medium of exchange.

If these considerations are correct, then using a non-human primate as an economic model is by no means a problem, as long as one can induce an economic behavior in it, by manipulating the environmental constraints as we can do in a lab. The results that we obtained suggest that it is entirely possible to do so: we brought monkeys to bet, a slight complication of the task may have made them speculate, and undoubtedly, many other economic behaviors are possible to be induced in the rhesus monkey (i.e. behaviors associated with strategies of competition, cooperation, exchange or even anticipation of future consumption).

COGNITIVELY MICROFOUNDING ECONOMICS: A QUESTION AT THE CROSSROADS OF MULTIPLE DISCIPLINES? In order to bring answers to the question of the cognitive micro-foundation of economics, we used concepts and methods from at least three disciplinary fields: biology, computer science and economics.

Among the many advantages to stand at the frontiers of multiple disciplines, one is to gain access to a population of agents of different types: artificial agents, humans, and non-human primates. The former thus enabled us to include in our models very strong computational and informational constraints that would have been otherwise difficult to integrate into an axiomatic system, in the sense that it would have made the production of theorems extremely difficult. The use of artificial agents was also a mean to obtain fine predictions on what could be expected with human subjects. Thus, it helped us to define the experimental conditions in which we had to place our subjects to obtain the desired

contrasts. Conversely, human subjects allowed us to test the validity of the predictions made using artificial agents. Besides, non-human primates allowed to work at a fundamental level of the microfoundations of economics, questioning the relevance of its use as a model and enabling preparatory work to be carried out to investigate the neuronal mechanisms underlying economic decision-making. This raises questions about the contribution that other disciplinary fields could provide in regard to a microfoundational approach.

Regarding the study on spatial competition, an interesting perspective would be to associate econometric tools with those used in the study proposed here. This would make it possible to evaluate the accuracy of the predictions made by our model, and its adaptability to existing competitive phenomena.

The study on the emergence of money would have, without a doubt, benefited from the contribution of anthropological or historical work. As a matter of fact, a limitation of this study is that it remains fairly close to monetary prospecting models in terms of environmental design. We have in fact ignored the observations made by historians and anthropologists on the emergence of money. If we did so, it is because there is a need to proceed step by step: we could not test several hypothesis at the same time. In case of null results—as it happens with human subjects in our study—, it is important to know which alternative hypothesis are plausible. However, once the results on the possibility of money emergence under strong constraints on information access and computational abilities are strengthened, it would certainly be beneficial to include hypotheses of a historical and anthropological nature in our models.

It is (unfortunately) unlikely that an anthropologist will take over the study on money

because of the tightness of disciplinary boundaries. However, as I am writing these lines, an electrophysiological study of the neuronal processes underlying the treatment of losses has just been undertaken. It is too early to report the results here, but the idea of continuity through a new form of interdisciplinarity itself is very pleasing.

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Appendix

In parallel to my PhD projects, I engaged myself in two side-projects. One was a collaboration with Mathieu Bourdenx and the team of Erwan Bezard (IMN, Bordeaux, France) where he belongs when we started the project. The project mainly consisted in applying tools from machine learning to data obtained using a baboon model of Parkinson's disease based on injection of α -synuclein, where application of standard statistical tools was not a relevant option. The study aims to identify new targets potentially implicated in the development of Parkinson's disease and we proceed to a variable selection using artificial neural networks that led to surprising results, as the fact that some heavy metals as iron was a good predictor of the disease. This led to the writing of an article which is currently under review. A copy of this article is joined to the present document.

The second side-project, of a very different nature, led me to continue to work in philosophy. Indeed, during the second year I have been invited to participate in a working group on free-will with monthly sessions at the Collège de France (Paris, France) by Jean-Baptiste Guillon. It has been the opportunity to work on the publication of a study that I had started during the internships of the first year of master, in collaboration with Florian Cova and Paul Egré, and of a study that I had started during the internship of the second year of master. These works have been published as chapters of a collective book. A copy of these chapters are joined to the present document.

1
2 **Machine learning reveals different pathological signatures of patient-derived α -**
3 **synuclein extracts in non-human primates : variable selection using multiple-layer**
4 **perceptrons**

5
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42
43 **Manuscript information:** 15 text pages; 4 figures; 6 supplementary figures; 2 supplementary
44 tables; Machine Learning Code: 10.5281/zenodo.1240558; Raw data: supplementary table 2

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46
47 **INTRODUCTORY PARAGRAPH (146)**

48 Intracellular α -synuclein (α -syn)-rich protein aggregates termed Lewy bodies and neuronal
49 death are commonly found in the brains of Parkinson's disease (PD) patients. Clinical,
50 neuropathological and experimental evidence strongly suggests that α -syn plays a role not
51 only as a trigger of pathology but also as a mediator of disease progression, through its
52 pathological spreading. These properties of α -syn have been described in rodents and non-
53 human primates, but still remain controversial. Building up on this recent literature, we here
54 used an unbiased machine learning-based approach to unravel unique signatures of
55 degeneration induced by distinct α -syn assemblies derived from PD patients in non-human
56 primates. Our results pinpoint the long anticipated, yet unproved, primate-specific
57 susceptibility to α -syn toxicity thus reinforcing the need of preclinical research in this species.
58 Furthermore, our results provide evidence supporting the true multifactorial nature of PD as
59 multiple causes can induce similar outcome regarding dopaminergic degeneration.

60

61 **TEXT (1706)**

62 The seminal work of Braak and colleagues suggesting that Lewy body (LB) pathology
63 follows a predictable pattern of progression within the brain in Parkinson's disease (PD) ^{1,2}
64 led to the development of experimental models based on the inoculation of α -synuclein (α -
65 syn) assemblies^{3,4}. The most widely accepted paradigm postulates that pre-fibrillar oligomers,
66 as opposed to mature fibrils, represent the neurotoxic entities in PD^{5,6}. Such notion has been
67 established primarily using large doses of recombinant α -syn applied to cell cultures or
68 injected in adult mice, generally overexpressing mutant and less often wild-type α -syn.
69 However, we showed that intracerebral inoculation of low doses of α -syn-containing LB
70 extracts purified from the *Substantia Nigra pars compacta* (SNpc) of PD brains promotes α -
71 syn pathology and dopaminergic neurodegeneration in wild-type mice and non-human
72 primates⁷, an event directly linked to the presence of α -syn in LB extracts. The selective
73 vulnerability of SNpc dopamine neurons in PD⁸ owes notably to their unique cellular

74 architecture⁹. In fact, the large and complex axonal arbor of dopamine neurons makes them
75 particularly vulnerable to factors that contribute to cell death. Moreover, in primates, their
76 axonal arbor is ten-fold the size of the one measured in rodent⁹, and dopamine neurons
77 display unique molecular characteristics (e.g. the primate-specific presence of neuromelanin).
78 Thus, we hypothesize that non-human primates could be highly sensitive to low doses of
79 misfolded α -syn. Accordingly, we here comprehensively compare the pathological and
80 behavioral signatures of intrastriatal inoculation in baboon monkeys (n=4-6 per experimental
81 group) of either LB-enriched fractions containing pathological α -syn or non-LB (noLB)
82 fractions containing lower density α -syn assemblies, both fraction types purified from the
83 same *postmortem* PD brains.

84 NoLB and LB fractions were obtained from the SNpc of five sporadic PD brains exhibiting
85 conspicuous LB pathology, processed through differential ultracentrifugation in sucrose
86 gradient, and analyzed for the presence of α -syn aggregates by filter retardation assay
87 (**Supplementary Fig. 1A**)⁷. Further characterization of noLB and LB fractions was
88 performed by colocalization of α -syn and Thioflavin S staining, electron microscopy, as well
89 as biochemical characterization of assemblies stability (**Supplementary Fig. 1B-F**). While
90 total α -syn content was comparable between selected fractions, LB fractions showed higher
91 resistance to proteinase K treatment (noLB $t_{1/2}$ =15.23minutes vs LB $t_{1/2}$ >60minutes)
92 (**Supplementary Fig. 1D**) as well as greater resistance to multiple detergents, including 8M
93 Urea (**Supplementary Fig. 1E**). The physical separation through sarkosyl treatment of
94 soluble monomeric and insoluble aggregated α -syn within noLB and LB fractions of PD
95 patients (n=5 each) was performed by velocity sedimentation and density floatation to
96 quantify these two respective populations and determine their relative ratios in each fraction
97 (**Supplementary Fig. 2A-H**). Strikingly, while LB fractions contain ~90% of aggregated α -
98 syn, noLB fractions are composed of ~10% of this pathological form of the protein

99 (Supplementary Fig. 2I). Micro-Infrared Spectroscopy of LB and noLB fractions in the
100 range of 1,590-1,700 cm^{-1} confirmed that the LB group contained a fraction of amyloid
101 aggregates with larger amyloid structures than those in the noLB group (Supplementary Fig.
102 3). Altogether, these results suggest that LB fractions primarily contain large aggregated α -
103 syn fibrils while noLB fractions contain soluble α -syn and smaller α -syn aggregates.

104 Data from several studies suggest that both recombinant α -syn preformed fibrils¹⁰⁻¹² and
105 patient-derived α -syn⁷ can promote dopaminergic neurodegeneration in SNpc. Accordingly,
106 fractions were tested for their ability to kill dopamine neurons in primary mesencephalic
107 cultures (Supplementary Fig. 4A) as well as *in vivo* in wild-type mice and non-human
108 primates. Four months after supranigral injection, LB-injected mice displayed dopaminergic
109 degeneration, while noLB inoculations in mice had no impact on dopaminergic neurons up to
110 almost 17 months post-injection (Supplementary Fig. 4B) as previously reported⁷.

111 Two years after administration, LB-injected monkeys displayed a loss of dopamine neurons
112 and fibers (Fig. 1) without parkinsonism, since lesion remained below the threshold for
113 symptom appearance; i.e. 45% of cell loss¹³, compared to age-matched control monkeys.
114 However, at odds with mice, noLB-injected monkeys showed as well degeneration of the
115 nigrostriatal pathway of the same extent as that observed in LB-injected monkeys (Fig. 1),
116 suggesting a primate-specific susceptibility to various α -syn species. Facing such peculiar
117 finding, we addressed the identification of specific signatures of the pathological mechanisms
118 involved in α -syn toxicity induced by each fraction independently using machine learning. To
119 avoid selection and reporting bias, we performed an exploratory approach followed by a truly
120 unbiased variable selection using machine-learning. To do so, we investigated a large number
121 of variables tapping on behavioral, histological, biochemical, transcriptional and biophysical
122 approaches (Fig. 2A) applied to several brain areas (n=40 - Fig. 2B), totalizing the
123 quantification of 180 variables for each individual (Supplementary Fig. 5 for variable

124 abbreviation nomenclature; **Supplementary Table 1** for exhaustive list of variables;
125 **Supplementary Table 2** features **all raw data**).

126 To overcome the roadblock associated to the “ $p > n$ ” problem that occurs when the number of
127 variables measured is greater than the sample size, we developed a distributed algorithm using
128 multiple layer perceptron (MLP), a classic algorithm that can approximate virtually any
129 functions (**Fig. 2C**)¹⁴. It is now well accepted that machine-learning algorithms can be trained
130 to detect patterns much better than humans¹⁵. However, instead of classification algorithms
131 (the algorithm learns to identify in which category belongs a sample) that were mostly used in
132 recent applications of machine-learning in biology,¹⁶ we chose to predict continuous and
133 biologically-relevant, variables. MLPs with one hidden layer were trained to predict 3
134 relevant variables in the context of PD: levels of dopaminergic degeneration in (i) the SNpc,
135 (ii) the putamen and (iii) the caudate nucleus. To both alleviate the overfitting problem and
136 tackle the ‘black-box’ issue that is often opposed to the use of machine-learning (e.g. perform
137 variable selection)¹⁷, we used MLPs with a constrained architecture to predict actual
138 neurodegeneration with, as input, all possible combinations of 3 variables (total number:
139 $C_3^{163}=708,561$) that could explain the neurodegeneration (each combination being cross-
140 validated over 50 instances of MLP)¹⁸. This approach allowed us to rank input variables
141 according to their explanatory power and therefore to extract the strongest predictors of
142 neurodegeneration for each experimental group¹⁸. As a control for the learning process, we
143 used random data as input for the MLP with the same output; as expected, performances were
144 significantly lower (**Supplementary Fig. 6**). We selected the best predictors based on their
145 occurrence in the top 1% of the best combinations (**Fig. 2C**) for both for LB-exposed (**Fig.**
146 **2D**) and noLB-exposed monkeys (**Fig. 2E**). This method allowed us to identify differential
147 variable sorting patterns for both experimental groups despite similar level of nigrostriatal
148 degeneration (**Fig. 2D-E**).

149 Next, we compared the LB and noLB signatures using rank-rank hypergeometric overlap
150 (RRHO) test (**Fig. 3A**). Interestingly, low similarity was observed for the highly ranked
151 variables suggesting specific differences in the biological response to the injection of LB or
152 noLB (**Fig. 3B**). Focusing on the 20 first variables that showed low similarity between
153 groups, we found that LB-exposed monkeys were characterized by both quantitative and
154 qualitative changes in α -syn levels (i.e. phosphorylation at Ser129 and aggregation) especially
155 in cortical areas corroborated by distinct methodologies as well as by a dysfunctional
156 equilibrium in neurochemistry of basal ganglia output structures classically associated to
157 parkinsonism^{19,20} (**Fig. 3C**). Conversely, noLB-exposed monkeys exhibited a more diverse
158 nigrostriatal-centric signature with variables related to α -syn aggregation, proteostasis and Zn
159 homeostasis (**Fig. 3D**). Overall, using this unbiased methodology, we confirmed the interest
160 of highly-expected variables but more importantly also unexpected variables that appear to be
161 excellent predictors of α -syn-associated dopaminergic degeneration. The first hit for LB-
162 injected animals was phosphorylated α -syn in the entorhinal cortex (as we previously
163 showed) followed by synucleinopathy in para-hippocampal cortex (unexpected) and
164 microglial activation (expected). Conversely, Zn homeostasis was a strong predictive variable
165 (unexpected) followed by α -syn aggregation-related terms (expected) in noLB-injected
166 animals. Together, we identified specific signatures for both groups with low overlap (35% -
167 7/20) for an identical level of degeneration.

168 As we used combinations of 3 variables and because of the structure of MLPs, one could
169 expect that some combinations would complement each other to allow finer prediction of
170 neurodegeneration levels. To address this question, we used a classic measurement of
171 association in the field of data-mining: lift²¹ and plotted the results as network plots showing
172 association (edge size) and enrichment in the best learners (node size). Lift calculation was
173 corrected for error prediction to avoid detrimental association between variables. The first

174 observation is that the most enriched variables (top 3 to 5) appeared to be self-sufficient to
175 predict in neurodegeneration levels with minimal error (**Fig. 4**). Some variables, with modest
176 enrichment, showed strong positive associations that were specific to each experimental
177 group. Associated variables in LB-injected monkeys were related to: (i) α -syn-related
178 variables along the SNpc-striatum-cortex axis and an impairment of locomotion as well as of
179 the ethologically-defined orientation of the animals towards its environment (**Fig. 4 top left**
180 **inset**); (ii) a strong association between oligomeric α -syn species measured in the midbrain
181 and striatum equally associated, but to lesser extent, with α -syn levels in cortex and plasma
182 (**Fig. 4 top right inset**).

183 In noLB-injected animals, the analysis shed light upon the relative abundance of two
184 members of the macroautophagy pathway (**Fig. 4B top left**) as well as the balance between
185 monomeric and high-molecular weight species of α -syn into the putamen (**Fig. 4B bottom**
186 **right**). Such disruption of the nigrostriatal pathway has already a repercussion upon the basal
187 ganglia physiology as GABA levels in their output structure, the internal *globus pallidus*, was
188 associated with a decreased social behavior (**Fig. 4B bottom left inset**).

189

190 In conclusion, our findings point to a primate-specific susceptibility to dopaminergic
191 neurodegeneration and synucleinopathy induced by patient-derived aggregates. These
192 findings involve two immediate outcomes. First, as only non-human primates display such
193 induced degeneration, it spots clear species differences^{22,23} and calls for a systematic appraisal
194 of proteinopathies in primates in particular for validating therapeutic strategies before clinical
195 testing²⁴. Second, the present study highlights and corroborates the multifactorial origin of
196 synucleinopathies as distinct assemblies can induce similar degeneration (that would probably
197 lead to similar clinical manifestation in patients) through different mechanisms, nigrostriatal
198 or extranigral brain pathways, calling for molecular diagnosis to identify patient sub-

199 populations before launching large-scale, heterogeneous in nature, clinical trials. Finally, we
200 developed a machine-learning approach allowing unbiased and quantitative assessment of the
201 explanatory power of a given set of variables compatible with the constrained sample size of
202 experimental biology.

203

204 **METHODS**

205 Methods, including hyperlinks to fully available data set and machine-learning code, are
206 available in the online version of the paper.

207

208 **ACKNOWLEDGMENTS**

209 The authors thank Carmen Lagares Martínez (Head, Veterinary Service, University of
210 Murcia) for administrative assistance; Maria Fermina Ros Romero and Josefa Martínez
211 Rabadán (University of Murcia) for veterinary and husbandry support; Ana Luisa Gil, Lorena
212 Cuenca and Ignacio Mascarell from Clinical and Experimental Neuroscience group
213 (University of Murcia) for their technical help with various parts of the In Vivo part of these
214 complex experiments. We would like to thank Philippe Hantraye (MIRCen) for providing
215 baboon stereotactic frame. The University of Bordeaux and the Centre National de la
216 Recherche Scientifique provided infrastructural support. This work was supported by a grant
217 from the Michael J Fox Foundation (Project Grant No. 2013-8499), Fundacion de
218 Investigacion HM Hospitales (Madrid, Spain), the Fundación Séneca (Project Grant No:
219 FS19540/PI/14), the TARGET PD ANR grant and The Simone and Cino Del Duca Prize from
220 French Academy of Sciences. MB and MLA were supported by a Ministère de
221 l'Enseignement Supérieur et de la Recherche fellowship and the France Parkinson Foundation
222 (MB). The help of the Bordeaux Imaging Center, part of the national infrastructure France

223 BioImaging, granted by ANR-10INBS-04-0, is acknowledged. The Human α -Synuclein
224 aggregation TR-FRET immunoassay was done in the Biochemistry and Biophysics Platform
225 of the Bordeaux Neurocampus at the Bordeaux University funded by the LABEX BRAIN
226 (ANR-10-LABX-43) with the help of Y. Rufin. Computing time for this study was provided
227 by MCIA (Mesocentre de Calcul Intensif Aquitain), the public research HPC-center in
228 Aquitaine, France. The samples were obtained from the Brain Bank GIE NeuroCEB (BRIF
229 number 0033-00011), funded by the patients' associations France Alzheimer, France
230 Parkinson, ARSEP, and "Connaître les Syndromes Cérébelleux" to which we express our
231 gratitude. The synchrotron Diamond is acknowledged for provision of beam time (exp.
232 SP13009).

233

234 **AUTHOR CONTRIBUTIONS**

235 M.B., M.V., J.O., P.D., B.D. and E.B. conceived and designed the study. M.B., G.P., I.T.D.,
236 C.E., N.G.C., M.T.H., B.D. and E.B. performed surgeries. S.C. and C.E. performed
237 behavioral analysis. M.G. set up the actimetry behavioral platform. S.D., A.P. and P.A.
238 performed histologic and immunohistochemical analysis of the data. S.D., A.P. and M.L.A.
239 performed imaging experiments. E.D. performed electron microscopy analysis. F.L., M.L.A.
240 and M.L.T. performed biochemistry experiments. C.P. performed and analyzed primary
241 cultures experiment. S.B. and B.D. performed synchrotron analysis. C.S. performed infrared
242 microscopy. N.K. and B.M. performed biological fluids analysis. S.N. and M.M. performed
243 HPLC analysis. T.L.L. performed mRNA extraction and qPCR analysis. M.B., A.N., S.D.,
244 M.L.A., S.C., N.P.R., S.B., C.S., F.L., N.K., B.M., S.N., M.M., C.P., A.R., M.T.H., P.D.,
245 M.V., J.O., B.D. and E.B. analyzed the data. M.B., A.N. and N.P.R. developed the MLP
246 approach. M.B., M.V., J.O., B.D. and E.B. wrote the paper. All authors discussed the results,

247 assisted in the preparation and contributed to the manuscript. All authors approved the final
248 version of the manuscript.

249

250 **COMPETING FINANCIAL INTERESTS STATEMENT**

251 EB a director and a shareholder of Motac neuroscience Ltd. Other authors declare no conflict
252 of interest.

253

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308

309 **FIGURE LEGENDS**

310 **Fig. 1. Intracerebral inoculation of Lewy bodies (LB) and noLB fractions from**
311 **Parkinson's disease patients induces nigrostriatal neurodegeneration in baboon**
312 **monkeys. (A)** Tyrosine hydroxylase (TH) staining at striatum and substantia nigra pars
313 compacta (SNpc) levels. A green fire blue LUT (lookup table) was used to enhance contrast
314 and highlight the difference between non-injected, LB-injected and noLB-injected baboon
315 monkeys at striatum level. Scale bars = 5mm (striatum) and 10 μ m (SNpc). **(B)** Scatter plot of
316 TH immunostaining in SNpc. $F_{(2,14)}=9.439$, $p=0.0025$. Control vs LB-injected: $p=0.0029$.
317 Control vs noLB-injected: $p=0.0248$. **(C, D)** Scatter plots of mean grey values of striatal TH
318 immunoreactivity in the putamen ($F_{(2,14)}=7.313$, $p=0.0067$; Control vs LB-injected: $p=0.0059$)
319 **(C)** and in the caudate ($F_{(2,14)}=16.25$, $p=0.0002$; Control vs LB-injected: $p=0.0008$; Control vs
320 noLB-injected: $p=0.0008$) **(D)** in non-injected, LB-injected and noLB-injected baboon
321 monkeys. The horizontal line indicates the average value per group \pm standard error of the
322 mean. Comparison were made using One-Way ANOVA and Tukey's correction for multiple
323 comparison. * $p < 0.05$ compared with non-injected animals.
324

325 **Fig. 2. Multiple-layer perceptron (MLP)-based identification of specific signature. (A)**
326 Several endpoints ($n=180$) were measured using multiple methods (colors). Endpoints can be
327 grouped as clusters: 1. Behavior, 2. Dopaminergic degeneration, 3. α -syn-related pathology.
328 4. Non- α -syn related pathology. 5. Putative biomarkers. **(B)** Multiple brain regions ($n=40$)

329 were investigated from coronal sections at 2 levels: anterior commissure (ac.) -3mm (striatum,
330 entorhinal cortex) and -7mm (SNpc, hippocampus). (C) Detailed methodology. 1.
331 Representative scheme of one MLP predicting 3 neurodegeneration-related variables (ND₁,
332 ND₂, ND₃) with 3 experimental variables as input (var₁, var₂, var₃). Out of the 180 variables
333 measured in total, 163 were used as inputs for the MLP. 2. One MLP was trained for every
334 unique combination of 3 variables. 3. Combinations were ranked based on their prediction
335 error and top1% were selected for further analysis. 4. Combinations were deconvoluted to
336 extract single variables and count occurrence of individual variables. 5. Variables were sorted
337 based on the number of occurrence in the top1% of the best combination. (D) Raw ranking
338 obtained for LB-injected animals. Color code highlights measurement methods as in A. (E)
339 Raw ranking obtained for noLB-injected animals. Color code highlights measurement
340 methods as in A.

341

342 **Fig. 3. Direct comparison of MLP-derived signatures shows specific pattern between**
343 **experiment groups.** (A) Rank-rank hypergeometric overlap (RRHO) test between variable
344 sorting of LB and noLB-injected animals. Highly enriched variables are in the lower left
345 corner. Diagonal (highlighted by a red dashed line) was extracted to do a bin-to-bin
346 comparison between LB and noLB signatures. (B) Signatures were aligned with RRHO and
347 show low similarity in highly enriched variables (light orange background) and higher
348 similarity for lower rank variables (pale blue background). (C, D) First 20 enriched variables
349 for both LB-injected animals (C) and noLB-injected animals (D). Color code is similar to Fig.
350 2A. Detailed of variable names can be found in **Supplementary Table 1**. Bars are mean +/-
351 99% confidence interval estimated by bootstrap.

352

353 **Fig. 4. Association metric shows independence of strong predictors and beneficial**
354 **association of weaker predictors.** Both network plots were build using number of counts in
355 the top1% as node size and color, and lift (association measure) as edges. To allow better
356 visualization, only 10% of the strongest edges are shown. (A) Network plot for LB-injected
357 animals showing independence of strong predictors: S129 phosphorylated α -syn (psyn) in the
358 entorhinal (*h.psyn.ctx.er*) and the para-hippocampal cortex (*h.psyn.ctx.phipp*), microglia-
359 activation in the putamen (*h.ibal.put*), α -syn in the cingulate cortex (*h.syn.ctx.cg*) and the
360 supplementary motor area (*h.syn.ctx.sma*) and GABA levels in the internal part of the globus
361 pallidus (*hlpc.gaba.gpi*). Upper right box highlights association between actimetry measure
362 (*actim*) and a scan-sampling measure of body direction toward a closed environment (*ss.enf*)
363 with α -syn levels in the caudate nucleus (*h.syn.cd*), the red nucleus (*h.syn.rm*) and psyn in the
364 sensorimotor cortex (*h.psyn.ctx.sm*). Lower right box highlights association between
365 pathological α -syn in the putamen (*wb.syn.put* and *db.syn.put*) and the SNpc (*db.syn.sn*) as
366 well as psyn in the ventral tegmental area (*h.psyn.vta*) and peripheral levels of α -syn in the

367 plasma (*bm.plasma*). **(B)** Network plot for noLB-injected animals showing independence of
368 strong predictors: levels of Zn in the SNpc (*s.zn.sn*), pathological α -syn in the putamen
369 (*db.syn.put*), α -syn in the supplementary motor area (*h.syn.ctx.sma*) and aggregated α -syn in
370 the SNpc (*wb.synHMW.sn*). Upper left box highlights association between autophagosomes
371 (*wb.lc3.put*) and lysosomes (*wb.lamp2.put*) levels in the putamen and α -syn in the SNpc
372 (*wb.syn.sn*). Lower left box highlights association between GABA levels in the internal part
373 of the globus pallidus (*hlpc.gaba.gpi*), α -syn in the caudate nucleus (*wb.syn.cd*) and microglia
374 activation in the entorhinal cortex (*h.ibal.ctx.er*). Lower right box highlights association
375 between soluble (*wb.syn.putc*) and aggregated (*wb.synHMW.putc*) levels of α -syn in the
376 putamen.

377
378
379

380 **Supplementary Fig. 1. Purification and characterization of Lewy bodies (LB) and noLB**
381 **inocula from Parkinson disease (PD) brains.** **(A, left)** Immunohistochemistry image of α -
382 synuclein-positive LB (arrows) in nigral postmortem brain samples (PD #1; α -synuclein in
383 brown, neuromelanin in dark-brown) before sucrose gradient purification. The pie chart
384 indicates the relative contribution of the 5 patients to the final pool of LB and noLB inocula
385 **(A, middle)** Schematic representation of the sucrose gradient fractionation procedure used to
386 purify LB/noLB-containing fractions from freshly frozen postmortem nigral brain tissue of 5
387 sporadic PD patients. **(A, right)** Filter retardation assay probed with a human α -synuclein
388 antibody to assess the presence of insoluble α -synuclein aggregates in the different fractions
389 obtained by sucrose gradient fractionation from freshly frozen postmortem nigral brain tissue
390 from sporadic PD patients (PD #1). Blue rectangles indicate the noLB-containing fraction and
391 red rectangles indicate the LB-containing fraction selected to prepare the mixture used for
392 inoculations. **(B)** Confocal examination of purified noLB and LB fractions with α -syn
393 immunofluorescence (red) and thioflavin S staining (green). Both LB and noLB present
394 thioflavin S-positive aggregates but much smaller in noLB fractions. Scale bar = 10 μ m. **(C)**
395 Ultrastructural examination of noLB and LB fractions by electron microscopy showing
396 massive fibrils in LB fractions while noLB fractions contain, besides soluble α -syn, some
397 punctiform small size aggregates. **(D)** NoLB and LB fractions derived from PD brains (left
398 panel) were treated with 1 μ g/ml proteinase K for 0, 15, 30, 45 and 60 min and analyzed by
399 immunoblotting with syn211 antibody. The EC50 value was determined as the concentration
400 at which this ratio is decreased by 50%. The corresponding EC50 value for LB (>60 min) was
401 approximately fourfold greater than with noLB (15.23 min) **(E)** NoLB and LB fractions were
402 treated for 6h with increasing concentrations of either urea or SDS or buffer as control.
403 Syn211 was used to detect the forms of α -synuclein. The LB fractions appear to be more
404 resistant to breakdown compared with noLB fractions. The horizontal line indicates the

405 average value per group \pm standard error of the mean. Comparison were made using Two-
406 Way ANOVA and Tukey's correction for multiple comparison. * $p < 0.05$ compared with
407 untreated condition. **(F)** TR-FRET immunoassay analysis of noLB and LB fractions.
408 Fluorescence measurements were taken 20h after antibody. Analysis by unpaired Student's t-
409 test. *: $P < 0.05$. Mean \pm s.e.m.

410

411 **Supplementary Fig. 2. Relative quantification of soluble and aggregated α -synuclein in**
412 **noLB/LB fractions by velocity sedimentation and density floatation gradient**
413 **fractionations.**

414 **(A)** Representative dot blots of the distribution of total α -synuclein (top, MJFR1 antibody, Abcam),
415 FILA-1 α -synuclein aggregates (middle, MJFR14-6-4-2 antibody, Abcam) and phosphorylated pS129 α -synuclein
416 (bottom, EP1536Y antibody, Abcam) on velocity sedimentation fractions (numbered from top to bottom of the gradient) for noLB
417 (green) and LB (blue). **(B-D)** The relative amounts of total α -synuclein **(B)**, FILA-1-positive
418 α -synuclein **(C)** and pS129 α -synuclein **(D)** per fraction were quantified from noLB (green,
419 $n=5$ PD patients) and LB (blue, $n=5$ same PD patients) velocity sedimentation fractionations.
420 Mean curves (bold lines) with SEM (lighter shade areas) for each group. Velocity fractions
421 containing soluble α -synuclein (1 to 6) are identified with a black line, while fractions
422 containing aggregated insoluble α -synuclein (7 to 16) are identified with a red line. **(E)**
423 Representative dot blots of total α -synuclein (top, MJFR1 antibody, Abcam), FILA-1 α -
424 synuclein aggregates (middle, MJFR14-6-4-2 antibody, Abcam) and phosphorylated pS129
425 α -synuclein (bottom, EP1536Y antibody, Abcam) on density floatation gradient fractions
426 (numbered from top to bottom of the gradient) for noLB (green) and LB (blue). **(F-H)** The
427 relative amounts of total α -synuclein **(F)**, FILA-1-positive α -synuclein **(G)** and pS129 α -
428 synuclein **(H)** per fraction were quantified from noLB (green, $n=5$ PD patients) and LB (blue,
429 $n=5$ same PD patients) equilibrium density floatation fractionations. Mean curves (bold lines)
430 with SEM (lighter shade areas) for each group. Density fractions containing soluble α -
431 synuclein (9 to 12) are identified with a black line, while fractions containing aggregated
432 insoluble α -synuclein (5 to 8) are identified with a red line. **(I)** Relative ratios of soluble
433 monomeric (velocity fractions 1-6 and density fractions 9-12) versus insoluble aggregated
434 (velocity fractions 7-16, and density fractions 5-8) α -synuclein forms were calculated from
435 each fractionation of noLB (green) and LB (blue) of each PD patient ($n=5$) and are
436 represented respectively as black and red bars with SEM, together with individual values of
437 each fractionation ($n=5$ velocities, $n=5$ densities).

438

439 **Supplementary Fig. 3. Analysis of the amyloid structure of LB and noLB protein**
440 **aggregates by infrared microspectroscopy.**

441 **(A).** Mean spectra of LB (blue) and noLB
442 (green) aggregates in the amide I and II bands. The spectra exhibited the typical amide I and
amide II bands characteristic of protein samples. The amide I band in the two groups showed

443 a strong shoulder at around 1630 cm^{-1} which is characteristic for the β -sheet component (**B**)
444 Second derivative of the 3 groups separated by principal component analysis (PCA). A total
445 of 37 no-LB and 53 LB vector normalized second derivative spectra were analyzed. The
446 second derivative spectra allowed finding the exact position of the β -sheet component at
447 1626.7 cm^{-1} . The $1627\text{ cm}^{-1}/1653\text{ cm}^{-1}$ ratio does not completely separate the 2 groups by the
448 intensity of their amyloid signal. One group containing about 40% of the LB spectra (red
449 ellipse) presented a higher amyloid signal than the rest of the LB spectra and a 2 cm^{-1} shift in
450 the position of the amyloid peak (black arrow) (**C**) PCA score plot showing the clustering of
451 the spectra in 3 groups (in ellipses) formed by principal components 1 (PC-1) and 2 (PC-2).
452 The PCA score plot shows that most LB and no LB spectra cluster on the negative part of PC-
453 1 axis while over 40% of the LB spectra cluster on the positive part of PC-1 axis (red ellipse).
454 In the negative part of PC-1 axis, LB and noLB groups can be separated along the PC-2 axis
455 (in the green and blue ellipses). (**D**) PCA loadings of PC-1 and PC-2. Loadings of the PC-1
456 (blue) showing peaks at 1658 , 1647 and 1620 cm^{-1} associated respectively with alpha-helices,
457 random coil, and amyloid domains in the aggregates. Loadings of PC-2 (red) showing peaks
458 at 1695 , 1652 , 1645 and 1628 cm^{-1} associated respectively with antiparallel beta-sheet, alpha-
459 helix, random coil, parallel beta-sheet signal.

460

461 **Supplementary Fig. 4. *In vitro* and *in vivo* nigral toxicity of Lewy bodies (LB) and noLB**
462 **inocula from Parkinson disease (PD) brains. (A, top)** In mouse primary mesencephalic
463 culture, immunofluorescent labeling for tyrosine hydroxylase (TH) (green) following 7 days
464 of treatment with $1\mu\text{l}$ and $5\mu\text{l}$ of noLB or LB fractions. Scale bars = $10\mu\text{m}$. (**A, bottom**)
465 Number of TH-positive primary mesencephalic neurons following the different treatments at
466 1 day (in white), 2 days (in blue), 5 days (in green) and 7 days (in black). Analysis by Two-
467 Way ANOVA followed by Tukey test for multiple comparisons. In all panels, $n=2-6$ per
468 experimental group. *: $p<0.05$ compared with 1d; #: $p<0.05$ compared with 2d. (**B, top**)
469 Representative photomicrographs of tyrosine hydroxylase (TH)-positive substantia nigra pars
470 compacta (SNpc) neurons (brown; thionin staining in purple) in non-injected, noLB or LB-
471 injected mice at 4 months after inoculations. Scale bars= $500\mu\text{m}$. (**B, bottom**) Quantification
472 of TH-positive substantia nigra pars compacta (SNpc) neurons by stereology in control, LB-
473 and noLB-injected mice. Control mice, $n=10$, LB-injected mice at 4 months, $n=10$, No-LB-
474 injected mice at 4 months, $n=10$. One-way analysis, followed by Tukey test for multiple
475 comparisons. *: $p<0.05$ compared with control and noLB-injected side at 4 months.

476

477 **Supplementary Fig. 5. Guideline for variable naming.**

478

479 **Supplementary Fig. 6. Performances of multiple-layer perceptrons.** A matrix of similar
480 size filled with randomly generated values was used as control. (**A**) Data histogram for LB-
481 injected group (left panel - blue) shows significant decrease (Cohen's $d=0.468$, $t=-278.755$,

482 $p < 10^{-6}$) in mean square error. Right panel shows similar data presented as boxplots. **(B)** Data
483 histogram for noLB-injected group (left panel - blue) shows significant decrease (Cohen's $d =$
484 0.543 , $t = -323.013$, $p < 10^{-6}$) in mean square error. Right panel shows similar data presented as
485 boxplots.

486

487 **Supplementary Table 1. List of variables used in multiple-layer perceptron analyses.**

488

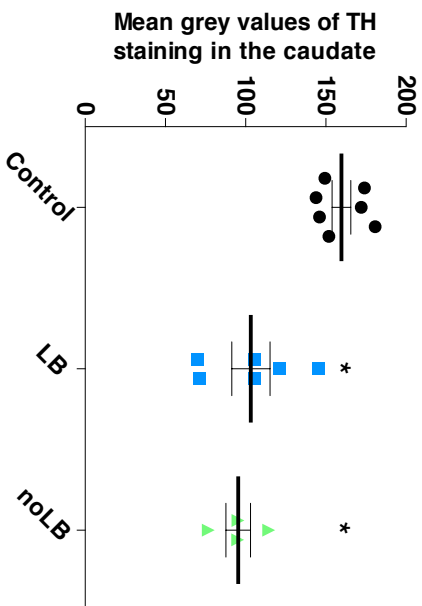
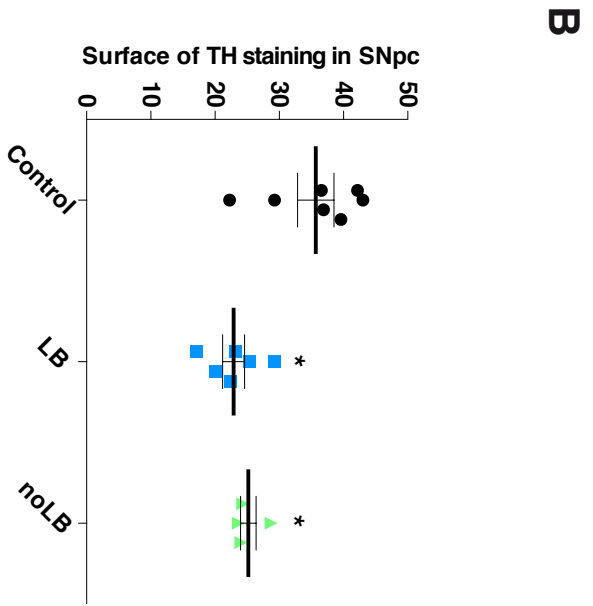
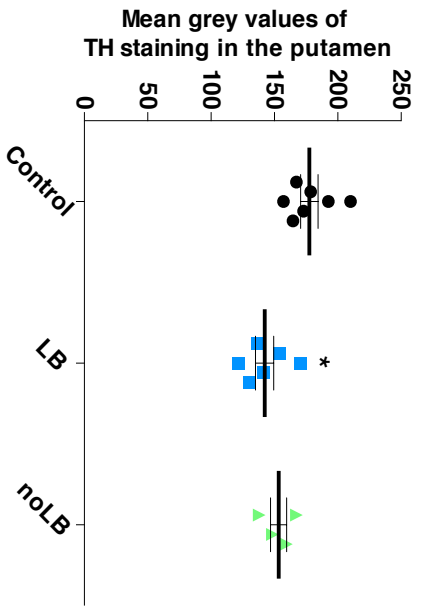
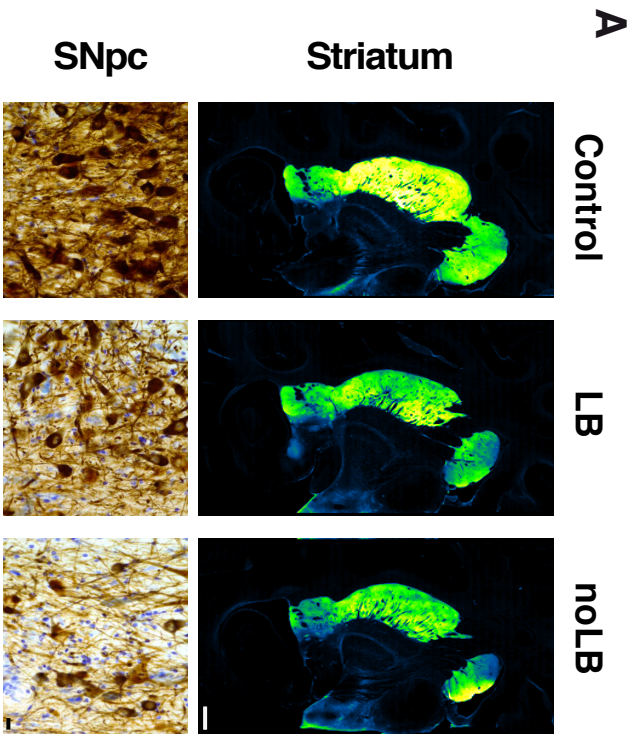
489 **Supplementary Table 2. Raw data that served for the multiple-layer perceptron analyses**

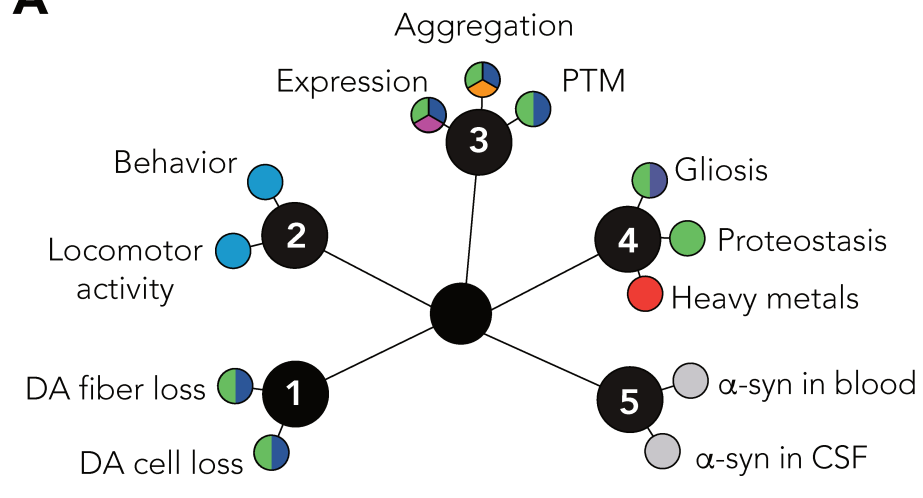
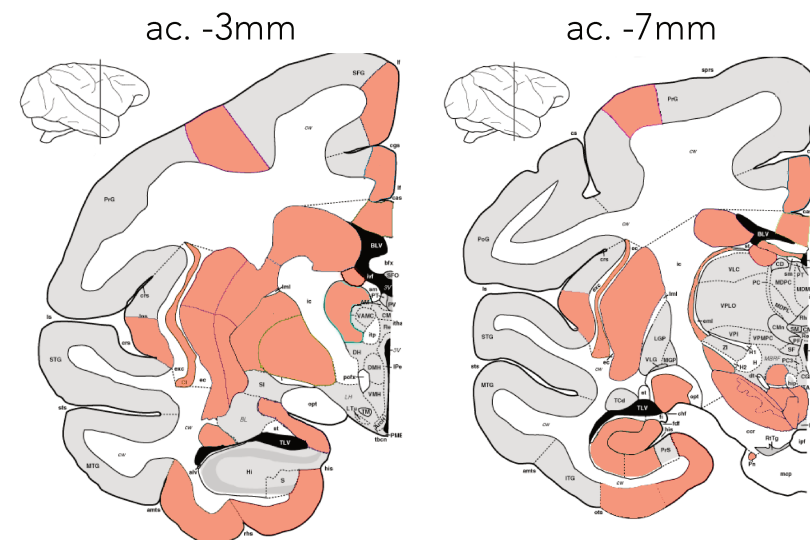
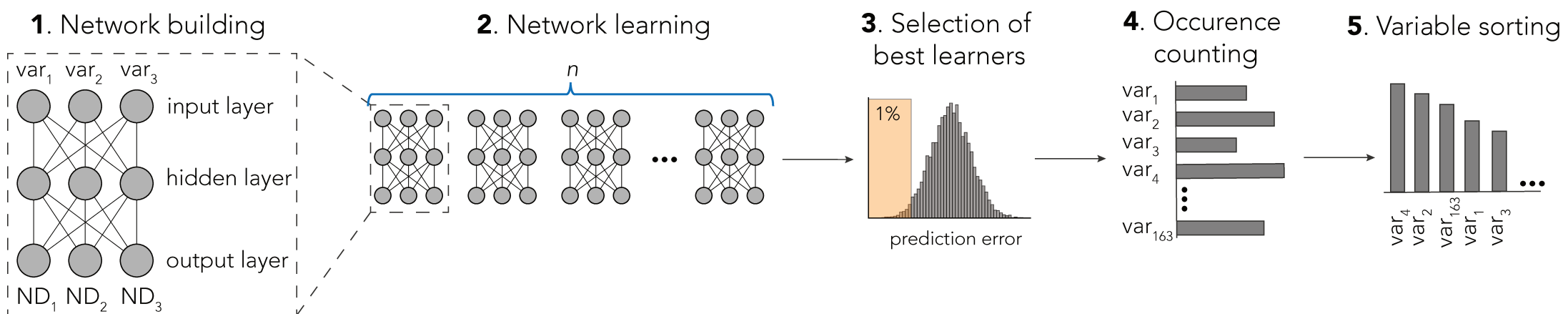
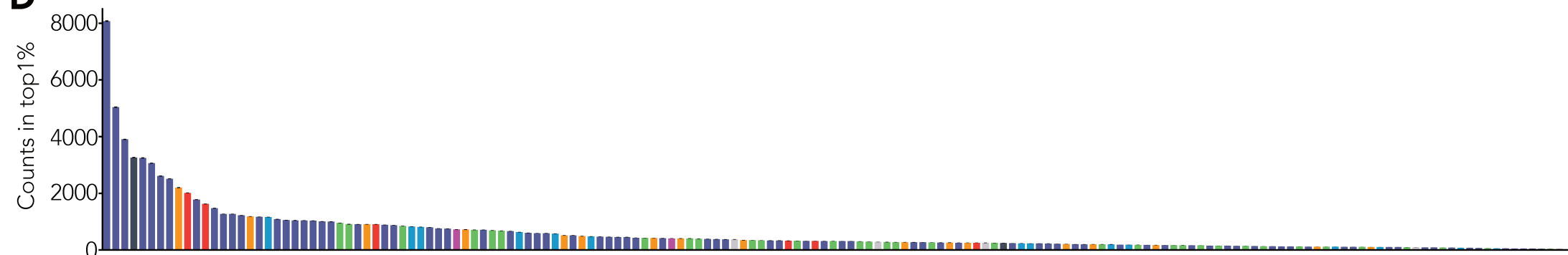
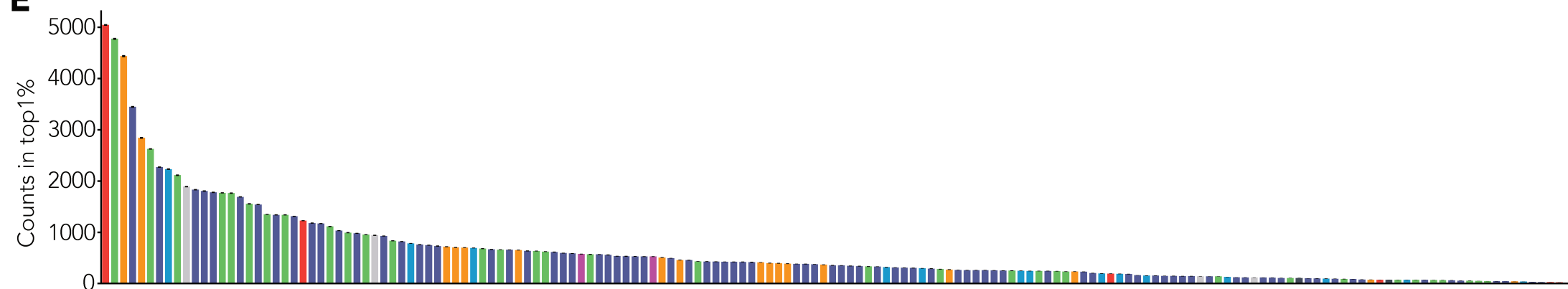
490 for all behavioral, histological, biochemical, transcriptional and biophysical approaches

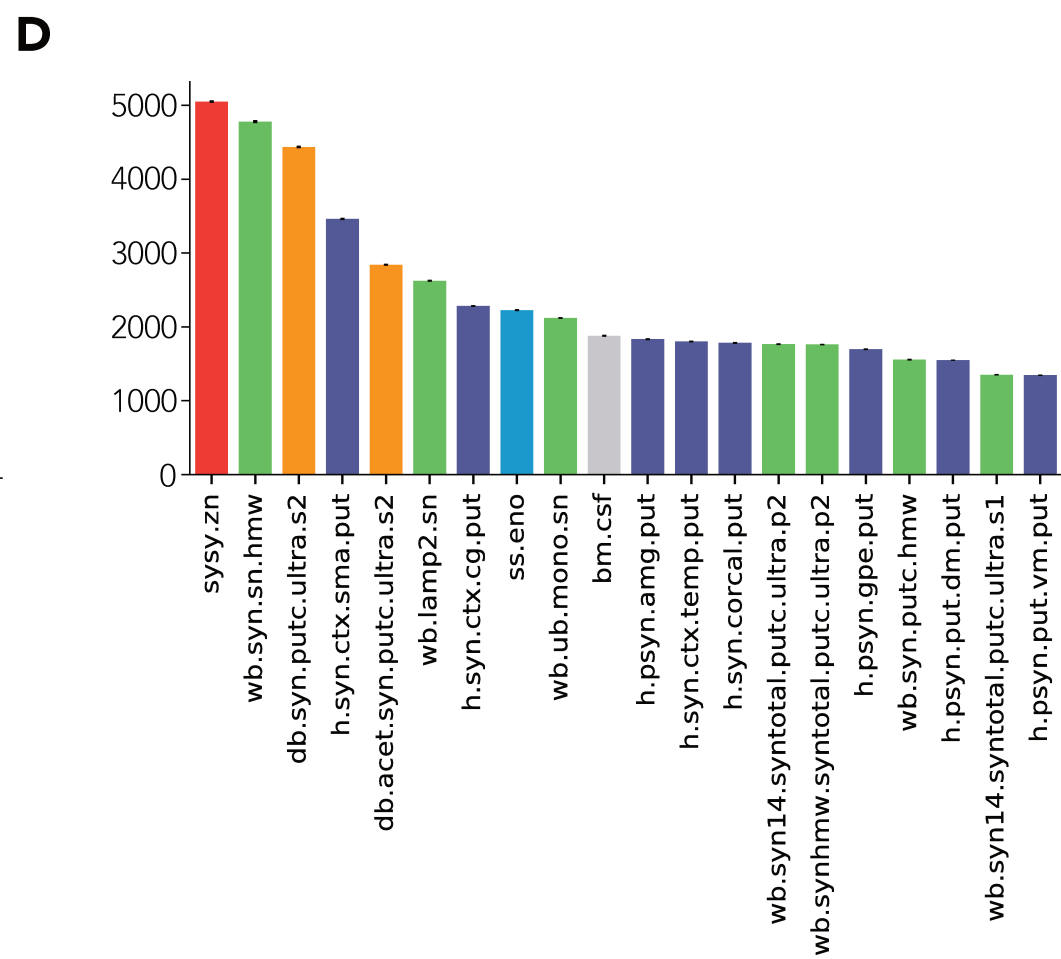
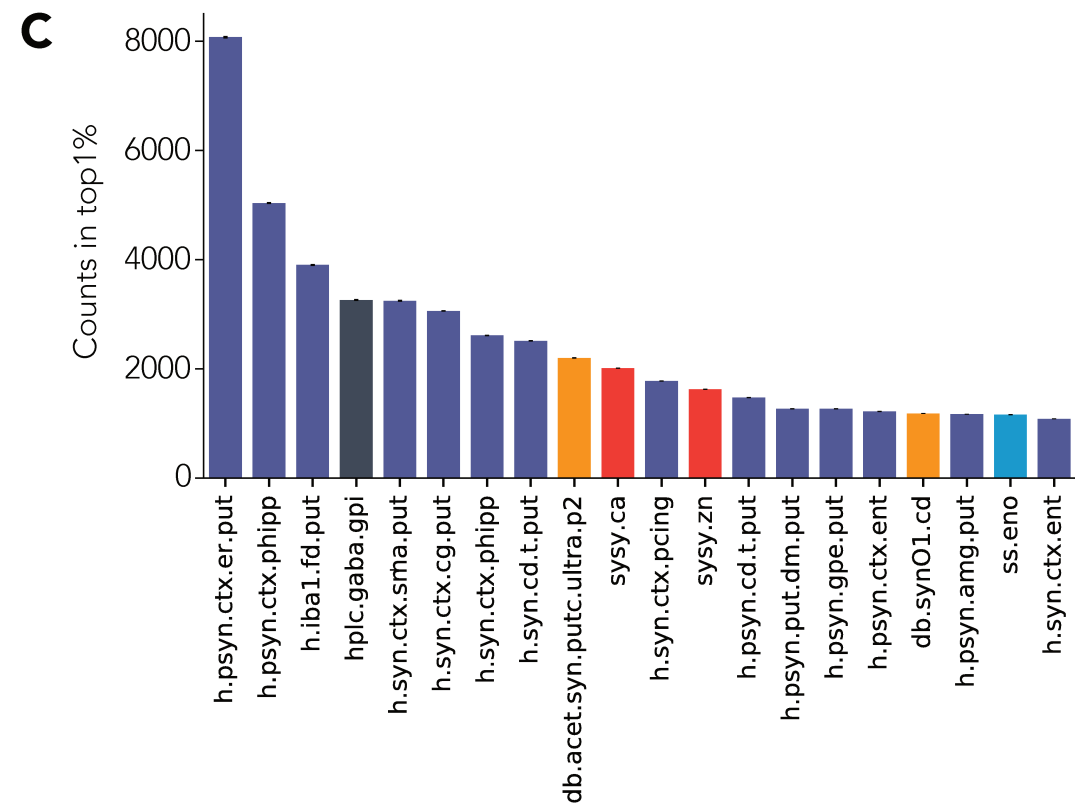
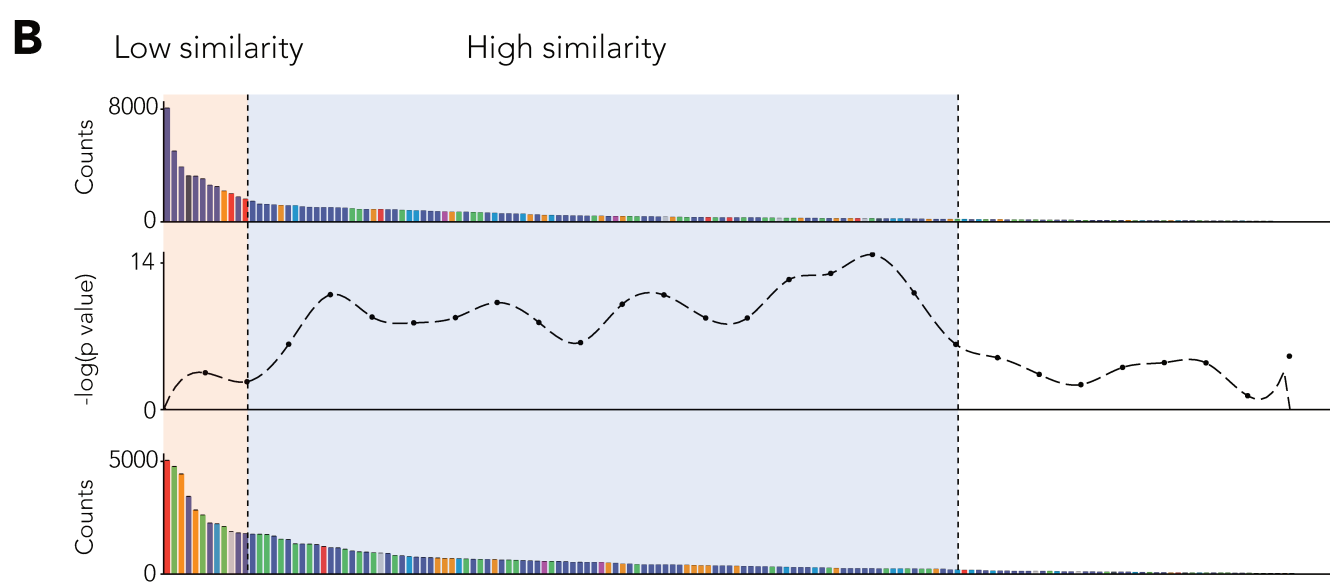
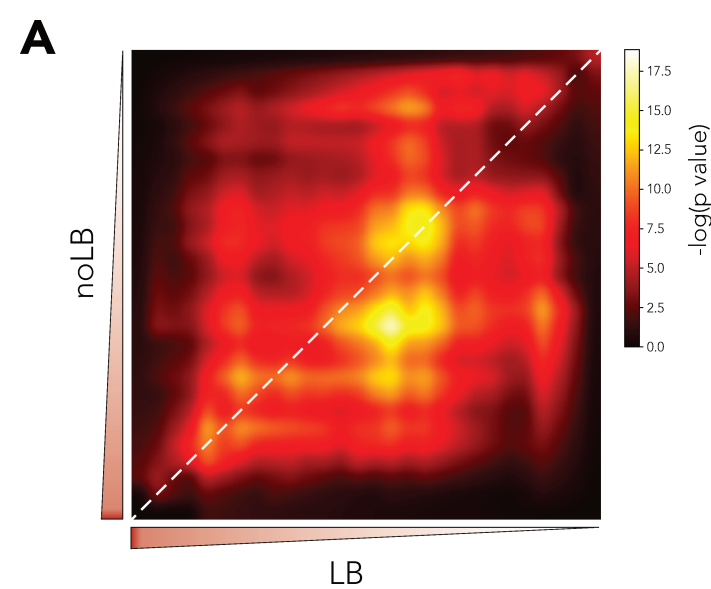
491 (applied to several brain areas, totalizing the quantification of 180 variables for each

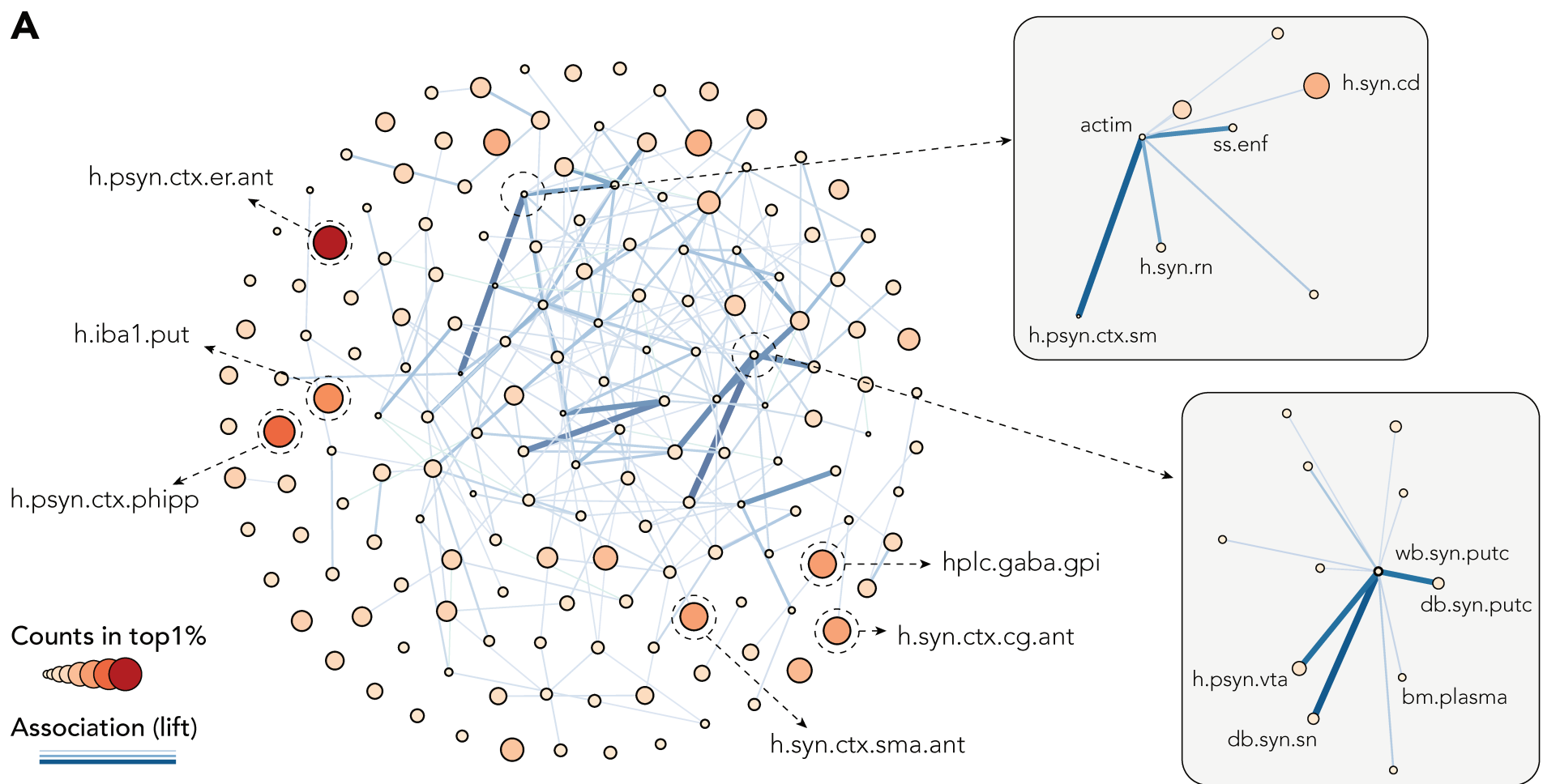
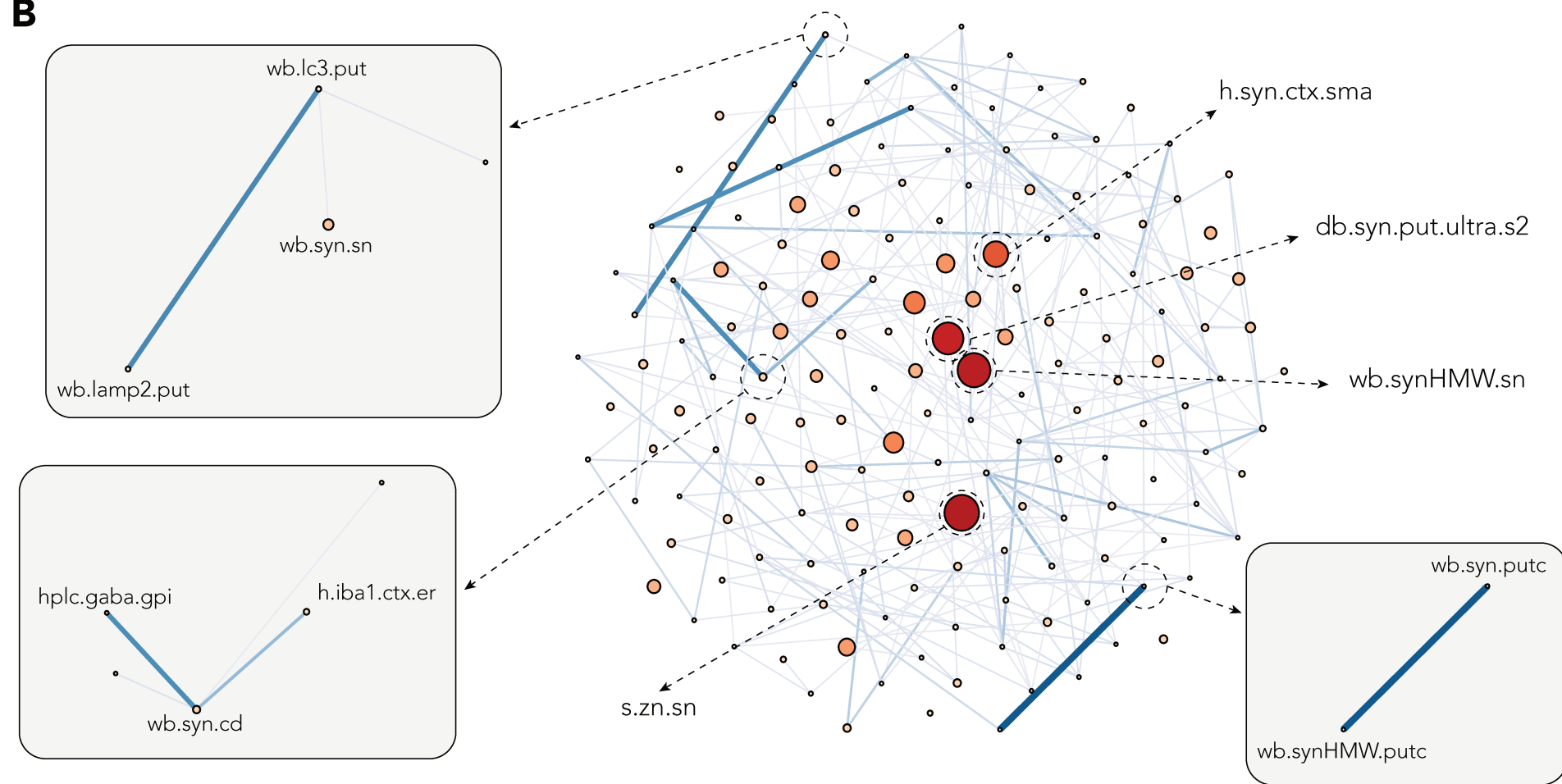
492 individual).

493



A**B****C****D****E**



A**B**

1 METHODS

2 Methods, including statements of data availability and any associated accession codes and
3 references, are available in the online version of the paper.

4 *Note: Any Supplementary Information and Source Data files are available in the online*
5 *version of the paper.*

7 ONLINE METHODS

8 Purification of Lewy bodies from human PD Brains

9 The samples were obtained from brains collected in a Brain Donation Program of the Brain
10 Bank “GIE NeuroCEB” run by a consortium of Patients Associations: ARSEP (association
11 for research on multiple sclerosis), CSC (cerebellar ataxias), France Alzheimer and France
12 Parkinson. The consents were signed by the patients themselves or their next of kin in their
13 name, in accordance with the French Bioethical Laws. The Brain Bank GIE NeuroCEB
14 (Bioresource Research Impact Factor number BB-0033-00011) has been declared at the
15 Ministry of Higher Education and Research and has received approval to distribute samples
16 (agreement AC-2013-1887). Human SNpc was dissected from fresh frozen postmortem
17 midbrain samples from 5 patients with sporadic PD exhibiting conspicuous nigral LB
18 pathology on neuropathological examination (mean age at death: 75 ± 2.75 years; frozen post-
19 mortem interval: 31.8 ± 7.45 h; GIE Neuro-CEB BB-0033-00011). Tissue was homogenized
20 in 9 vol (w/v) ice-cold MSE buffer (10 mM MOPS/KOH, pH 7.4, 1M sucrose, 1mM EGTA,
21 and 1mMEDTA) with protease inhibitor cocktail (Complete Mini; Boehringer Mannheim)
22 with 12 strokes of a motor-driven glass/teflon homogenizer. For LB purification, a sucrose
23 step gradient was prepared by overlaying 2.2 M with 1.4 M and finally with 1.2 M sucrose in
24 volume ratios of 3.5:8:8 (v/v). The homogenate was layered on the gradient and centrifuged at
25 $160,000 \times g$ for 3 h using a SW32.1 rotor (Beckman). Twenty-six fractions of 1500 μ l were
26 collected from each gradient from top (fraction 1) to bottom (fraction 26) and analyzed for the
27 presence of α -synuclein aggregates by filter retardation assay, as previously described¹.
28 Further characterization of LB fractions was performed by immunofluorescence, α -synuclein
29 ELISA quantification and electron microscopy as previously described¹. For stereotactic
30 inoculations, LB-containing fractions from PD patients were mixed together in the same
31 proportion (PD#1, fractions 19 and 20; PD#2, fractions 19 and 20; PD#3, fraction 22; PD#4,
32 fractions 17,18 and 19; PD#5, fractions 20, 21 and 23). NoLB-containing fractions (i.e.
33 fraction 3, at the beginning of the 1,2M interface) derived from the same PD patients (which
34 contain soluble or finely granular α -synuclein) but lacks large LB-linked α -synuclein

35 aggregates were obtained from the same sucrose gradient purification. NoLB and LB
36 fractions were adjusted to ~24 pg α -synuclein per microliter of injected samples, as measured
37 by a specific enzyme-linked immunosorbent assay (ELISA) kit against human α -synuclein
38 (Invitrogen, #KHB0061) according to the manufacturer's instructions. In all cases, samples
39 were bath-sonicated for 5 min prior to *in vitro* and *in vivo* inoculations.

40

41 **Characterization of noLB and LB fractions**

42 *Electron microscopy.* Briefly, carbon-coated nickel grids were covered for 1 min with
43 corresponding fractions of interest, then washed 3 times with distilled water. They were then
44 washed again in distilled water and stained for 5 min with 2% uranyl acetate, before being air-
45 dried. Digital images were obtained with a computer linked directly to a CCD camera (Gatan)
46 on a Hitachi H-7650 electron microscope. In all cases, samples were bath-sonicated for 5 min
47 prior to the *in vitro* applications.

48 *Immunofluorescence analysis of noLB and LB fractions.* Indicated fractions from the sucrose
49 gradient were spread over slides coated with poly-D lysine and fixed with 4%
50 paraformaldehyde (PFA) in PBS for 30 min. Fixed slides were stained with 0.05% thioflavin
51 S for 8 min and then washed three times with 80% EtOH for 5 min, followed by two washes
52 in PBS for 5 min. Finally, all samples were washed 3 times with PBS and blocked with 2%
53 casein and 2% normal goat serum for 30 min. For immunofluorescence analyses, samples
54 were incubated with human α -synuclein specific antibody (clone syn211, Thermo Scientific,
55 1:1000) for 30 min, washed three times with PBS, incubated with a goat anti-mouse TRITC
56 (Jackson, 1:500), before being cover-slipped for microscopic visualization using fluorescence
57 mounting medium.

58 *Dot-blotting analysis.* To evaluate PK-resistant α -synuclein contained in noLB and LB
59 fractions derived from PD brains, each fraction was subjected to digestion with 1 μ g/ml
60 proteinase K for 0, 15, 30, 45, and 60 min. The reaction was stopped by boiling for 5 min
61 before dot-blotting with syn211 antibody. To analyze their stability, noLB and LB fractions
62 were treated with increasing concentrations of urea (7 and 8M) or sodium dodecyl sulphate
63 (SDS) (0.5, 1 and 2%) for 6 h at room temperature. α -Synuclein was visualized as described
64 above.

65 *Human α -Synuclein aggregation TR-FRET immunoassay.* Time-resolved Förster's resonance
66 energy transfer (TR-FRET)-based immunoassays were validated for total and oligomeric α -
67 synuclein². Ten microliters of noLB and LB samples were analyzed for total α -synuclein

68 quantification with the TR-FRET immunoassays kit against human α -synuclein aggregation
69 kit (Cisbio, #6FASYPEG) according to the manufacturer's instructions.

70 *Velocity sedimentation and density floatation α -synuclein profiles in noLB and LB fractions.*

71 Frozen noLB and LB fractions aliquots (100 μ L) were thawed and solubilized in
72 solubilization buffer (SB) to reach 10 mM Tris pH 7.5, 150 mM NaCl, 0.5 mM EDTA, 1 mM
73 DTT, Complete EDTA-free protease inhibitors (Roche), PhosSTOP phosphatase inhibitors
74 (Roche), 1 U/ μ L Benzonase (Novagen), 2 mM MgCl₂ and 2% (w/v) N-lauroyl-sarcosine
75 (sarkosyl, Sigma) final concentrations, by incubating at 37°C under constant shaking at 600
76 rpm (Thermomixer, Eppendorf) for 45 minutes.

77 For velocity sedimentations, a volume of 400 μ L of solubilized noLB / LB fraction was
78 loaded on top of a 11 mL continuous 5-20% iodixanol gradient (Optiprep, Sigma) in SB
79 buffer containing 0.5% w/v final sarkosyl concentration, linearized directly in ultracentrifuge
80 11 mL tubes (Seton) with a Gradient Master (Biocomp). For density floatation gradients, a
81 volume of 400 μ L of solubilized noLB / LB fraction was mixed to reach 40% iodixanol in SB
82 buffer with 0.5% w/v final sarkosyl concentration and loaded within an 11 mL 10-60%
83 discontinuous iodixanol gradient in SB buffer with 0.5% w/v final sarkosyl concentration.

84 The gradients were centrifuged at 180,000 g for 3 hours (velocity) or for 17 hours (density) in
85 a swinging-bucket SW-40 Ti rotor using an Optima L-90K ultracentrifuge (Beckman
86 Coulter). Gradients were then segregated into 16 equal fractions from the top using a piston
87 fractionator (Biocomp) and a fraction collector (Gilson). Fractions were aliquoted for further
88 analysis of their content by dot-blot. Gradient linearity was verified by refractometry.

89 For dot blotting, aliquots of the collected native fractions were spotted onto Hybond PVDF
90 0.2 μ m membranes (GE Healthcare) using a dot blot vacuum device (Whatman). For total
91 (MJFR1) and phosphorylated pS129 (EP1536Y) α -synuclein immunolabelling, a step of
92 fixation in PBS - 0.1% glutaraldehyde was performed at this point, followed by 3 washes in
93 PBS. Membranes were then blocked with 5 % (w/v) skimmed milk powder in PBS - 0.1%
94 (v/v) Tween and probed with anti-human α -synuclein (MJFR1, rabbit 1:10000, Abcam), anti-
95 phospho pS129 α -synuclein (EP1536Y, rabbit 1:5000, Abcam) or anti α -synuclein aggregate
96 specific FILA-1 (MJFR14-6-4-2, rabbit 1:10000, Abcam) primary antibodies in PBS-T - 4%
97 (w/v) BSA, and secondary goat anti rabbit IgG HRP-conjugated antibodies (1:10000, Jackson
98 Laboratories) in PBS-T 1% (w/v) milk. Immunoreactivity was visualized by
99 chemiluminescence (GE Healthcare). The amount of the respective protein in each fraction
100 was determined by the Image Studio Lite software, after acquisition of chemiluminescent

101 signals with a Chemidoc imager (Biorad). Profiles obtained by immunoblot were normalized
102 and plotted with SEM using the Prism software.

103 *FTIR microspectroscopy.* 1-2 μL of each suspension was deposited on a CaF_2 window and
104 dried at room pressure and temperature giving aggregates varying from a few to hundreds of
105 microns in size. The protein aggregates were then measured in transmission at $50 \times 50 \mu\text{m}^2$
106 spatial resolution with an infrared microscope³. Depending on its size it was possible to
107 collect one to twenty spectra inside each aggregate. The infrared microscope was a Thermo
108 Scientific Continuum equipped with a MCT detector and a 32x 0.65 NA Refflachromat
109 objective and matching condenser, coupled to a Thermo Scientific Nicolet 8700 spectrometer
110 with a globar source and KBr beamsplitter. The microscope was operated in dual path single
111 aperture mode. Spectra were recorded between $650\text{-}4000 \text{ cm}^{-1}$ at 2 cm^{-1} resolution, with
112 Happ-Genzel apodization and Mertz phase correction. Spectra were processed in Omnic 9.2
113 for automatic atmospheric correction to remove water vapor contribution. Regarding the data
114 analysis, spectra were analyzed by Principal Component Analysis (PCA). PCA is a
115 multivariate statistical analysis technique that captures independent sources of variance in the
116 data and represents them in Principal Components (eigenvectors) that carry the underlying
117 spectral information and in a Score plot that shows the relation between spectra and can be
118 used to cluster the data based on the spectral information. PCA were performed in The
119 UnscramblerX 10.3 (Camo Software) using the SVD algorithm with leverage correction. Two
120 series of preprocessing were applied prior to PCA and compared. Spectra were either baseline
121 corrected in the amide I region between 1590 and 1700 cm^{-1} and vector normalized, or their
122 second derivatives were computed and vector normalized.

123

124 **Ethics Statement**

125 Experiments were performed in accordance with the European Union directive of September
126 22, 2010 (2010/63/EU) on the protection of animals used for scientific purposes. The Animal
127 Experimentation Ethical Committee (CEEA) of the Vall d'Hebron Institute of Research
128 (VHIR) approved experiments under the license number CEEA 81/13 (rats). The Institutional
129 Animal Care and Ethical Committee of Bordeaux University (CE50, France) approved
130 experiments under the license number 5012099-A (mice). The Institutional Animal Care and
131 Ethical Committee of Murcia University (Spain) approved experiments under the license
132 number REGA ES300305440012 (monkeys).

133

134 **Rat Ventral Midbrain Primary Cultures**

135 Postnatally derived ventral midbrain cultures were prepared essentially as described⁴. Briefly,
136 cultures were prepared in two steps. In the first step, rat astrocyte monolayers were generated
137 as follows. The entire cerebral cortex from a single rat pup (postnatal days 1–2) was removed,
138 diced, and then mechanically dissociated by gentle trituration. The isolated cells were plated
139 at a concentration of 80,000 cells onto wells under which a laminin-coated coverslip was
140 affixed. The cells were housed at 37°C in an incubator in 5% CO₂ and were fed on glial media
141 (89% MEM, 9.9% calf serum, 0.33% glucose, 0.5 mM glutamine, and 5 µg/mL insulin). Once
142 confluence had been attained (about 1 week in vitro), fluorodeoxyuridine (6.7 mg/mL) and
143 uridine (16.5 mg/mL) were added to prevent additional proliferation. In the second stage,
144 which occurred 1 week later, rat pups aged between 1 and 2 days were anesthetized and 1-
145 mm³ blocks containing ventral midbrain neurons were dissected from 1-mm-thick sagittal
146 sections taken along the midline of the brain. Tissues were collected immediately into cold
147 phosphate buffer and were treated enzymatically using papain (20 U/mL) with kynurenate
148 (500 µM) at 37°C under continuous oxygenation with gentle agitation for 2 h. A dissociated
149 cell suspension was achieved by gentle trituration and was then plated onto the preestablished
150 glia wells at a density of 0.5–1.7 million neurons per well. Cultures were maintained in
151 specially designed neuronal media (47% MEM, 40% DMEM, 10% Hams F-12 nutrient
152 medium, 1% calf serum, 0.25% albumin, 2 mg/mL glucose, 0.4 mM glutamine, 10 µg/mL
153 catalase, 50 µM kynurenic acid, 10 µM CNQX, 25 µg/mL insulin, 100 µg/mL transferrin, 5
154 µg/mL superoxide dismutase, 2.4 µg/mL putrescine, 5.2 ng/mL Na₂SeO₃, 0.02 µg/mL
155 triiodothyronine, 62.5 ng/mL progesterone, and 40 ng/mL cortisol) containing 27 µM
156 fluorodeoxyuridine and 68 µM uridine to control glial outgrowth and in 10 ng/mL glial cell
157 derived neurotrophic factor (GDNF). They were incubated for a further 7–8 days until the
158 start of experiments. All tyrosine hydroxylase (TH) neurons were counted on each plate
159 following the addition of noLB and LB fractions after 1, 2, 5 and 7 days of treatment.

160

161 **Animals and Stereotactic Inoculations**

162 *Mice.* Wild-type C57BL/6 mice (4 months old) received 2µl of either LB fractions or noLB
163 fractions by stereotactic delivery to the region immediately above the right substantia nigra
164 (coordinates from Bregma: AP=-2.9, L= -1.3, DV=-4.5) at a flow rate of 0.4µl/min and the
165 pipette was left in place for 5 min after injection to avoid leakage. Mice were killed four
166 months after injection. Animals were euthanized after 4 months. Ten to fifteen mice were
167 used in each group.

168 *Monkeys.* Animals were located from the research animal facility of the University of Murcia
169 (Murcia, Spain) and housed in 2 multi-male multi-female exterior pens, were studied in a
170 breeding farm over 2 years (Murcia, Spain). Animals were fed fruits, vegetables and monkey
171 pellets twice a day before 9 am and after 5pm. Water was available ad libitum. 17 healthy
172 adult olive baboons have been used in this study. Group sizes were chosen assuming a one-
173 tailed alpha of 0.05, with sample size of at least three per group, which provided >80% power
174 to detect a difference between the treatment groups and the control group, using a Fisher's
175 exact test. Animals were randomized into treatment or control groups. Six baboons were used
176 for LB inoculations, four were used for noLB inoculations and seven were untreated control
177 animals. Intrastratial inoculations of either LB fractions or noLB fractions were performed at
178 2 rostrocaudal levels of the motor striatum (anterior commissure [AC], -1mm and -5mm)
179 under stereotactic guidance as previously described⁵⁻⁸. The total injected volume per
180 hemisphere was 100µl (2 injection sites with 50µl each at 3µl/min at each location site). After
181 each injection, the syringe was left in place for 10 min to prevent leakage along the needle
182 track. A number of parameters were monitored during the course of the two-year study,
183 including survival and clinical observations. At the end of the experiment (24 months post-
184 injection), all monkeys were terminated with pentobarbital overdose (150mg/kg i.v.),
185 followed by perfusion with room-temperature 0.9% saline solution (containing 1% heparin) in
186 accordance with accepted European Veterinary Medical Association guidelines. Brains have
187 been removed quickly after death. Each brain was then dissected along the midline and each
188 hemisphere was divided into three parts. The left hemisphere was immediately freshly frozen
189 by immersion in a cold isopentane bath at -50°C during at least 5 min and stored at -80°C for
190 biochemistry investigation. The right hemisphere was post-fixed one week in 10 vol/tissue of
191 4% paraformaldehyde at 4°C, cryoprotected in two successive gradients of 20 then 30%
192 sucrose in phosphate buffered saline (PBS) before being frozen by immersion in a cold
193 isopentane bath (-50°C) during at least 5 min and stored immediately at -80°C until
194 sectioning. CSF and blood samples (plasma, serum, whole blood) in the 17 animals have been
195 carefully collected before sacrifice for further analysis. No samples were excluded from
196 analysis in these studies.

197

198 **Non-Human Primate Behavioral Assessment**

199 Following a 4-hour minimum habituation phase performed one day before the beginning of
200 the observations, baboon behavior was observed outside the feeding and cleaning times, in a
201 random order at two-time points (morning and afternoon), over 4 to 9 days (8 sessions per

202 group). On the 1st observational time point (i.e. 1-month post-surgery), the habituation phase
203 was performed over 3 days allowing the observer to recognize individually the animals. We
204 used a scan-sampling method, appropriate for time budgeting⁹, in which behavioral
205 parameters were assessed every 5 minutes during 2-hour sessions, resulting in 192 scans per
206 individual. Extra observational sessions were performed to avoid missing data. A unique
207 trained observer (SC; intra-observer reliability: Spearman rank order correlation $R=0.987$)
208 collected the data live on the 2-time points of the study: at 1 and 24 months post-surgery. The
209 observer was standing 1 m away from the outdoor cages. We focused on behavioral profiles
210 rather than single items and used two repertoires: one reports the interaction with the
211 environment and one describes the position within the environment, according to published
212 protocols¹⁰⁻¹². We investigated the percentages of occurrence of each item with regard to the
213 total number of scans in order to obtain mean behavioral and postural time budgets, body
214 orientation and location profiles.

215

216 **Histopathological analysis.**

217 *Extent of lesion.* To assess the integrity of the nigrostriatal pathway, tyrosine hydroxylase
218 (TH) immunohistochemistry was performed on SNpc and striatal sections. Briefly, sections
219 from three representative levels of the striatum (anterior, medial and posterior) and serial
220 sections (1/12) corresponding to the whole SNpc were incubated with a mouse monoclonal
221 antibody raised against human TH (Millipore, MAB318, 1:5000) for one night at RT and
222 revealed by an anti-mouse peroxidase EnVisionTM system (DAKO, K400311) followed by
223 DAB visualization. Free-floating SNpc sections were mounted on gelatinized slides,
224 counterstained with 0.1% cresyl violet solution, dehydrated and cover-slipped, while striatal
225 sections were mounted on gelatinized slides and cover-slipped. The extent of the lesion in the
226 striatum was quantified by OD. Sections were scanned in an Epson expression 10000XL high
227 resolution scanner and images were used in ImageJ open source software to compare the grey
228 level in each region of interest: i.e. caudate nucleus and putamen. TH-positive SNpc cells
229 were counted by stereology blind with regard to the experimental condition using a Leica
230 DM6000B motorized microscope coupled with the Mercator software (ExploraNova, France).
231 The substantia nigra was delineated for each slide and probes for stereological counting were
232 applied to the map obtained (size of probes was $100 \times 80 \mu\text{m}$ spaced by $600 \times 400 \mu\text{m}$). Each TH-
233 positive cell with its nucleus included in the probe was counted. The optical fractionator
234 method was finally used to estimate the total number of TH-positive cells in the SNpc of each
235 monkey hemisphere. In addition, we measured Nissl cell count, the volume of SN, and the

236 surface of TH-occupied in SN to fully characterize the pattern of dopaminergic cell loss in the
237 SN.

238 *α -synuclein pathology.* Synucleinopathy has been assessed with a mouse monoclonal antibody
239 raised against human α -synuclein (syn211) and phosphorylated α -synuclein (Wako, 015–
240 2191, 1:5000) immunostaining as we previously reported^{1,13}. Briefly, selected sections at two
241 rostro-caudal levels were specifically identified and incubated in a same well to allow direct
242 comparison of immunostaining intensity. Sections were incubated over-night at room
243 temperature with the aforementioned antibodies. The following day, revelation was performed
244 with anti-specie peroxidase EnVision system (DAKO) followed by 3,3'-diaminobenzidine
245 (DAB) incubation. Sections were then mounted on gelatinized slides, dehydrated, counter-
246 stained if necessary and cover-slipped until further analysis. Grey level quantification or
247 immunostaining-positive surface quantification in forty brain regions (**Fig. 2B**) were
248 performed as previously described¹³.

249 *Inflammation.* Inflammatory process in the striatum, in the entorhinal cortex and in the white
250 matter of noLB and LB-injected monkeys was measured through GFAP/S-100 (DAKO,
251 Z0334/Abnova, PAP11341) and Iba1 (Abcam, ab5076) immunohistochemistry. Striatal
252 sections of all animals were incubated together over night with a mix of rabbit antibodies
253 raised against GFAP and S-100 for the astroglial staining (respective dilutions 1:2000 and
254 1:1000) and with a goat anti-Iba1 antibody for the microglial staining (dilution 1:1000). These
255 signals were reveled with anti-specie peroxidase EnVision system (DAKO) followed by 3,3'-
256 diaminobenzidine (DAB) incubation. Sections were mounted on slides, counter-stained in
257 0.1% cresyl violet solution, dehydrated and cover-slipped. Sections stained by GFAP-S-100
258 were numerized at x20 magnification with a NanoZoomer (Hamamatsu, France) and the
259 quantification of GFAP-positive astrocytic reaction was estimated by a immunostaining-
260 positive surface quantification at regional levels with the Mercator software (ExploraNova,
261 France). Sections stained by Iba1 were used for the microglial morphology analysis through
262 fractal dimension quantification based on microscopic acquisitions, as previously described¹⁴.
263 All analyses were performed blinded to the researcher.

264

265 **mRNA extraction and qRT-PCR.** Substantia nigra samples were homogenized in Tri-
266 reagent (Euromedex, France) and RNA was isolated using a standard chloroform/isopropanol
267 protocol¹⁵. RNA was processed and analyzed following an adaptation of published
268 methods¹⁶. cDNA was synthesized from 2 μ g of total RNA using RevertAid Premium
269 Reverse Transcriptase (Fermentas) and primed with oligo-dT primers (Fermentas) and

270 random primers (Fermentas). QPCR was performed using a LightCycler® 480 Real-Time
271 PCR System (Roche, Meylan, France). QPCR reactions were done in duplicate for each
272 sample, using transcript-specific primers, cDNA (4 ng) and LightCycler 480 SYBR Green I
273 Master (Roche) in a final volume of 10 µl. The PCR data were exported and analyzed in an
274 informatics tool (Gene Expression Analysis Software Environment) developed at the
275 NeuroCentre Magendie. For the determination of the reference gene, the Genorm method
276 was used¹⁷. Relative expression analysis was corrected for PCR efficiency and normalized
277 against two reference genes. The proteasome subunit, beta type, 6 (Psmb6) and eukaryotic
278 translation initiation factor 4a2 (EIF4A2) genes were used as reference genes. The relative
279 level of expression was calculated using the comparative ($2^{-\Delta\Delta CT}$) method¹⁷.
280 Primers sequences: Psmb6 (NM_002798) forward: CAAGAAGGAGGGCAGGTGTACT;
281 Psmb6 (NM_002798) reverse: CCTCCAATGGCAAAGGACTG; EIF4a2 (NM_001967)
282 forward: TGACATGGACCAGAAGGAGAGA; EIF4a2 (NM_001967) reverse:
283 TGATCAGAACACGACTTGACCCT; SNCA (CR457058) forward: GGGCAAGAATGAA
284 GAAGGAGC; SNCA (CR457058) reverse: GCCTCATTGTCAGGATCCACA.

285

286 **Biochemical analysis.**

287 *Total protein extraction and quantification.* Immunoblot analyses were performed on
288 substantia nigra, putamen and caudate nucleus. Tissue patches (n=5) were extracted on ice
289 using 100µl of RIPA buffer (50 mM Tris-HCl pH 7.4, 150 mM NaCl, 1.0% Triton X-100,
290 0.5% Na-deoxycholate, 0.1% sodium dodecyl sulfate) with a protease inhibitor cocktail tablet
291 (Complete Mini, Roche Diagnostics). The lysate was incubated on ice for 20 min, centrifuged
292 at 14,000rpm for 15 min at 4°C. The supernatant was collected and the Bicinchoninic Acid
293 (BCA) Assay was used to determine the total amount of protein in the lysates, and then stored
294 at -80°C.

295 Based on total protein concentrations calculated from the BCA assays, aliquots of tissue
296 lysates corresponding to known amounts of total protein per lane were prepared for each
297 animal in Laemmli buffer (Tris-HCl 25mM pH=6.8, Glycerol 7.5%, SDS 1%, DTT 250mM
298 and Bromophenol Blue 0.05%) for immunoblotting experiment.

299 *Biochemical fractionation.* This technique was performed as described¹⁸. Tissue patches
300 (n=10) were homogenized in 200µl of high-salt (HS) buffer (50 mmol/L of Tris, 750 mmol/L
301 of NaCl, 5 mmol/L of EDTA, and a cocktail of protease inhibitors and phosphatase
302 inhibitors). Samples were sedimented at $100,000 \times g$ for 20 minutes, and supernatants were
303 removed for analysis. Pellets were rehomogenized in successive buffers, after which each was

304 sedimented, and supernatant was removed: HS containing 1% Triton X-100 (HS/Triton)
305 (Variable names terminated as ultra.s1), RIPA (50 mmol/L of Tris, 150 mmol/L of NaCl, 5
306 mmol/L of EDTA, 1% NP40, 0.5% Na deoxycholate, and 0.1% SDS) (Variable names
307 terminated as ultra.s12, and SDS/urea (8 mol/L of urea, 2% SDS, 10 mmol/L of Tris; pH 7.5)
308 (Variable names terminated as ultra.p2). Sodium dodecyl sulfate sample buffer was added,
309 and samples (except for the SDS/urea fractions) were heated to 100°C for 5 minutes prior to
310 immunoblot analysis.

311 *Western blot analysis.* Western blots were run in all conditions from 20µg of protein
312 separated by SDS-PAGE and transferred to nitrocellulose. Incubation of the primary
313 antibodies was performed overnight at 4°C with rabbit anti-LC3 (1:1000, Novus Biologicals),
314 rabbit anti- LAMP-2 (1:1000, Santa Cruz Biotechnology), mouse anti-TH (1:1000, Millipore),
315 goat p62 (1:1000, Progen), mouse anti human- α -synuclein (1:1000, Thermo Scientific). For
316 detection of ubiquitinated proteins, proteins were transferred on polyvinylidene fluoride
317 membranes (Millipore) and subjected to Western blot analysis using a rabbit anti-Ubiquitin
318 (1:1000, Sigma U5379). Anti-actin (1:5000, Sigma) was used to control equal loading.
319 Appropriate secondary antibodies coupled to peroxidase were revealed using a Super Signal
320 West Pico Chemiluminescent kit (Immobilon Western, Chemiluminescent HRP substrate,
321 Millipore). Chemiluminescence images were acquired using the ChemiDoc+XRS system
322 measurement (BioRad). Signals per lane were quantified using ImageJ and a ratio of signal on
323 loading per animal was performed and used in statistical analyses.

324 *Dot-blot analysis of α -synuclein.* This technique was performed as we previously described¹
325 ¹⁹. After heating at 100 °C for 5 min, 20 µg of protein extract was diluted in buffer (25 mM
326 Tris-HCl, 200 mM Glycine, 1% SDS) and filtered through either a nitrocellulose membrane
327 or an acetate cellulose membrane (Bio-Rad, 0.2 µm pore size). Membranes were then
328 saturated in 5% dry-skimmed milk in PBS and probed with antibodies against α -synuclein
329 (syn211, 1:1000), both α -synuclein fibrils and α -synuclein oligomers (Syn-O1, 1:10000^{20, 21})
330 (kindly provided by Prof. Omar El-Agnaf). Revelation was done as described in the previous
331 Materials and Methods section.

332

333 **Synchrotron radiation X-ray fluorescence (SR-XRF) microscopy elemental mapping of** 334 **brain tissue cryosections**

335 The synchrotron experiments were carried out at Diamond Light Source, Harwell Science and
336 Innovation Campus (Didcot, UK) with a 3 GeV energy of the storage ring and 300 mA
337 currents with top-up injection mode. All SR-XRF microscopy investigations reported herein

338 were carried out on the microfocus spectroscopy beamline (I18)²². The micro X-ray
339 fluorescence (μ -XRF) elemental mapping were acquired at room temperature with an incident
340 X-ray energy set to 12 keV using an Si(111) monochromator and resulting in a X-ray photon
341 flux of $2 \cdot 10^{11}$ ph/s. The substantia nigra of each animal were collected from free-floating
342 sections and mounted onto an X-ray transparent metal-free 4 μ m thickness Ultralene® foil
343 (SPEXCert Prep, Metuchen, NJ, U.S.A.) secured to a customized Polyetheretherketone
344 (PEEK) holder ensuring contamination-free samples and reduced X-ray scattering
345 contribution. The samples were affixed to a magnetic plate that connects to the sample stage.
346 The 4-element Si drift Vortex ME4 energy dispersive detector (Hitachi Hi-Technologies
347 Science America) with Xspress-3 processing electronics, was operated in the 90° geometry,
348 as such it minimizes the background signal. The sample-detector distance was fixed (75 mm).
349 The sample was held at 45° to the incident X-ray beam and rastered in front of the beam
350 whilst the X-ray fluorescence spectra were collected. An area of 500 μ m x 500 μ m within the
351 substantia nigra pars compacta (SNpc) was mapped for each sample with a step-size that
352 match the beam size (5 μ m) and a dwell time of 1 s per pixel due to low concentration of the
353 element. A thin (100 μ m) pellet of the NIST standards reference materials SRM1577c (bovine
354 liver material, NIST, Gaithersburg, MD, USA) was measured to calibrate experimental
355 parameters as well as a thin-film XRF reference material (AXO Dresden GmbH). This was
356 followed by elemental quantification through the open-source software PyMCA²³ in which
357 both the reference material and the sample are modelled in terms of main composition,
358 density and thickness. The fluorescence spectrum obtained from each pixel was fitted, the
359 elemental concentration (μ g/g dry weight or ppm) maps were generated and an average
360 elemental concentration of the SNpc regions was obtained.

361

362 **Measurement of α -synuclein in monkey biological fluids samples.** Multi-Array 96-well
363 plates (MesoScale Discovery, Gaithersburg, MD, USA) were coated with 30 μ l 3 μ g/ml MJFR1
364 (abcam, Cambridge, UK) as capture antibody and incubated overnight at 4°C without
365 shaking. The next day plates were washed 3 times with 150 μ l PBS-T [PBS (AppliChem,
366 Darmstadt, Germany) supplemented with 0,05% Tween-20 (Roth, Karlsruhe, Germany)] per
367 well. Unspecific binding of proteins was prevented by incubation with 150 μ l 1% BSA
368 (SeraCare Life Sciences, Milford, MA, USA)/PBS-T/well for 1 hour and shaking at 700rpm.
369 Calibrators (kindly provided by Prof. Omar El-Agnaf) were prepared from single use aliquots
370 of α -synuclein (1 μ g/ml stored at -80°C until use) and ranged from 25000pg/ml to 6,1pg/ml in
371 serial fourfold dilutions. 1% BSA/PBS-T served as blank. For the different specimen the

372 following dilutions were applied: 1 in 10000 for whole blood and 1 in 8 for serum, plasma
373 and CSF. All dilutions were prepared in 1% BSA/PBS-T. After washing the plates 25µl
374 calibrator solutions and diluted samples were applied to the wells and incubated as indicated
375 above. Plates were washed again and 25µl Sulfo-TAG labeled Syn1 antibody (BD
376 Biosciences, Heidelberg, Germany) diluted to 1µg/ml in 1% PBS-T were applied to the wells
377 as detection antibody. Sulfo-TAG labeling was done according to the manufacturer's
378 instruction using MSD Sulfo-TAG NHS-Ester (MSD). Incubation was for 1 hour at 700rpm.
379 Plates were washed, 150µl 2x Read Buffer (MSD) was applied and the plates were read on a
380 MSD SectorImager 2400. Data analysis was performed using WorkBench software (MSD).

381

382 **Neurotransmitter analysis.** Brain patches were dissected out on ice-cold plate, weighed and
383 put into 1.5 ml Eppendorf tubes. Samples were homogenized in methanol/water (50:50% v/v),
384 then centrifuged at 14000 rpm for 15 min at 4°C²⁴. The supernatant was aliquoted and stored
385 at -80°C until amino acid derivatization. Glutamate and GABA content in the samples was
386 measured by HPLC coupled with fluorometric detection (FP-2020 Plus fluorimeter, Jasco,
387 Tokyo, Japan) after precolumn derivatization with o-phthaldialdehyde/mercaptoethanol
388 (OPA) reagent²⁵. Thirty microliters of OPA reagent were automatically added to 28 µL
389 sample by a refrigerated autosampler kept at 4°C (Triathlon, Spark Holland, Emmen, The
390 Netherlands). Fifty microliters of the mixture were injected onto a 5-C18 Hypersil ODS
391 column (3 X 100 mm; Thermo-Fisher, USA) perfused at 0.48 mL/min (Jasco PU-2089 Plus
392 Quaternary Pump; Jasco, Tokyo, Japan) with a mobile phase containing 0.1 M sodium
393 acetate, 10% methanol, 2.2% tetrahydrofuran (pH 6.5). Chromatograms were acquired and
394 analysed using a ChromNav software (Jasco, Tokyo, Japan). Under these conditions, the
395 limits of detection for glutamate and GABA were ~1 nM and ~0.5 nM, and their retention
396 times ~3.5 min and ~18.0 min, respectively.

397

398 **Multiple-Layer Perceptrons**

399 Each Multiple-layer Perceptron (MLP) had the same architecture rule: 3 neurons as input, 3
400 neurons in the hidden layer and 3 neurons as output. Activation function of neurons was the
401 hyperbolic tangent. Each network was trained over 1,000 presentations of a subset of the
402 dataset. We used as error measure the mean square of differences between the expected
403 output and the actual output. Our implementation comprises two parameters: a learning
404 rate set at 0.05 (regulating the learning speed), and a momentum set at 0.05 (introducing
405 purposefully a conservatism bias). Prior to learning, inputs were scaled and centered

406 and normalized between -0.5 and 0.5. For every combinations of 3 variables used as inputs,
407 50 instances of MLP were trained with different subsets of the dataset. 80% of available data
408 has been used for learning and the remaining 20% for testing the performance of the network
409 (elements of each subset were randomly (and uniformly) drawn for each network). The
410 performance from a given set of input variables was the mean of the error of the 50 instances
411 of MLP that had data for these variables as inputs. Code was written using Python and the
412 Python scientific stack²⁶⁻²⁸ (Jones, 2001; Walt, 2011; Hunter, 2007). The code is fully
413 available here (DOI: 10.5281/zenodo.1240558). Computation has been done using the Avakas
414 cluster of the Mesocentre de Calcul Intensif Aquitaine (MCIA). Rank-rank hypergeometric
415 overlap (RRHO) test was performed as previously described²⁹ using RRHO package (1.14.0)
416 in R³⁰ on variable list after ranking between experimental groups. Plotting was made using
417 matplotlib in Python environment.

418 The association metric was based on lift calculation. Let a and b be the two variables and n_x
419 the number of combinations including variable x and n the total number of combinations
420 considered in the analysis. Lift calculation was then:

$$Lift_{ab} = \frac{n_{ab}/n_b}{n_a/n}$$

421 The lift calculation was then corrected for performance to avoid selection of detrimental
422 association by being divided by the mean prediction error of the duo.

423

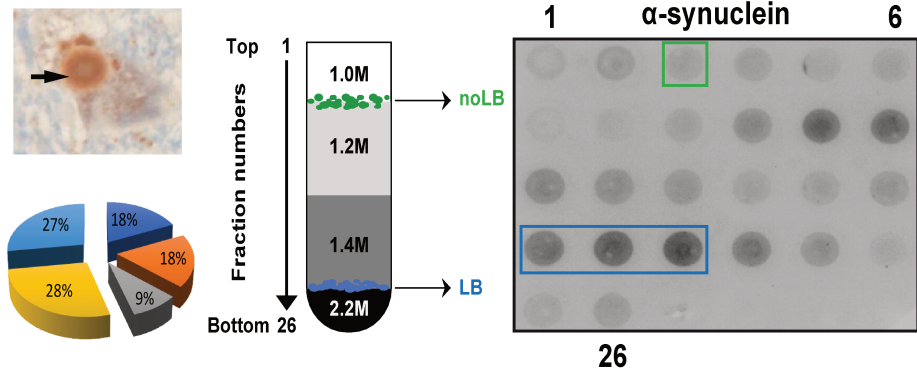
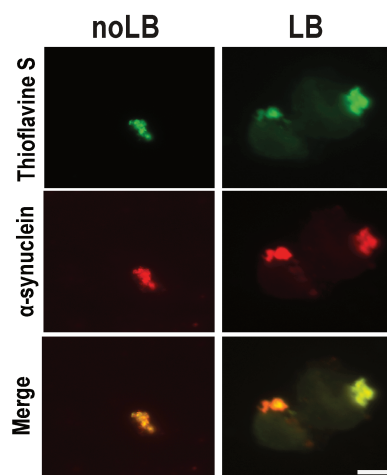
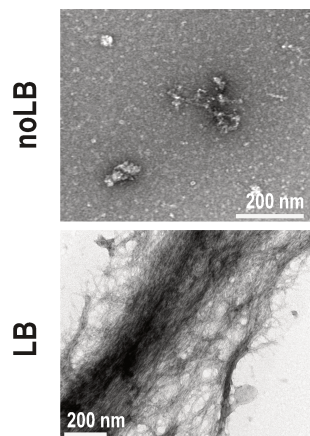
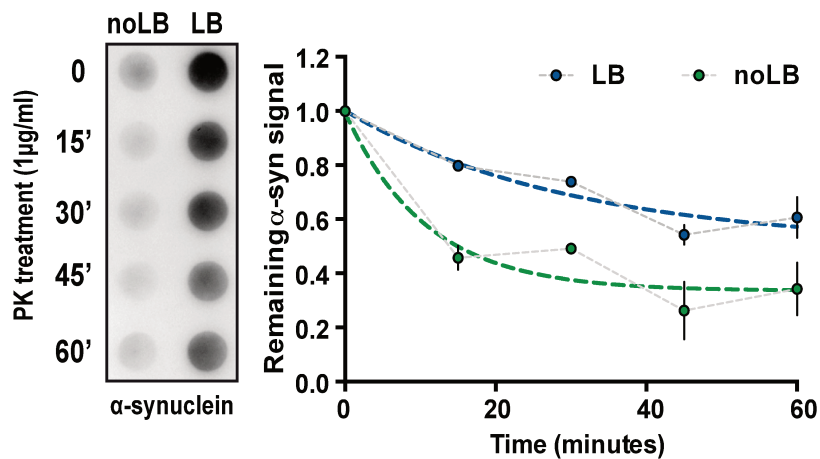
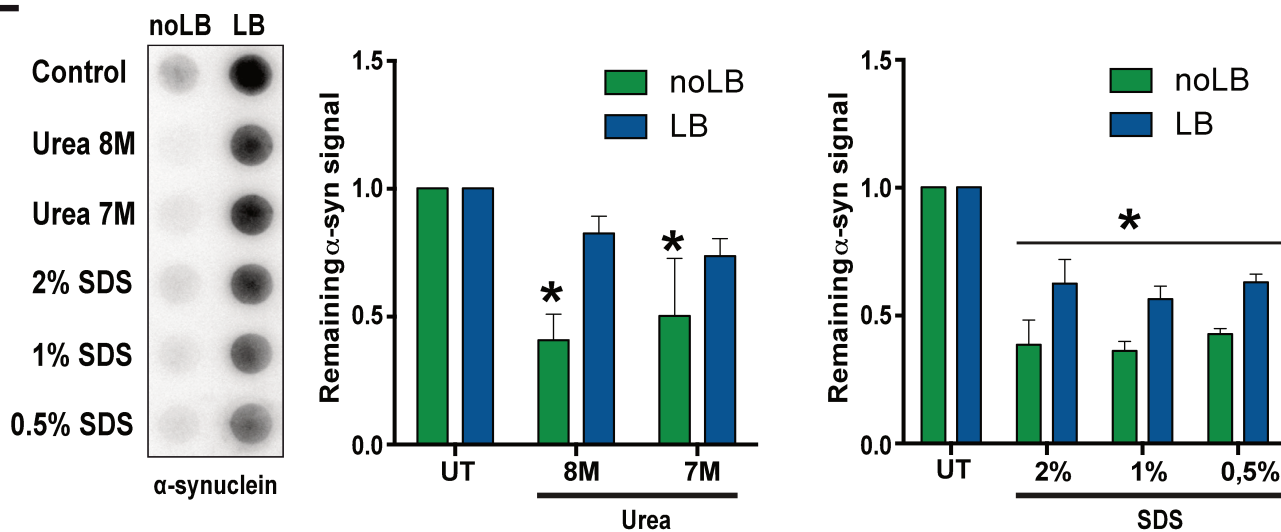
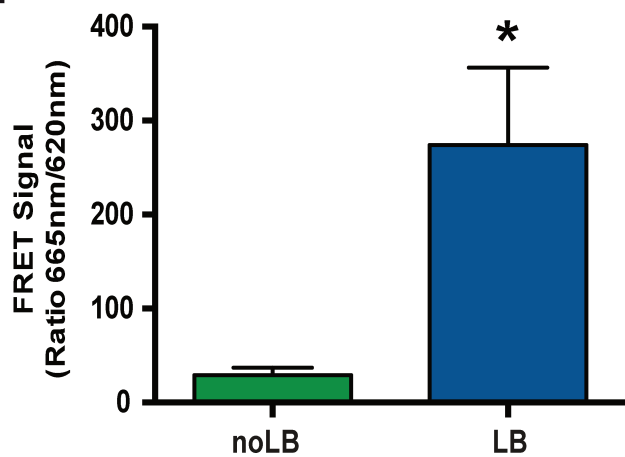
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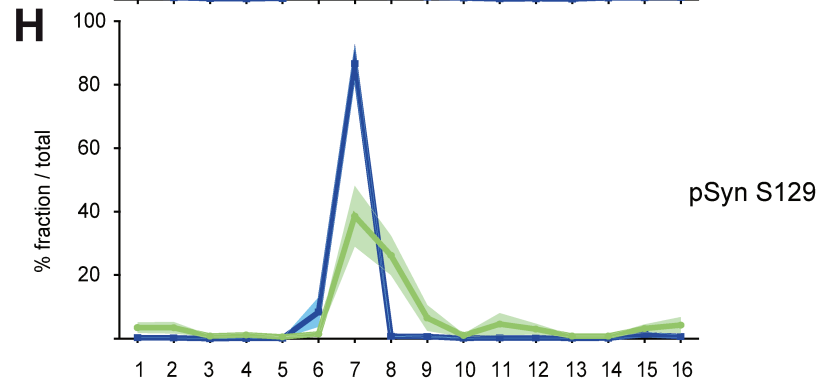
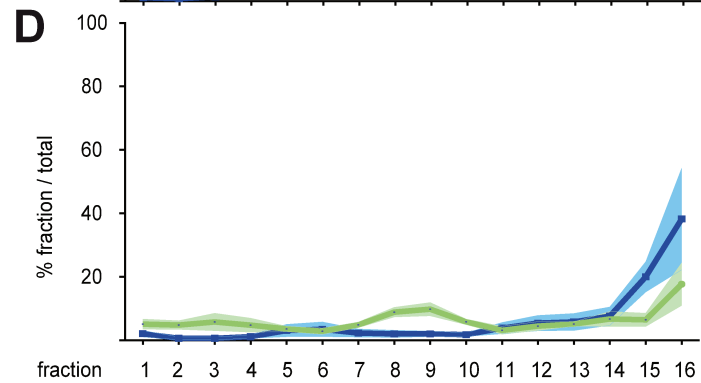
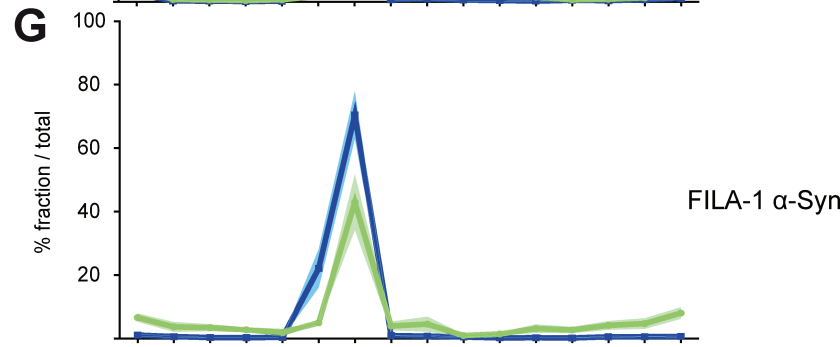
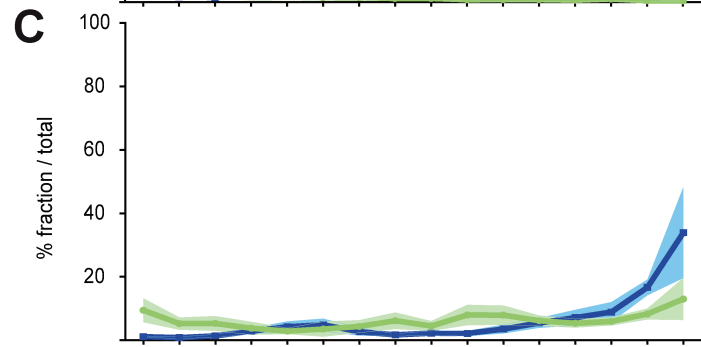
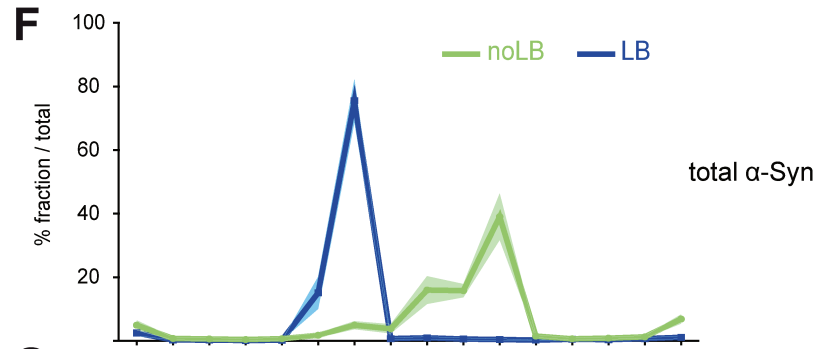
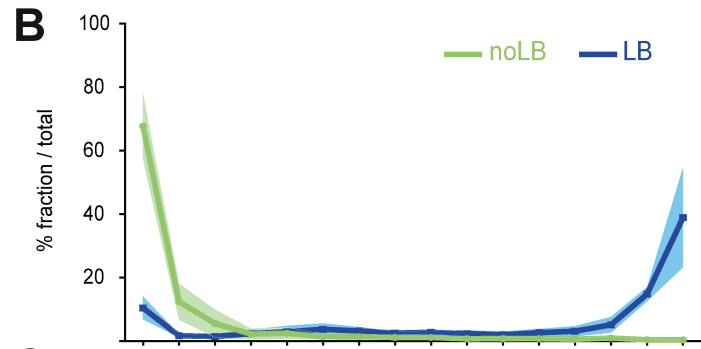
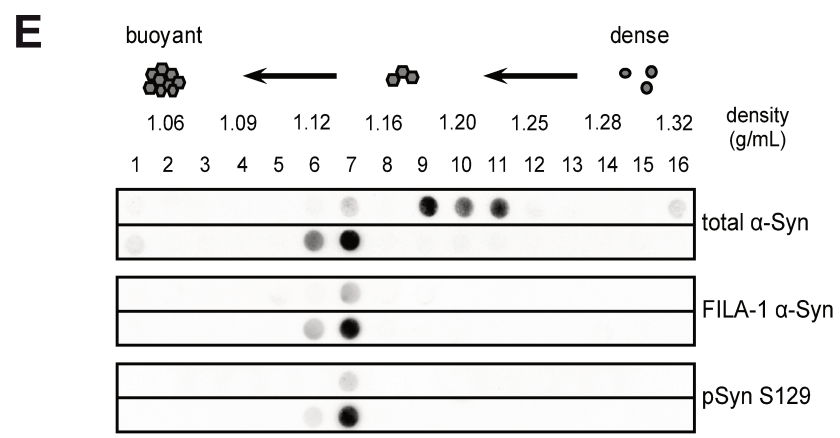
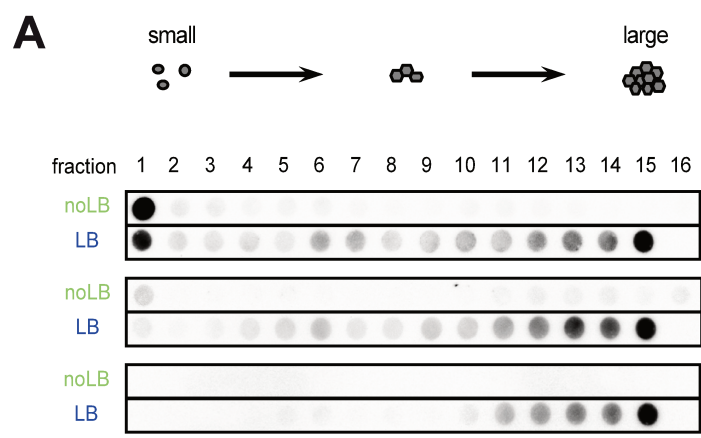
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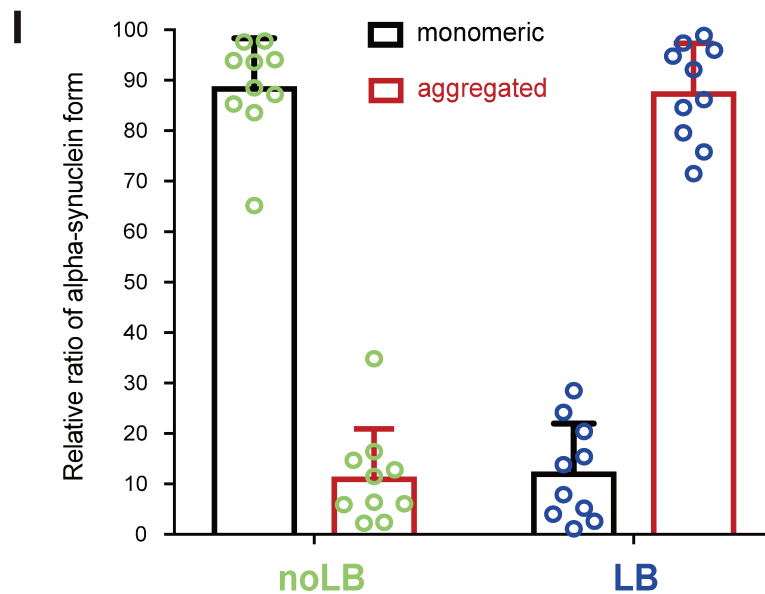


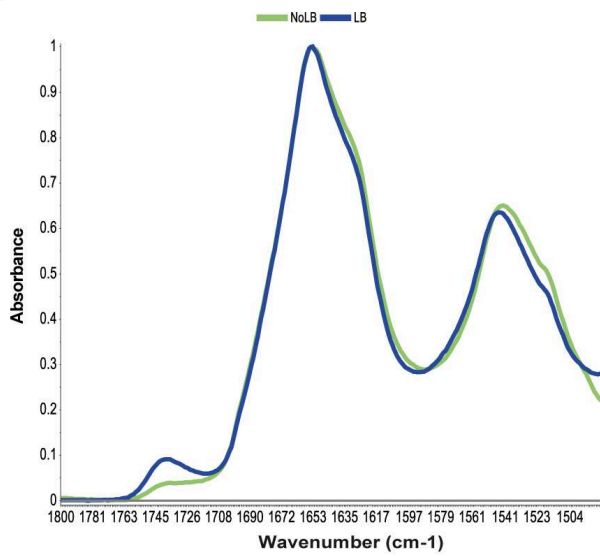
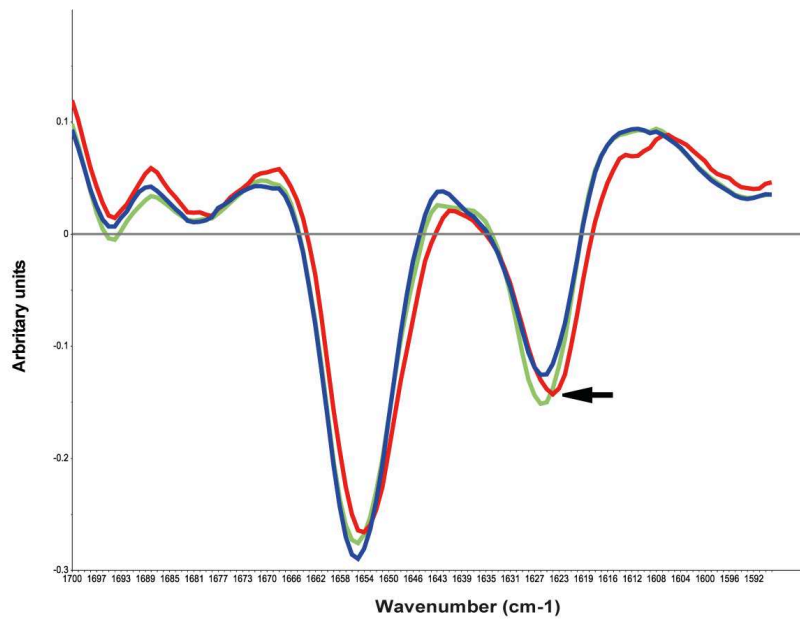
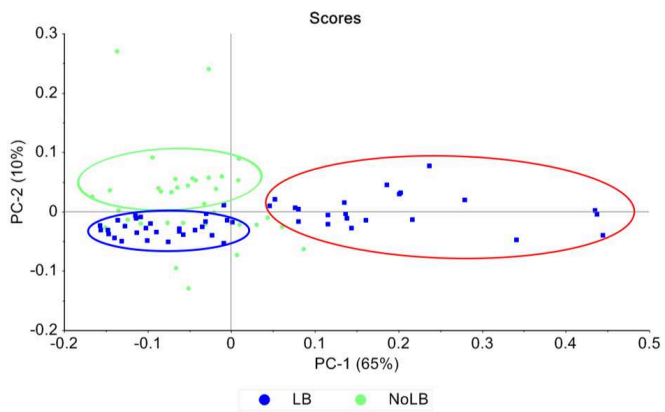
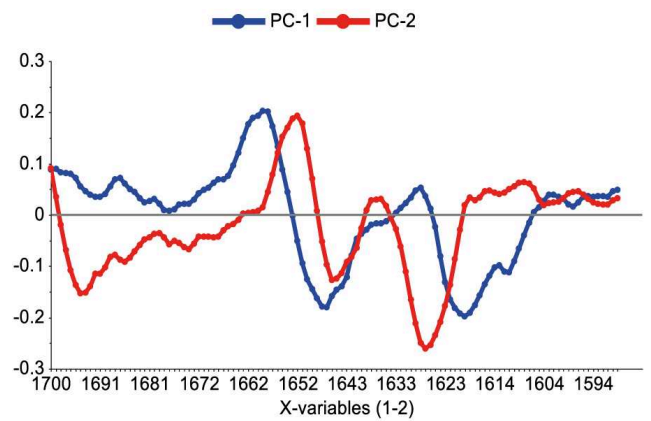
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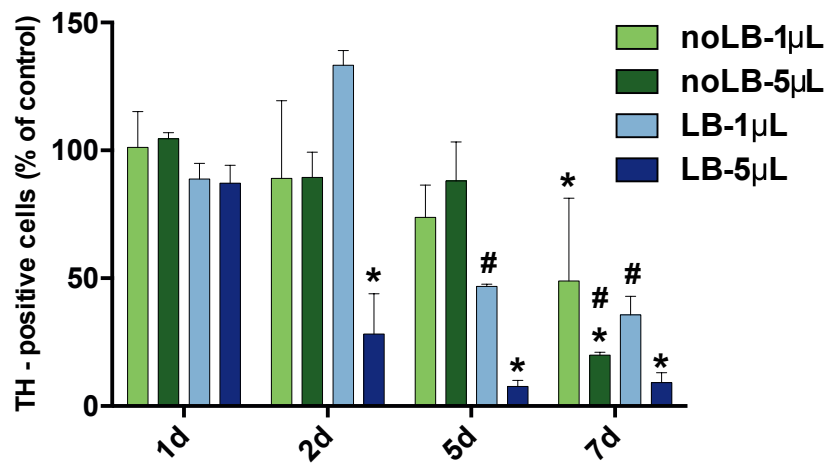
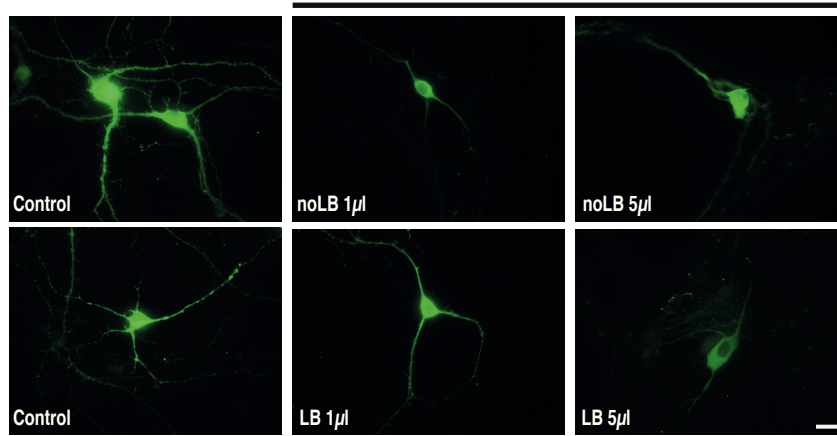
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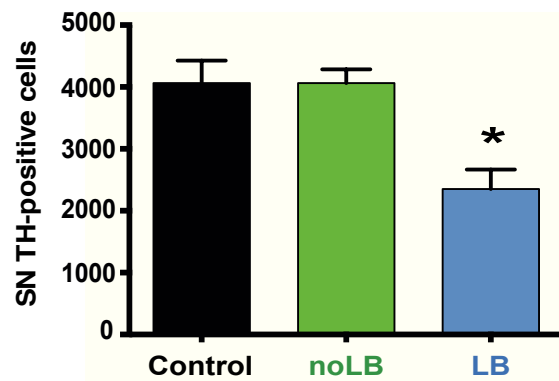
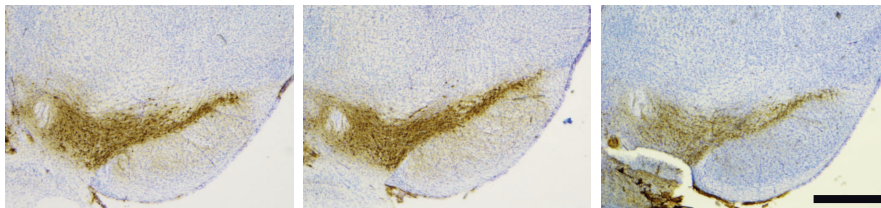
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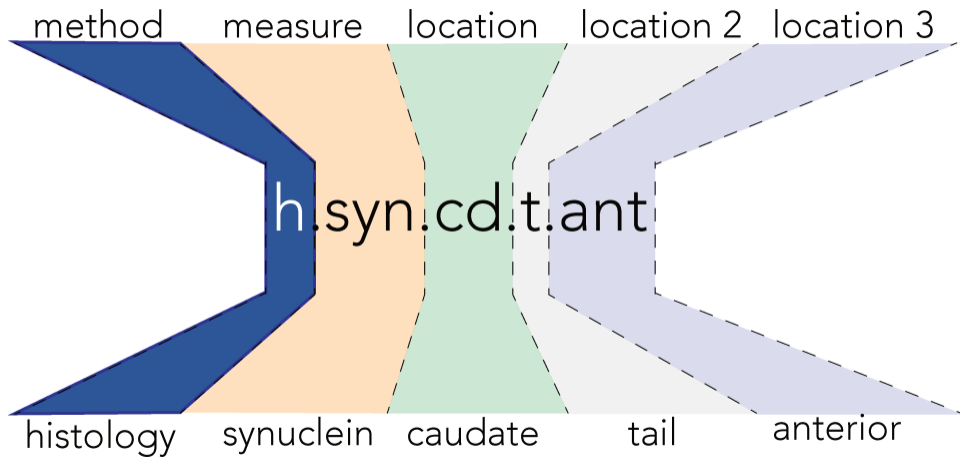
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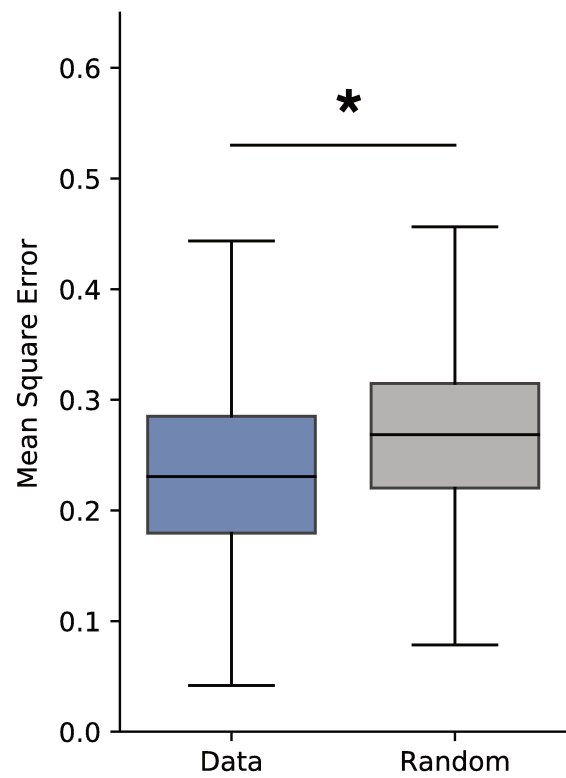
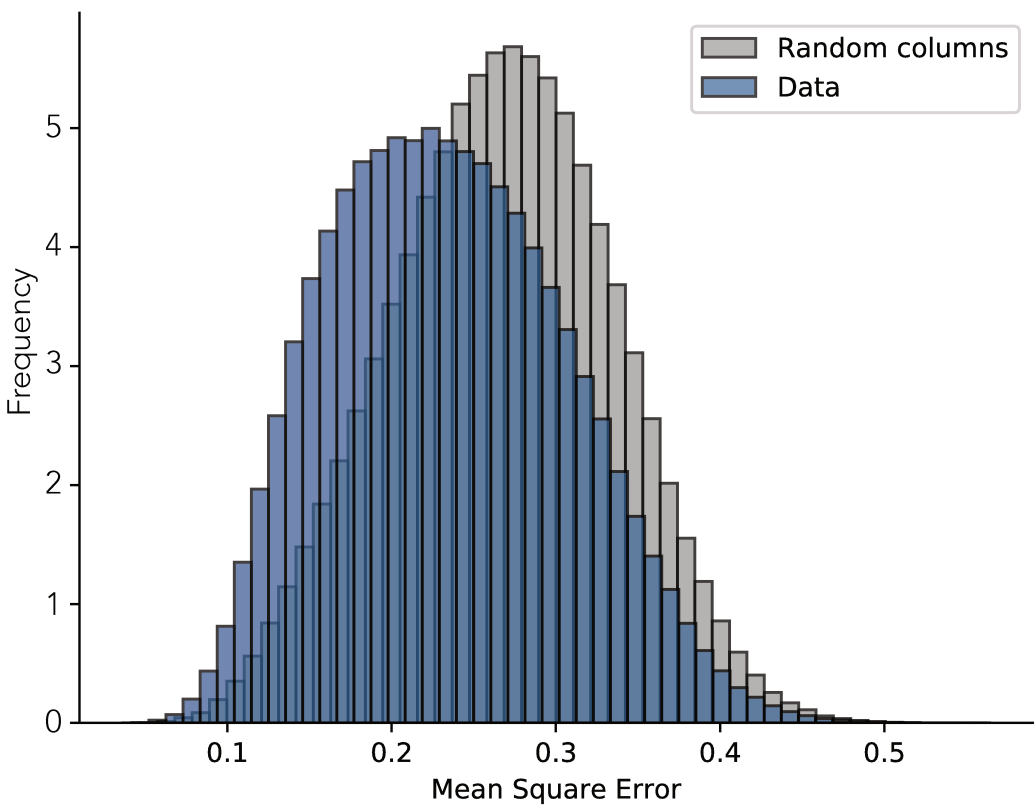
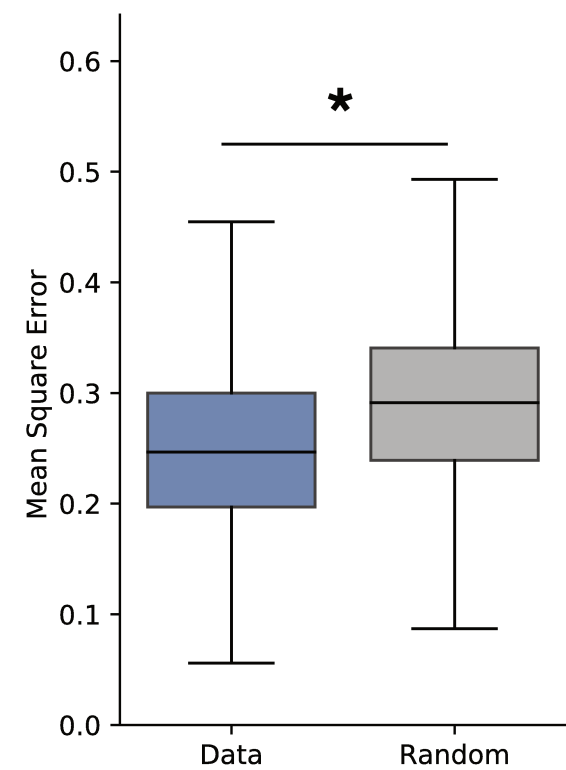
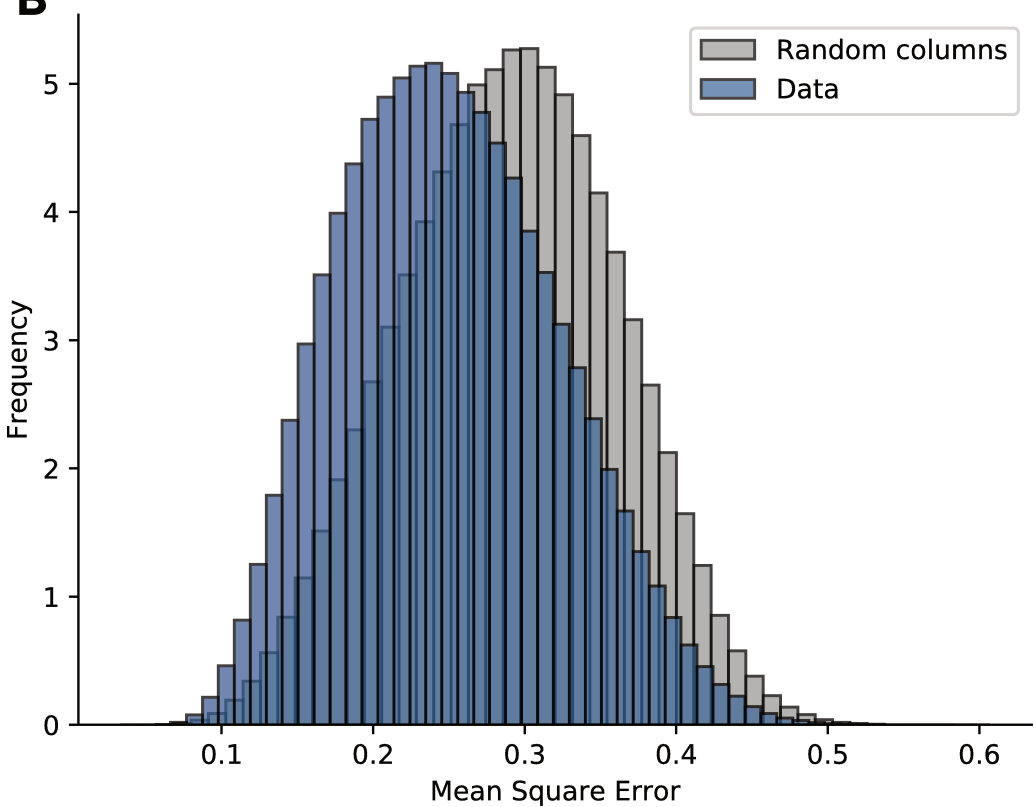
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Collège de France



Le libre arbitre | Jean-Baptiste Guillon

Chapitre 9

Exercer son libre arbitre : un processus décisionnel

Aurélien Nioche

Entrées d'index

Mots clés :

compatibilisme des alternatives, conception hiérarchique du libre arbitre, déterminisme rationnel, théorie de la décision

Texte intégral

- 1 La question de savoir s'il est possible d'agir selon son propre libre arbitre continue de faire l'objet de nombreuses discussions, formelles et plus informelles, sérieuses et moins sérieuses et les positions adoptées par les protagonistes de telles discussions font souvent preuve d'une grande diversité. Une manière de situer ces positions les unes par rapport aux autres est de considérer l'attitude prise par rapport à l'argument suivant qui défend une incompatibilité entre exercice du libre arbitre et véracité de la thèse du déterminisme (nous laisserons pour l'instant le lecteur "libre" d'apporter à "thèse déterministe" la signification qu'il souhaite mais prendrons le temps d'y revenir un peu plus loin).
 - 1) On agit de son propre libre arbitre si l'on a le contrôle de son action.
 - 2) Avoir le contrôle d'une action nécessite d'être la source ultime de cette dernière,
 - 3) et d'avoir la capacité d'agir autrement qu'on l'a effectivement fait.
 - 4) Si la thèse du déterminisme est vraie, alors nous ne sommes la source ultime d'aucune de nos actions, et
 - 5) nous n'avons pas la possibilité d'agir autrement que nous l'avons effectivement fait.
 - 6) Comme il est possible que la thèse du déterminisme soit vraie, il est donc possible que le libre arbitre soit une pure illusion.

- 2 La place que l'on occupe sur l'échiquier du débat contemporain sur le libre arbitre va donc être déterminée par le fait que l'on accepte l'argument ou bien, si on le refuse, par la prémisse que l'on rejette.
- 3 Accepter les conclusions d'un tel argument laisse place à deux options : soit prendre une place proche de celle des déterministes durs (Honderich [2012]) qui, pour ainsi dire, acceptent l'argument tel quel, soit prendre une place proche des libertariens¹. Ces derniers, s'ils ne refusent pas la possibilité de la véracité de la thèse du déterminisme dans le monde actuel, défendent toutefois la plausibilité d'une forme d'indéterminisme indépassable qui serait à même de fonder l'exercice du libre arbitre (Kane [2007]). Cependant, cela revient à bien vouloir fonder l'exercice du libre arbitre sur un processus stochastique, ce qui, comme nous le verrons, n'est peut-être pas ce que l'on souhaite.
- 4 Il y a aussi de nombreuses manières de considérer cet argument comme fallacieux. La position la plus radicale vise sans doute à refuser la première prémisse selon laquelle le libre arbitre nécessite le contrôle de son action. Il y a alors au moins deux manières de procéder. L'une est de fonder l'exercice du libre arbitre sur la possibilité d'agir de manière inconsidérée et imprévisible – de même que nous verrons en quoi fonder l'exercice du libre arbitre sur un processus stochastique ne nous apparaît pas souhaitable, nous verrons pourquoi fonder l'exercice du libre arbitre sur la capacité à agir de manière déraisonnée ne nous paraît pas souhaitable non plus. L'autre est de défendre l'inconsistance du concept de libre arbitre, et donc l'impossibilité de supputer des conditions nécessaires à son exercice – c'est la carte jouée par les *hard incompatibilists* (Pereboom [2007]). Bien que ces positions ne soient pas sans intérêt, nous nous concentrerons ici sur les positions qui ont pour conséquence la possibilité de l'existence du libre arbitre, et ce sans supposer pour autant que les actions issues de l'exercice du libre arbitre sont des actes de folie.
- 5 La première de celles-ci consiste à refuser la deuxième et troisième prémisse de l'argument, en soutenant le fait qu'avoir le contrôle de son action ne nécessite ni d'être la source ultime de celle-ci, ni d'avoir la capacité d'agir autrement qu'on l'a effectivement fait. Il s'agit sûrement de l'option la plus populaire pour argumenter en faveur d'une compatibilité entre véracité de la thèse déterministe et exercice du libre arbitre – autrement dit, l'option *compatibiliste* la plus largement répandue. On peut penser par exemple à Frankfurt (1969), qui, par le biais d'une expérience de pensée, donne un argument assez célèbre contre la nécessité de l'existence de possibilités alternatives. Si l'on devait résumer l'expérience de pensée en quelques mots seulement, ce pourrait être "John tue Jones, mais s'il ne l'avait pas fait, M. Black l'y aurait contraint ; n'a-t-on pas envie de considérer que John est moralement responsable de son acte, alors même qu'il lui était impossible d'agir autrement ?". Force est alors de supposer que ce qui est vrai de la responsabilité morale l'est aussi du libre arbitre : le pouvoir d'agir autrement n'est nullement requis. Pour nier les deuxième et troisième prémisses de l'argument, une stratégie possible est donc de soutenir qu'une adéquation entre la volonté et l'acte est suffisante pour que l'on puisse parler de contrôle de l'action. En élaborant un peu l'argument, on peut par exemple distinguer deux sens de contrôle de l'action, l'un faible – et parler à la manière de Fischer (1994) de *guidance control* – et l'autre fort – et parler alors de *regulative control* – tout en assumant que le sens faible de contrôle, qui ne nécessite pas de possibilités alternatives, suffit comme fondation à l'exercice d'un libre arbitre. Le prix à payer en adoptant une position de ce type est sans doute d'affaiblir le sens que l'on peut donner à "faire un choix" en même temps que l'on affaiblit le sens donné à "contrôle", ce du fait de l'absence d'alternative – nous verrons comment il nous semble possible de ne pas faire ce sacrifice.

- 6 Une deuxième possibilité pourrait consister à refuser les prémisses 3 et 4. En d'autres termes, on pourrait soutenir le fait qu'avoir le contrôle de son action ne requiert pas l'existence de possibilités alternatives, mais seulement d'être la source ultime de celle-ci, et qu'être la source ultime de nos actions est possible quand bien même la thèse du déterminisme est vraie. Toutefois, il semble qu'il y ait très peu de défenseurs d'une telle position – sûrement quant à la difficulté d'affirmer une compatibilité entre véracité de la thèse du déterminisme et possibilité d'être la source ultime de nos actions.
- 7 Une autre possibilité ne rencontrant pas davantage d'engouement est, en procédant de manière symétrique au raisonnement précédent, de refuser les deuxième et cinquième prémisses, et défendre l'idée selon laquelle avoir le contrôle de nos actions ne nécessite pas d'être la source ultime de nos actions, mais se fonde plutôt sur l'existence de possibilités alternatives, et que l'existence de possibilités alternatives est – dans un sens qu'il appartient de définir – compatible avec la véracité de la thèse du déterminisme. C'est cette position, peut-être d'apparence un peu scabreuse, que nous tâcherons de défendre ici. Nous nous ferons donc l'avocat d'un libre arbitre "des alternatives" compatible avec la véracité de la thèse du déterminisme, tout en se posant la contrainte de ne pas faire du libre arbitre un phénomène surnaturel.
- 8 Pour montrer que notre position est raisonnable, nous devons montrer trois choses : (1) avoir le contrôle de nos actions ne nécessite pas d'être la source ultime de celle-ci ; (2) l'existence de possibilités alternatives est – au moins dans un certain sens – compatible avec la véracité de la thèse du déterminisme ; (3) l'existence de possibilités alternatives – comprise au sens où nous l'entendons dans (2) – est suffisante pour fonder l'exercice du libre arbitre ou bien exprimer les autres conditions nécessaires. Commençons donc par montrer la première.

1. Être (ou ne pas être) la source ultime de nos actions

- 9 Admettons (en nous inspirant de McKenna [2016]) que (1) si un agent a est la source ultime de x alors il y a au moins une condition x_i nécessaire pour x qui apparaît avec a et (2) si une condition x_i apparaît avec a , alors il n'y a pas de conditions suffisantes pour cette condition x_i indépendantes de a .
- 10 Il est clair qu'être la source ultime de son action est impossible s'il est vrai que nous vivons dans un monde déterministe. Dans un tel cas, et si l'on admet pour la simplicité du propos que l'hypothèse du Big Bang est vraie, alors, par transitivité, toutes nos actions ont une condition nécessaire et suffisante : le Big Bang et les lois de la Nature (que l'on suppose existantes même si nous n'en connaissons pas la formulation). La recherche de sources ultimes paraît ainsi une quête du surnaturel dans le sens où il faut aller chercher dans la brisure de l'enchaînement logique des conditions le fondement d'un contrôle de l'action et cela apparaît quelque chose de ce point de vue assez peu souhaitable.
- 11 Il semble que l'on puisse répondre à l'intuition à laquelle fait implicitement appel l'argument qui viserait à fonder le libre arbitre sur cette notion par une condition plus faible : si un agent a a le contrôle de son action, alors le choix que l'agent a fait d'effectuer cette action en est la cause. Nul n'est besoin alors de supposer une quelconque brisure de l'enchaînement logique des conditions qui permettent tel ou tel événement.
- 12 Cette nouvelle condition, bien que plus faible, n'est pas sans soulever des difficultés. La première réside dans le fait de référer au concept de causalité, qui a fait à lui seul couler beaucoup d'encre. Comme ce n'est pas le propos d'entrer ici dans une discussion sur la causalité, nous adopterons d'emblée, et sans aucune forme de justification autre que celle qu'il s'agit désormais d'une conception assez

conventionnelle, une conception contrefactuelle du terme, en référence au cadre conceptuel proposé par Lewis (1986, 2004).

- 13 Dans un tel cadre conceptuel, on considère que l'évènement a cause l'évènement b si et seulement si a est survenu dans le monde actuel et b lui a succédé, et dans le monde contrefactuel le plus proche au monde actuel où a n'a pas eu lieu, b n'a pas eu lieu non plus². Un tel cadre nous donne donc les moyens de statuer sur le fait qu'un agent est bien la cause de son action.
- 14 Qu'un agent soit la cause de son action est tout à fait compatible avec la véracité de la thèse du déterminisme : il n'est pas nécessaire d'assumer la fausseté de la thèse du déterminisme pour pouvoir faire une analyse causale de la situation. Il est même au contraire nécessaire que le monde que nous considérons montre certaines régularités, au risque de devoir abandonner toute analyse causale fructueuse.
- 15 Une critique pourrait toutefois être la suivante. Si l'on suppose que notre monde est déterministe, et s'il est bien sûr possible de se livrer à des analyses causales, est-il pour autant possible qu'un choix soit la cause d'une action ? Est-il même possible que des états mentaux en général soient des causes des actions ? En effet, selon Kim (1998), si l'on accepte le principe de clôture causale du monde physique selon lequel un évènement physique a toujours un ensemble nécessaire et suffisant d'autres évènements physiques, alors les états mentaux ne peuvent être que des épiphénomènes. Pour parer à cette critique, nous nous contenterons de citer la réponse de List et Menzies (2009) à Kim. En s'appuyant sur la définition de la causalité en termes de contrefactuels – Kim était resté évasif quant au cadre conceptuel dans lequel il s'inscrivait pour parler de causalité – les auteurs montrent qu'il est plus pertinent de considérer des états mentaux comme causes des actions que des évènements purement physiques tels qu'un certain *pattern* d'activité neuronal, et ce du fait de la multi-réalisabilité des états mentaux. Bien qu'il y aurait beaucoup à dire ici aussi, nous tiendrons cette réponse pour satisfaisante et considérerons donc que si nous substituons la condition d'être la source ultime d'une action pour en avoir le contrôle au simple fait d'en être la cause au sens contrefactuel, nous réglons l'un des deux problèmes de compatibilité avec le déterminisme. Attaquons-nous donc maintenant au deuxième problème qui est celui de la compatibilité entre existence de possibilités alternatives et déterminisme.

2. Possibilités alternatives et déterminisme

- 16 L'argument qui vise à montrer une incompatibilité entre exercice du libre arbitre et véracité du déterminisme du fait d'une incompatibilité entre existence de possibilités alternatives et véracité de la thèse du déterminisme peut être formulé de la manière suivante (McKenna [2016]) :
- 1) Un agent a produit une action x selon son propre libre arbitre si et seulement si a a le contrôle sur x .
 - 2) a a le contrôle sur x seulement si a a la capacité de sélectionner parmi plusieurs plans d'action le fait de produire x .
 - 3) Si a a la capacité de sélectionner parmi plusieurs plans d'action le fait de produire x , alors il y a d'autres plans d'action que x réalisables par a (c'est-à-dire que a aurait pu produire d'autres actions que x).
 - 4) Si le déterminisme est vrai, alors il y a un seul futur possible étant donné le passé actuel et les lois de la nature étant ce qu'elles sont.
 - 5) Si un seul futur est possible étant donné le passé actuel et les lois de la nature étant ce qu'elles sont, alors il n'y a pas plusieurs options de plans d'action

réalisables par un agent donné (c'est-à-dire qu'aucun agent n'aurait pu agir autrement qu'il l'a effectivement fait).

6) En conséquence, si le déterminisme est vrai, il n'est pas le cas qu'un agent *a* produit *x* selon son propre libre arbitre.

17 De cet argument, nommé par ailleurs le *Garden of Forking Paths argument* (McKenna, [2009]), nous allons préciser la quatrième prémisse, ce qui aura pour conséquence de rendre fausses les cinquième et sixième propositions.

18 Cependant, avant de montrer comment il est possible de rendre compatibles déterminisme et existence de possibilités alternatives, raisonnons quelque peu par l'absurde et supposons pour un temps la fausseté de la thèse du déterminisme pour examiner en quoi cela pourrait nous aider à formuler un concept de choix plus fort. En effet, une idée *a priori* séduisante est que si le monde est indéterministe, alors, du fait de l'existence de possibilités alternatives, un agent est réellement capable d'un choix entre plusieurs plans d'action, et alors d'exercer son libre arbitre – ce qui est une idée largement défendue par les libertariens (Kane [2007]).

19 Toutefois, si c'est le fait que le monde soit indéterministe qui rend possible un "réel" choix, alors ce sont des caractéristiques telles que la présence de processus stochastiques ou l'impossibilité d'établir des prédictions qui vont être amenées à fonder l'exercice du libre arbitre. Or, si le processus de prise de décision a pour élément fondamental un lancer de dé, plutôt que les circonstances environnementales et les préférences de l'agent en train de prendre une décision, alors il est évident que dans bien des cas, l'action qui en résulte sera considérée par quelque observateur que ce soit comme inconsiderée et irréfléchie. Ce sont pourtant des caractéristiques que l'on ne souhaite pas associer à l'exercice d'un libre arbitre. Le choix même des mots "libre arbitre" en français fait penser à l'exercice de la raison plutôt qu'à des choix effectués aux dés. Il n'est donc pas souhaitable, comme le fait remarquer Carnap (1966), de fonder le libre arbitre sur un processus stochastique :

Imaginez un homme sur le point de prendre une décision. S'il se manifeste, à un moment précis, un type d'indétermination pareil à celui que manifeste un saut quantique, il faudra dire que la décision prise à ce moment est également due au hasard. L'idée d'un hasard de telle sorte n'est d'aucune aide pour donner un sens fort à l'expression de "libre arbitre". Autant dire qu'il n'y a pas de choix du tout, qu'il s'agit d'un événement fortuit, d'une décision prise au hasard qui résulterait d'un coup de dés (Carnap [1973], p. 213).

20 Cette idée est déjà présente chez Hume (1748), qui insiste sur l'idée qu'un choix "libre" est un choix fait selon les préférences de l'agent et les conditions environnementales – et certainement pas donc un choix tributaire du hasard qui n'ait aucun lien d'aucune sorte avec les préférences de l'individu, ni même qu'avec les circonstances :

Car que veut-on dire par liberté, quand on applique le mot aux actions volontaires ? Nous ne pouvons certainement pas vouloir dire que les actions ont si peu de connexion avec les motifs, les inclinations et les circonstances que les unes ne s'ensuivent pas des autres avec un certain degré d'uniformité et que les uns n'offrent pas d'inférences par lesquelles nous pouvons conclure l'existence des autres ; car ce sont des choses de fait évidentes et reconnues. Par liberté, alors, nous ne pouvons vouloir dire qu'un *pouvoir d'agir ou de ne pas agir selon les déterminations de la volonté*.

21 Si l'on suppose en conséquence que le libre arbitre porte avant tout sur l'exercice de la raison et que fonder la possibilité de son existence sur des processus stochastiques n'est sûrement pas souhaitable, il nous reste alors à montrer

comment l'idée d'un "réel" choix entre plusieurs alternatives, s'il est incompatible avec l'indéterminisme, l'est avec le déterminisme.

- 22 Avant d'entamer cette discussion, prenons le temps de nous arrêter quelques instants sur le terme "déterminisme" pour lui ôter tout reste de mysticisme. La définition sans doute la plus citée est celle de Laplace (1814), ne nous privons donc pas d'une énième relecture de ce court passage de son *Essai philosophique sur les probabilités* :

Nous devons envisager l'état présent de l'univers comme l'effet de son état antérieur, et comme la cause de celui qui va suivre. Une intelligence qui, pour un instant donné, connaîtrait toutes les forces dont la nature est animée et la situation respective des êtres qui la composent, si d'ailleurs elle était assez vaste pour soumettre ces données à l'analyse, embrasserait dans la même formule les mouvements des plus grands corps de l'univers et ceux du plus léger atome : rien ne serait incertain pour elle, et l'avenir, comme le passé, serait présent à ses yeux.

- 23 Notons pour commencer que "déterministe" est un prédicat qui s'applique aux "mondes", ou pour être plus précis, à des systèmes complexes pour signifier qu'il est possible de formuler une théorie exhaustive de ces "mondes". Aussi, il convient sûrement de comprendre la question comme avant tout épistémique : un système est déterministe s'il est possible de connaître chacun des mécanismes qui le composent et de pouvoir tirer de cette connaissance et de l'état initial dans lequel il est, la façon dont il se comportera par la suite³.

- 24 Notons également que le démon de Laplace ne contrôle pas le monde, il ne fait que le contempler : il semble en effet que par trop souvent, il y ait une confusion entre contrainte et déterminisme. Cette confusion, délétère quand il s'agit de considérer la question de la compatibilité entre libre arbitre et déterminisme, est probablement due, comme le soulève Russell (1913), à une compréhension anthropomorphique du concept de déterminisme :

L'idée [qu'il existe un lien entre la question du libre arbitre, la conscience subjective de la liberté et le déterminisme] repose sur la croyance que les causes contraignent leurs effets ou que la nature exige l'obéissance à ses lois de la même façon que les gouvernements. Ce sont là de pures superstitions anthropomorphiques, dues à l'assimilation des causes avec les volitions et les lois de la nature avec les décrets humains (Russell [2006]).

- 25 Aussi, considérons un exemple donné par Carnap (1966) dans lequel la dissociation entre contrainte et déterminisme est rendue particulièrement sensible :

J'ai un ami qui a une prédilection pour des compositions musicales de Bach qu'on interprète rarement. J'apprends qu'un ensemble de musiciens de qualité donnent une audition privée de Bach chez un autre ami et que certaines compositions figurent au programme. L'on m'invite et on me fait savoir que je peux venir accompagné. J'appelle mon premier ami, l'amateur de Bach, en étant quasiment certain d'avance qu'il voudra venir. Sur quoi se fonde ma prévision ? Sur la connaissance que j'ai des goûts de mon ami et de certaines lois psychologiques. Supposez maintenant qu'il m'accompagne comme prévu. A-t-il été contraint de venir ? Non ; il est venu de lui-même. Il n'est jamais plus libre, en fait, que devant un choix de ce genre (Carnap [1973], p. 213).

- 26 Utilisant les connaissances qu'il a sur son ami (probablement imaginaire), l'auteur peut prédire avec exactitude le fait qu'il viendra à ce concert privé. Comme il n'y est pas contraint, on a semble-t-il l'intuition que l'action que cet ami a accomplie en venant était bien sous son contrôle, non pas parce que la thèse du déterminisme était fautive, mais parce qu'il a agi sans contrainte.

- 27 Dans la même idée, on peut penser à un prisonnier enfermé pendant des années dans des conditions épouvantables de détention dans une petite pièce. Si

quelqu'un venait à ouvrir la porte, on pourrait prédire que le prisonnier, pour peu qu'il ait encore l'usage de ses jambes, en franchirait le pas. Admettons que cet évènement ait lieu. On a alors la même intuition que l'agent a tout à fait eu le contrôle de son action en sortant, et ce, non parce que la thèse du déterminisme est fausse, mais parce qu'il l'a fait sans contrainte.

- 28 En gardant en mémoire qu'avoir le contrôle de son action est bien plus une question d'absence de contrainte que de déterminisme, et en nous rappelant d'autre part que la question du déterminisme est avant tout épistémique – elle vise à savoir si en connaissant l'état du système à un temps t , on peut en prédire avec exactitude l'état à un temps $t + \delta$ – revenons donc sur la pierre angulaire de l'argument : "si la thèse du déterminisme est vraie, alors il n'y a qu'un seul futur possible".
- 29 Comme le rappelle Dennett (2003)⁴, un seul futur adviendra dans tous les cas, que le monde tel que nous le connaissons soit déterministe ou non. Si le monde est déterministe, une intelligence supérieure, ou une science à l'état "achevé" pourrait savoir de quoi ce futur sera fait. Dans le cas contraire, ce serait impossible. D'aucuns pourraient alors répliquer que c'est ici l'adjectif "possible" qui compte. Alors nous ne parlons plus du monde actuel, de "ce qui est", mais de ce qui pourrait être, ou encore en d'autres termes, de choses contrefactuelles.
- 30 Par la formule "existence de possibilités alternatives", il est facile de se livrer à – comme pourrait le dire Wittgenstein – un jeu de langage. Si l'on cherche à analyser rétrospectivement l'action d'un agent pour savoir s'il aurait pu agir autrement qu'il l'a fait, et que l'on s'intéresse aux possibilités alternatives qui ont "existé" à ce moment-là, nous parlons bien évidemment non pas ce qui est ou a été, mais de ce qui *aurait* pu être dans le monde actuel. Les possibilités alternatives caractérisent donc, au moins d'un point de vue rétrospectif, ce qui aurait pu être et, de ce fait, on pourrait se laisser aller à jouer avec les mots et parler, au lieu de l'existence de possibilités alternatives, de l'existence de ce qui aurait pu exister. Comme il n'est pas de notre intérêt ici de rendre confus le propos, nous allons arrêter ici ces jeux de mots en nous concentrant sur la question qui nous intéresse : peut-on parler de possibilités alternatives dans un monde déterminisme ?
- 31 Si l'on garde à l'esprit que ce qu'on veut analyser ici est l'action d'un individu, la question est : peut-on considérer dans un monde déterministe, c'est-à-dire un monde dont on pourrait connaître tous les mécanismes à l'œuvre, des possibilités alternatives à l'action d'un individu ? Si l'on cherche à effectuer une analyse causale de cette action en termes de contrefactuels, la réponse est presque triviale. Bien évidemment, pour déterminer si le choix de l'agent est bien la cause de son action, nous allons considérer des possibilités alternatives, c'est-à-dire considérer les mondes contrefactuels où l'agent a fait d'autres choix. D'ailleurs, soulignons encore une fois que c'est parce que le monde fait preuve de régularités que cette analyse peut porter ces fruits ; si le monde était chaotique et qu'il nous était impossible de faire une quelconque prédiction – c'est-à-dire un monde très clairement indéterministe où même une intelligence supérieure ne saurait faire de prédictions correctes – alors une telle analyse n'aurait aucun sens.
- 32 Retenons donc de ces considérations qu'au moins dans un sens faible, nous sommes fondés à parler de possibilités alternatives dans un monde déterministe. Acceptons par la même occasion la quatrième prémisse de l'argument selon laquelle il n'y a qu'un seul futur si le monde est déterministe – car il n'y aura qu'un seul futur dans tous les cas –, mais refusons la cinquième : il est possible de considérer qu'il existe plusieurs plans d'action dans un monde déterministe – si l'on considère une action passée, un seul d'entre eux a eu lieu, mais nous pouvons toutefois (pour les besoins d'une analyse par exemple) en considérer d'autres qui

auraient pu avoir lieu, et si l'on considère une action future, un seul sera actualisé parmi tous ceux qui peuvent être considérés comme possibles actuellement.

3. Possibilités alternatives et exercice du libre arbitre

- 33 Si l'on veut éviter d'ouvrir une discussion dont le but serait de se prononcer sur le statut ontologique exact de ces "possibilités alternatives", il nous appartient néanmoins de défendre que le sens qu'on leur donne est suffisant pour fonder l'exercice du libre arbitre. Pour ce faire, nous proposons de situer la discussion au niveau du mécanisme qui sous-tend la prise de décision à l'origine du choix de l'action dont on veut statuer si elle est ou non le fruit de l'exercice d'un libre arbitre.
- 34 Dans une telle démarche, la question qu'il convient de se poser est : quel type de prise de décision doit-on considérer comme paradigmatique ? Il semble en effet qu'il faille davantage porter son attention sur des prises de décision impliquant un certain degré de raisonnement ou, en d'autres termes, de considérer les mécanismes qui supportent les choix dont on sait qu'ils sont le fruit de la raison.
- 35 On pourrait nous opposer à ce stade de faire grand cas d'un point de détail. Quelle différence cela peut-il faire ? La première réponse que l'on peut apporter fait appel à l'intuition du lecteur : n'y a-t-il pas quelque chose de sensiblement différent lorsque nous appuyons sur le bouton de la machine à café, ou lorsque nous signons un contrat d'engagement sur 10 ans ? Dans lequel des deux cas semble-t-il que nous faisons appel à notre libre arbitre ? La deuxième réponse, sans doute plus sérieuse, est que les mécanismes de prise de décision impliqués dans l'un ou l'autre sont sans doute radicalement différents. On sait en effet par ailleurs que selon la difficulté de la tâche à laquelle on est confronté, les mécanismes mis en œuvre sont différents. On peut illustrer cela avec un résultat de Lee et al. (2005) qui, bien qu'obtenu pour le besoin de répondre à une autre question que celle qui nous anime ici, permettra d'appuyer notre critique. Cette étude visant à étudier les mécanismes d'apprentissage et de prise de décision fait état de macaques Rhésus qui, dans une étude où ils sont amenés à jouer à Pierre-Feuille-Ciseaux contre un ordinateur, vont soit faire preuve de biais forts à l'égard de certains objets et ce sans aucune justification stratégique possible, soit adopter un comportement tel que, pour le modéliser convenablement, il convient d'utiliser un modèle faisant intervenir des croyances sur ce que pense le concurrent⁵. Or, le passage de l'un à l'autre de ces extrêmes se fait non pas selon le goût du singe, mais selon la sophistication du programme contre lequel l'animal joue, programme qui soit effectue des choix purement aléatoires, soit utilise l'historique des choix et récompenses de l'animal. En montrant que les processus à l'œuvre peuvent être très différents selon la complexité de la tâche, ce genre de résultat montre en quoi considérer des actions répondant à une tâche trop simple, que ce soit pour une expérience de pensée ou une expérience en laboratoire, tient de l'erreur méthodologique si l'objet d'étude est le libre arbitre. En somme – et n'en déplaise à Libet (1983) – si notre objet d'étude est le libre arbitre, un lever de doigt n'est sûrement pas une action dont le processus décisionnel mis en œuvre est paradigmatique de l'exercice du libre arbitre.
- 36 Si nous devons en conséquence porter notre attention sur les choix qui exemplifient une certaine rationalité en supputant que certains doivent bien faire l'objet de l'exercice d'un libre arbitre, alors sûrement est-il de bon ton de se tourner vers la théorie de la décision, au moins pour convenir de ce que peuvent être des choix d'un tel type. Un cours d'introduction à la théorie de la décision fait rarement l'impasse sur Savage (1954) qui pose un des cadres axiomatiques permettant de définir très précisément ce qu'est un choix rationnel. Nous n'entrerons pas ici dans le formalisme de sa théorie, mais nous nous appuyerons

seulement sur l'un des fondements de la théorie qui est qu'un acte est une fonction qui associe à l'ensemble des états du monde une conséquence. Si l'agent est rationnel, selon la probabilité qu'il associe à chaque état du monde, il cherche alors à maximiser son utilité. En d'autres termes, sachant les probabilités subjectives qu'il associe à chaque *état du monde* et selon ses propres *préférences*, c'est-à-dire son propre système d'évaluation des conséquences des actions, l'agent choisit l'action qu'il pense être meilleure.

37 Le mécanisme à l'œuvre lors d'un choix rationnel peut donc être schématisé de la manière suivante : l'agent évalue quels sont les états du monde les plus probables, examine les conséquences les plus intéressantes, considère ainsi plusieurs plans d'actions possibles et porte son choix sur celui qui semble pouvoir lui donner la plus grande satisfaction. Pour peu que l'on suppose que ce mécanisme de choix est causal au sens contrefactuel, alors nous sommes fondés à assumer l'existence de plans d'action au sens où nous avons besoin de les supposer pour pouvoir expliquer l'action de l'agent : ces possibilités alternatives ne sont pas de simples supputations, mais sont impliquées dans le mécanisme permettant la production du choix, et ce même – ou plutôt surtout – si le monde est déterministe.

38 On pourrait supposer que la présence d'un tel mécanisme de choix est suffisant pour estimer qu'un agent a le contrôle de son action et ainsi exerce son libre arbitre – sous couvert bien sûr du fait qu'il agit sans contrainte, et que ce mécanisme de choix est bien causal : l'agent examine plusieurs plans d'action et sur cette base, exécute l'action qui lui semble la meilleure.

39 Il semble toutefois qu'il manque quelque chose de crucial. Pour s'en persuader, considérons l'exemple un peu saugrenu d'un robot aspirateur. Dans une machine de cette sorte sont implémentés un système perceptif qui lui permet d'avoir une distribution de probabilités sur les états du monde, un système d'évaluation des conséquences – certes rudimentaire – qui lui permet d'avoir des préférences sur les conséquences de ses actions – se retrouver bloqué face à un mur est clairement non souhaitable de son point de vue – et un système moteur – qui lui permet d'agir. Cette machine examine plusieurs plans d'action réalisables, et maximise son utilité en se déplaçant dans la direction qui semble la mieux convenir à la satisfaction de ses objectifs. Elle peut bien sûr parfois se tromper sur l'état du monde dans lequel elle est, ce qui la conduit à des erreurs, mais si notre souci n'est pas la propreté de la pièce dans laquelle se situe cette machine, ce n'est pas là le plus important. Notre souci étant plutôt d'arriver à une conception cohérente du libre arbitre, le problème principal réside davantage dans le fait qu'il est difficile de dire que cette machine a suffisamment de contrôle de son action et que de ce fait, elle bénéficie d'un libre arbitre.

40 Pour nous départir de ce problème, nous proposons de faire l'hypothèse que certains agents au moins sont capables d'effectuer des choix d'un ordre supérieur et que c'est la présence de ce second niveau de choix qui fonde le libre arbitre. Nous supposons en effet qu'il existe un second niveau de choix, qui se surajoute au choix de premier niveau portant sur l'action à effectuer et qui consiste à délibérer sur les buts à poursuivre. Ce choix de second niveau qui peut avoir pour effet de moduler les préférences de l'agent, vise à sélectionner l'information à traiter pour procéder à la prise de décision et sur les critères à utiliser pour évaluer les conséquences des actions. Cette proposition fait écho aux discussions contemporaines en théorie de la décision et en neurosciences de la décision dont l'intérêt s'est porté au cours des dix dernières années sur les processus dits métacognitifs. On peut ainsi penser du côté de la micro-économie aux travaux de Dietrich & List (2011, 2013a, 2013b) qui, en se concentrant sur la façon dont des agents peuvent établir des critères pour prendre leur décision, ont montré qu'il

était par la même occasion possible de résoudre des paradoxes classiques, tels que l'incohérence temporelle. Du côté des neurosciences, on peut penser à l'approche hiérarchique des processus de prise de décision, développée par Koechlin et ses collaborateurs (ex. Koechlin et al. [2003], Koechlin & Jubault [2006]) qui atteste de la pertinence de supposer plusieurs niveaux de choix lorsque l'on vise à expliquer le comportement de sujets humains lors de tâches dont la structure est plus sophistiquée qu'un simple enchaînement d'essais indépendants les uns des autres.

41 Pour donner une intuition claire de ce que nous appelons plusieurs niveaux de choix, prenons l'exemple d'un activiste politique de la fin des années 60 qui se trouve confronté à un choix cornélien entre deux moyens de mener sa lutte politique, sachant que l'objectif global de cette lutte est de faire accéder son propre parti politique au pouvoir. Le premier moyen consiste à utiliser les armes et fomenter une révolution, le second à construire des discours pour une ascension au pouvoir par les urnes. Pour résoudre ce dilemme, il semble que notre homme ait à délibérer sur quels sont *vraiment* les buts de son action. Par exemple, lui semble-t-il préférable de privilégier l'efficacité de la méthode – l'efficacité ici pouvant référer au temps demandé avant d'obtenir le résultat escompté – ou bien la sauvegarde de principes éthiques – ce qui l'empêcherait d'avoir recours à des actions violentes ? Il y a donc un premier niveau de choix qui porte sur l'alternative entre prendre les armes ou écrire un discours, et un choix de deuxième niveau sur la description des conséquences de l'action en termes éthiques ou bien temporels – choix de second niveau qui aura pour effet de moduler les préférences. Afin d'assurer la clarté de notre propos, l'on peut prendre un exemple plus prosaïque – mais isomorphe – qui consisterait en un choix de premier niveau entre une pomme et un morceau de moelleux au chocolat, et un choix de second niveau entre privilégier les aspects diététiques des deux aliments ou bien les sensations gustatives qu'ils sont à même de procurer.

42 Si l'on considère ce second niveau de choix comme nécessaire pour la forme de contrôle de l'action sur laquelle on souhaite fonder l'exercice du libre arbitre, cela a l'avantage d'exclure comme bénéficiant d'un libre arbitre les agents dont on pense intuitivement qu'il est impossible qu'ils le soient. Ainsi, nous excluons d'emblée les robots aspirateurs pour lesquels il est très clair qu'aucun mécanisme de prise de décision de second ordre n'est implémenté, et une large partie du règne animal.

43 Bien que situé sur un tout autre plan, un second avantage à cette proposition est que cela nous donne les moyens de redonner une consistance à l'idée classique de "suspension du jugement", en faisant de cette suspension du jugement une instance de choix de second niveau qui fait tout à fait sens. Aussi, si nous relisons Locke (1689) :

Je voudrais qu'on se demande sérieusement si la source et la mise en œuvre majeures de toute la *liberté* qu'ont les hommes, qu'ils peuvent acquérir, ou qui peut leur être utile, et dont dépend la tournure de leurs actions, ne réside pas en ce qu'ils peuvent *suspendre* leurs désirs, et les empêcher de déterminer leur *volonté* à une action jusqu'à ce qu'ils en aient soigneusement et correctement *examiné* le bien et le mal autant que l'exige l'importance de la chose.

44 Si l'on interprète cet extrait de l'*Essai sur l'entendement humain* à la lumière de notre distinction, il apparaît que la suspension des désirs dont parle l'auteur peut être interprétée comme un choix de second ordre de retarder l'exécution de l'action, qui permet d'effectuer un deuxième choix de second ordre, ce dernier portant sur l'adéquation des différents plans d'action aux principes éthiques de l'agent. L'accent est donc mis sur l'importance d'un processus de délibération, qui permet de temporiser le choix de premier niveau pour réfléchir aux buts

poursuivis, et ce notamment d'un point de vue éthique – et nous appelons les choix qui interviennent à ce niveau d'abstraction ou de généralité des choix de second niveau. Si nous ne pensons pas que les choix de second niveau sont nécessairement des choix éthiques, il est toutefois intéressant de considérer à ce propos ce que dit Kant (1785) dans les *Fondements de la métaphysique des mœurs* sur l'"autonomie de la volonté" :

Comme être raisonnable et, par suite, appartenant au monde intelligible, l'homme ne peut concevoir la causalité de sa propre volonté que sous l'idée de liberté ; car l'indépendance à l'égard des causes déterminantes du monde sensible (indépendance que la raison doit toujours s'attribuer) est la liberté. Or, à l'idée de liberté se rattache d'une manière insoluble l'idée d'*autonomie* et à cette dernière idée le principe général de la moralité, lequel est, au moins d'une manière idéale, le principe des actions de tous les êtres *raisonnables*, au même titre que les lois de la nature servent de principes à tous les phénomènes (Kant [1915], p. 105-106).

- 45 Les considérations morales servent chez Kant de fondement à l'autonomie de la volonté. Ainsi, en ayant une réflexion éthique – censée selon Kant être en conformité avec le fameux impératif catégorique⁶ –, l'agent s'affranchit en partie des contingences environnementales ("indépendance par rapport aux causes sensibles") et trouve la cause de son action en grande partie en lui-même. Kant avance ainsi l'idée que la volonté se détermine elle-même en établissant sa propre "loi" ; aussi trouve-t-on peu plus haut la formule suivante : "en effet ce devoir est à proprement parler un vouloir qui serait celui de tout être raisonnable" (*Ibid.*, p. 99). Là encore, si nous interprétons les propos de Kant à la lumière de notre distinction, un exemple de prise de décision tel que Kant le décrit est en fait un processus de décision en deux étapes : l'un vise à établir les principes éthiques qui doivent guider l'action et l'autre à évaluer la conformation des options disponibles à ces principes.
- 46 En ajoutant ce second niveau de choix, nous nous exposons au moins à deux critiques plus ou moins immédiates. La première est de considérer que nous ne faisons que repousser le problème d'un cran. La deuxième est pourquoi ne finalement supposer que deux niveaux alors qu'on pourrait en voir n autres.
- 47 Quant à la seconde, si l'on songe spécifiquement à la cognition humaine, il est clair qu'en tant qu'êtres biologiques nous sommes limités cognitivement – la limite cognitive la plus connue est sans doute la limite de nos capacités mnésiques, notamment en ce qui concerne la mémoire de travail (voir à ce propos le travail *princeps* de Miller [1956] qui établit avec une précision déconcertante la taille de notre empan mnésique, lui assignant ainsi, toutes choses étant égales par ailleurs, la capacité de contenir 7 plus ou moins 2 éléments). Il appartient donc au bon sens de supposer ce n suffisamment petit.
- 48 Quant à la première de ces deux critiques, Frankfurt (1971) se trouve confronté au même problème lorsqu'il forme sa distinction entre désirs de premier ordre et désirs de second ordre – si d'aucuns trouvaient cette distinction confuse, qu'ils pensent à l'exemple du désir de fumer comme désir de premier ordre et du désir d'arrêter de fumer comme désir de second ordre :

Une autre source de complications est qu'une personne peut avoir, surtout dans le cas où ses désirs de second niveau sont en conflit, des désirs et des volitions d'un niveau supérieur au second. Théoriquement, il n'y a pas de limite au nombre de niveaux du désir. Ce n'est que le bon sens et éventuellement une fatigue salvatrice qui peuvent empêcher un individu de refuser obstinément de s'identifier à un de ses désirs aussi longtemps qu'il n'a pas formé un désir d'un niveau immédiatement supérieur [Frankfurt [1995], p. 263].

- 49 Notons que la proposition de Frankfurt qui consiste à distinguer deux niveaux de désirs est en surface très semblable à notre proposition de distinguer deux

niveaux de choix, mais cette similitude disparaît aussitôt que l'on considère la position centrale que l'on donne au choix. En effet, si la possibilité de délibérer est ce que nous pensons fondamental à l'exercice du libre arbitre, alors il nous apparaît important de se focaliser sur la capacité à choisir entre plusieurs alternatives, et non seulement à désirer. Ceci étant dit, l'idée de l'identification du sujet à ses désirs chez Frankfurt paraît pouvoir se traduire dans notre cas par une conformité du choix de l'action à des principes supérieurs nés de la considération des buts de l'action en question, ce qui aurait pour effet de conclure le processus délibératif.

50 Nous pourrions compléter cette réponse en ajoutant qu'il nous semble inutile de vouloir caractériser les actions en deux catégories seulement dont l'une serait celles qui proviennent de l'exercice du libre arbitre et les autres non. Nous proposons au contraire qu'il y a une certaine continuité dans l'exercice du libre arbitre. Il apparaît de ce fait préférable d'ordonner les actions entre elles selon qu'elles font plus ou moins appel à l'exercice d'un libre arbitre, plutôt que de les trier en deux catégories. Ainsi, entre l'action quasi mécanique d'appuyer sur l'interrupteur de la machine à café et l'action de se porter candidat pour une offre d'emploi après une longue réflexion existentielle, nous supposons qu'il y a une myriade d'autres actions qui relèvent plus ou moins de l'exercice du libre arbitre. Si l'on fait cette supposition, alors il est possible d'apporter la réponse suivante à la première des deux critiques : si la présence d'au moins un second niveau de choix est une condition nécessaire à l'exercice du libre arbitre, l'ajout de niveaux supérieurs au second, en ajoutant une certaine profondeur à la prise de décision, ne peut avoir pour effet que d'exercer encore davantage un libre arbitre. En d'autres termes, si un deuxième niveau de choix semble nécessaire pour pouvoir parler de libre arbitre, on pourrait considérer qu'un agent effectuant une prise de décision faisant intervenir plusieurs autres niveaux de choix exerce davantage son libre arbitre qu'un agent ne faisant intervenir qu'un choix de second niveau.

51 Par conséquent, pour constituer un ordre entre les actions selon qu'elles proviennent plus ou moins de l'exercice d'un libre arbitre, nous disposons d'au moins deux critères pour évaluer les prises de décision qui en sont la cause : la profondeur de réflexion, c'est-à-dire le nombre de niveau de choix d'un ordre supérieur au second, et le nombre d'alternatives considérées lors de chacun de ces choix. Ainsi, si un deuxième niveau de choix semble nécessaire pour pouvoir parler de libre arbitre, on pourrait considérer qu'un agent effectuant une prise de décision faisant intervenir plusieurs autres niveaux de choix exerce davantage son libre arbitre qu'un agent ne faisant intervenir qu'un choix de second niveau.

52 Introduire cette notion de continuité permet par ailleurs de révéler en quoi l'exercice du libre arbitre va être dépendant d'une part de la quantité et de la qualité de l'information dont il dispose et d'autre part de ces aptitudes cognitives. En effet, plus un agent dispose d'une large quantité d'information, plus cette information est fiable, et plus il dispose de ressources computationnelles efficaces, plus cet agent va être à même d'une part de concevoir le problème de prise de décision auquel il est confronté sous plusieurs niveaux de choix organisés de façon hiérarchique, et d'autre part, de considérer plusieurs alternatives à chacun de ces niveaux – et par conséquent d'exercer son propre libre arbitre. Par conséquent, cela nous fournit un moyen de donner sens à l'intuition selon laquelle plus un sujet est "éclairé", plus il est à même d'exercer son libre arbitre.

4. Remarques finales

53 Nous nous étions fixé comme objectif de justifier les propositions suivantes : (1) avoir le contrôle de nos actions ne nécessite pas d'être la source ultime de celle-

ci ; (2) l'existence de possibilités alternatives est – au moins dans un certain sens – compatible avec la véracité de la thèse du déterminisme ; (3) soit l'existence de possibilités alternatives – comprise au sens où nous l'entendons dans (2) – est suffisante pour fonder l'exercice du libre arbitre, soit il existe une condition supplémentaire qu'il appartient de définir.

54 Par le fait qu'une recherche de sources ultimes s'apparente à chercher des ruptures de l'enchaînement logique des événements, nous avons jugé qu'il était préférable de lui substituer une condition plus faible qui est que la prise de décision soit cause au sens contrefactuel de l'action. Nous avons argumenté en faveur du deuxième point en insistant sur la prépondérance du rôle des possibilités alternatives dans le mécanisme sous-jacent au choix, rôle qui ne peut être que fondé sur la présence de régularités et non sur de l'indéterminisme. Cependant, et c'était notre réponse au troisième point, nous avons vu que la simple existence de ces possibilités alternatives ne suffisait pas à fonder l'exercice d'un libre arbitre. Nous avons donc proposé d'ajouter une autre condition qui est la présence d'au moins un choix de deuxième niveau, c'est à dire un choix portant sur la sélection de l'information pertinente et les critères d'évaluation des conséquences des actions.

55 Nous terminerons en ajoutant que cette contrainte nous permet de bénéficier d'au moins trois avantages. Le premier est qu'il permet de donner sens à l'intuition selon laquelle exercer son libre arbitre, c'est faire preuve de raison – alors même que cette intuition semble cruciale, elle est pourtant bien souvent absente des discussions contemporaines à propos du libre arbitre. Le deuxième avantage qu'apporte cette contrainte est qu'elle permet de comprendre le libre arbitre non comme quelque chose dont on disposerait pleinement ou aucunement, mais comme quelque chose auquel on peut plus ou moins faire appel – là aussi, il semble pourtant crucial de pouvoir situer sur un gradient le phénomène dont on parle. Enfin, en considérant qu'exercer son libre arbitre n'est rien d'autre que de prendre une décision en y apportant une certaine profondeur de réflexion – profondeur que l'on peut évaluer par le nombre de choix enchâssés et la diversité des alternatives considérées – et ce sans être sous la contrainte de quelqu'un ou de quelque événement, alors il n'est aucun doute que ce peut être compréhensible par le prisme des sciences cognitives et même appréhendable par elles. Les sciences cognitives n'ont-elles pas en effet parmi leurs objets d'étude les mécanismes sous-jacents à la prise de décision ?

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DOI : [10.2307/2678389](https://doi.org/10.2307/2678389)

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Notes

1. Notons que la position que les libertariens adoptent dans cette discussion n'a aucun lien avec une quelconque position politique.
2. Le lecteur peut se référer aux articles de Lewis (1986, 2004) pour une définition plus rigoureuse de ce qu'est un lien causal dans un tel cadre conceptuel.
3. Des exemples connus avec des automates cellulaires montrent la difficulté à prédire parfois la façon dont un système déterministe va se comporter à n pas de temps en connaissant uniquement l'état initial de ce système et les règles de passage d'un état à l'autre, sans procéder au calcul de chacune des étapes intermédiaires. Ce type de difficulté qui vaut à ce genre de phénomène l'étiquette "chaos déterministe" n'empêche toutefois pas que l'une des caractéristiques fondamentales de ce système est qu'il est prédictible, même si ce peut être laborieux.
4. Voir notamment les chapitres 2 et 3.
5. Les auteurs ont bien sûr procédé conformément à un certain rasoir d'Occam et testé des modèles plus simples, tel que des modèles d'apprentissage par renforcement, comparant chacun des modèles en utilisant des critères de comparaison prenant en compte outre la distance aux données, le nombre de paramètres libres, à savoir un critère d'information d'Akaike (*Akaike's Information Criteria* - AIC) et un critère d'information bayésien (*Bayesian Information Criterion* - BIC).
6. On en trouve plusieurs formulations dans les *Fondements de la Métaphysique des Mœurs*, mais la plus fameuse est sans doute : "Agis seulement d'après la maxime grâce à laquelle tu peux vouloir en même temps qu'elle devienne une loi universelle."

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NIOCHE, Aurélien. *Exercer son libre arbitre : un processus décisionnel* In : *Le libre arbitre : Perspectives contemporaines* [en ligne]. Paris : Collège de France, 2017 (généré le 09 août 2018). Disponible sur Internet : <<http://books.openedition.org/cdf/4965>>. ISBN : 9782722604797. DOI : 10.4000/books.cdf.4965.

Référence électronique du livre

GUILLON, Jean-Baptiste (dir.). *Le libre arbitre : Perspectives contemporaines*. Nouvelle édition [en ligne]. Paris : Collège de France, 2017 (généralisé le 09 août 2018). Disponible sur Internet : <<http://books.openedition.org/cdf/4937>>. ISBN : 9782722604797. DOI : 10.4000/books.cdf.4937.
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Chapitre 10

Les attitudes réactives et le déterminisme : une étude expérimentale

Aurélien Nioche, Paul Égré et Florian Cova

Entrées d'index

Mots clés :

attitudes réactives, compatibilisme, déterminisme, philosophie expérimentale, empathie

Texte intégral

1. Introduction

- 1 Le fait d'attribuer à un agent une responsabilité pour ses actions, comme de le punir pour un crime qu'il a commis, ou de le louer pour une action bonne, implique-t-il qu'il ait agi de manière non déterminée ? Selon le point de vue *incompatibiliste*, la réponse à cette question est positive : dans un monde où les actions humaines sont soumises au déterminisme, l'attribution d'éloge ou de blâme perdrait son fondement, car la notion même de responsabilité serait transférée de l'agent à l'ensemble des causes qui le déterminent. Selon le point de vue *compatibiliste*, à l'inverse, rétribution et punition jouent avant tout un rôle régulateur du comportement. Dans cette perspective, il resterait sensé de louer et de blâmer les agents même s'ils étaient soumis au déterminisme, parce que les attributions de responsabilité morale garderaient une fonction sociale incitative ou dissuasive. Au sein du grand édifice du déterminisme, leur contribution, entre autres causes du comportement des agents, serait de contrarier ou de favoriser certaines actions.
- 2 Dans un article devenu célèbre, Peter Strawson a donné un argument plus spécifique en faveur du compatibilisme, basé sur la notion d'*attitude réactive*. Strawson appelle "attitudes réactives" certains affects positifs ou négatifs suscités

par les comportements et les actions des autres qui semblent supposer un certain contrôle sur leur action de leur part (comme la haine, le ressentiment, mais aussi l'admiration ou la gratitude). Pour Strawson, les attitudes réactives constituent le fondement véritable de nos attributions de responsabilité morale, indépendamment de la question de savoir si nos actions sont déterminées ou pas. Selon lui, même si le déterminisme était avéré, nous ne cesserions pas pour autant d'avoir de telles attitudes, parce que ces attitudes prennent avant tout leur source dans les rapports inter-personnels. Pour Strawson, une attitude réactive est justifiée vis-à-vis d'un agent à condition de pouvoir exiger de lui une certaine dose de réciprocité ou de "bonne volonté". En revanche, elle cesse d'être justifiée, et pourra être suspendue ou inhibée, quand un agent manifeste par ses actions qu'il est inapte à entrer dans le système de réciprocité morale qui le lie à autrui. Face à un enfant, à un sujet fou, ou à un schizophrène, Strawson soutient que nous adoptons des attitudes *objectives* plutôt que réactives. En adoptant des attitudes objectives, nous exemptons en quelque sorte les agents concernés de la réciprocité à laquelle ils seraient soumis autrement.

3 Strawson mentionne ainsi que "voir quelqu'un comme pervers ou dérangé ou compulsif dans son comportement ou particulièrement malheureux dans les circonstances de son développement (...) tend à promouvoir des attitudes objectives". Si c'est le cas, cependant, une objection à Strawson semble être que nos attitudes réactives ne sont pas indépendantes de la question du déterminisme. Dans les cas mentionnés par Strawson, il semble que nous sommes d'*autant plus* enclins à suspendre nos attitudes réactives que nous percevons un sujet comme plus déterminé. Strawson n'envisage pas cette objection, car pour lui le déterminisme n'est pas une affaire de degré : ou bien nous sommes tous déterminés, ou bien nous ne le sommes pas, les cas d'exemption qu'il envisage étant vus plutôt comme des cas d'aliénation sociale, indépendants pour lui du problème métaphysique du déterminisme.

4 Cette réponse ne suffit pas à dissiper le doute. Comme l'ont souligné maints critiques de Strawson (voir Galen Strawson 1986, Kane 1996, Pereboom 2007, Nichols 2007), il semble plausible que nos attitudes réactives à l'égard d'un criminel s'estompent une fois que nous écoutons le récit de son enfance sordide. Kane (1996) rapporte l'expérience personnelle suivante : « Ce type d'intuitions incompatibilistes au sujet des attitudes réactives est très répandu, et je ne suis pas le dernier à les partager. Mes idées sur cette question m'ont été inspirées par le procès d'un jeune homme qui avait violé et tué une jeune fille de 16 ans non loin de chez moi. Je me mettais à la place d'un proche de la victime assistant chaque jour au procès. Mes premières pensées au sujet de ce jeune homme étaient pleines de colère et de rage. Mais, à force d'entendre jour après jour comment il en était venu à avoir le caractère mauvais et les motifs pervers qui étaient les siens – une histoire sordide mêlant négligence parentale, mauvais traitements, terribles modèles parentaux, etc. – une part de ma colère en est venue à s'atténuer et à être redirigée vers d'autres personnes, celles qui l'avaient maltraité et influencé. [...] Ainsi, certains changements dans nos attitudes réactives [...] dépendent de nos croyances dans la responsabilité ultime des agents. » (Kane, 1996, p. 84)

5 Ainsi, prendre connaissance du passé sordide d'un criminel aurait un impact sur nos attitudes réactives à son égard. Pour Kane, ce changement dans nos attitudes réactives est précisément lié à un transfert de responsabilité de l'agent vers les circonstances de sa formation. Nos attitudes réactives changent dans la mesure où nous considérons que le geste de l'agent était *déterminé* par son passé – ce qui montrerait, *pace* Strawson, que la vérité du déterminisme n'est pas une question sans rapport avec nos attitudes réactives.

- 6 Mais est-ce bien ce qui se produit ? Partant d'un autre exemple (celui du meurtre de deux jeunes hommes commis par Robert Harris, dont l'enfance fut aussi regrettable), Gary Watson donne une description plus nuancée de ce genre de situations. Pour lui : « Il serait plus juste de dire que, à la lumière de « toute » l'histoire, des réponses conflictuelles sont suscitées. La sympathie à l'égard du petit garçon qu'il était entre en conflit avec l'indignation qu'inspire l'homme qu'il est. Ces réponses entrent en conflit non pas au sens où la peur dissiperait la colère, mais au sens où la sympathie s'oppose à l'antipathie. En réalité, chacune de ces réponses est adéquate, mais prises ensemble elles ne nous permettent pas de répondre de manière cohérente à l'ensemble. » (Watson 1987 (2012), p.165).
- 7 En d'autres termes, la diminution des attitudes réactives pourrait être déclenchée par l'activation d'attitudes *empathiques* vis-à-vis de son enfance, plutôt que par une perception accrue du caractère déterminant de celle-ci. Un point important à noter est que la sympathie comme la pitié ne sont pas à proprement parler des attitudes réactives. Pour Strawson, les attitudes réactives s'exercent positivement ou négativement en lien avec une action, de sorte que la pitié n'en fait pas partie à proprement parler.
- 8 Autrement dit, l'objection incompatibiliste à l'argument de Strawson repose sur deux prémisses fondamentales. La première est qu'apprendre l'enfance d'un criminel a effectivement le pouvoir de *diminuer* nos attitudes réactives. La seconde est que cette diminution est causée par la perception du caractère *déterminé* des actions du criminel. Or, il s'agit là de deux prémisses décrivant (ou prétendant décrire) des faits au sujet de la psychologie humaine. En tant que telles, elles doivent faire l'objet d'un examen empirique, utilisant les méthodes de la psychologie.
- 9 Notre but dans cet article est d'éclairer ce débat, et en particulier de chercher à comprendre si les attitudes réactives sont ou non affectées par la perception du caractère déterminant des circonstances d'un agent. Pour cela nous présentons deux études expérimentales. La première est destinée à tester les intuitions de participants naïfs face au récit même sur lequel Gary Watson s'est appuyé dans sa discussion de Strawson, à savoir celui du meurtre commis par Robert Harris et de son enfance. Notre premier objectif est de vérifier si la lecture du récit de l'enfance malheureuse d'un meurtrier comme Robert Harris diminue effectivement les attitudes réactives négatives provoquées par le récit du meurtre qu'il a commis. Parallèlement, elle vise à mesurer la perception du caractère déterminant de l'enfance du meurtrier, pour voir si cette perception est accrue à la lecture de celle-ci. Dans une deuxième expérience, nous présentons une tentative plus fine pour départager l'hypothèse incompatibiliste de Kane, d'après laquelle les attitudes réactives seraient diminuées par la perception du caractère déterminant des circonstances d'un agent, de l'hypothèse affective de Watson, d'après laquelle le récit d'une enfance malheureuse viendrait simplement interférer avec nos attitudes réactives, indépendamment de la question du déterminisme.

2. Expérience 1 : apprendre l'enfance d'un criminel modifie-t-il réellement nos attitudes réactives ?

- 10 En premier lieu, il s'agit de déterminer si oui ou non apprendre l'enfance malheureuse de certains criminels nous conduit à changer nos *attitudes réactives* à leur égard. Comme nous l'avons vu, les philosophes qui considèrent que les attitudes réactives sont sensibles à la vérité du déterminisme font l'hypothèse qu'apprendre qu'un criminel a été maltraité durant son enfance nous conduira à avoir des attitudes réactives plus faibles à son égard : par exemple, à ressentir

moins de colère envers eux. C'est là la première et principale hypothèse que vise à mettre à l'épreuve cette étude.

- 11 En outre, nous avons vu que d'autres philosophes faisaient une seconde prédiction, parfaitement compatible avec la première, selon laquelle apprendre qu'un criminel a été maltraité pendant son enfance nous conduit à ressentir de l'empathie et de la sympathie à son égard. Appelons ces attitudes les *attitudes empathiques*. Dans cette étude, nous avons aussi cherché à déterminer l'impact du récit d'enfance sur ces attitudes empathiques.
- 12 Enfin, en troisième et dernier lieu, nous avons voulu explorer le lien entre ces deux types d'attitudes. Comme nous l'avons vu plus haut, Gary Watson semble supposer que la diminution (mais pas la disparition totale) de nos attitudes réactives est le fruit de leur conflit avec ces attitudes empathiques. Une façon de tester cette hypothèse est donc de voir si l'impact du récit de l'enfance sur les attitudes réactives est médié par leur impact sur les attitudes empathiques. Telle est la troisième hypothèse que nous testerons. En retour, il se pourrait que les choses aillent en sens inverse, et donc que l'impact du récit de l'enfance sur les attitudes empathiques soit en fait médié par leur impact sur les attitudes réactives. Par souci d'impartialité, il conviendra donc de tester cette quatrième et dernière hypothèse.

2.1. Matériel et méthodes

- 13 **Récit du crime.** Après avoir fourni quelques informations démographiques élémentaires (âge, sexe, langue maternelle), les participants recevaient pour instruction de lire attentivement un texte d'environ deux pages, directement inspiré des extraits de journaux présentés par Watson (1987). Le récit ressemblait le plus possible à celui de Robert Harris, si ce n'est que le nom du criminel avait été remplacé par le nom "Peter Watson". Nous avons fait le choix d'utiliser un long récit présenté sous forme d'article de presse plutôt qu'une courte vignette pour obtenir une situation expérimentale la plus proche possible des situations de la vie courante décrites par les philosophes travaillant sur la question.
- 14 Le récit, trop long pour être présenté ici dans son intégralité, racontait le crime horrible commis par Peter Watson et sa vie en prison. Il était raconté comment Peter Watson était accusé d'avoir tué deux jeunes hommes de sang-froid, juste pour le plaisir, et comment le meurtrier avouait ne ressentir aucun remords.¹
- 15 **Récit de l'enfance.** Après avoir lu le récit du crime, une moitié des participants (ceux dans la condition *avec* récit de l'enfance) devait lire un second texte d'environ deux pages. Le texte en question décrivait l'enfance de Peter Watson et les sévices dont il avait été victime. Là encore, le texte était largement inspiré de l'histoire vraie de Robert Harris. Il racontait comment Peter Watson était né deux mois plus tôt que prévu du fait des coups que son père donnait dans le ventre de sa mère, comment son père avait l'habitude de le battre, et le manque d'amour de la part de sa mère.
- 16 Les participants dans la condition *sans* récit de l'enfance passaient directement aux questions après avoir lu le récit du crime.
- 17 **Questions.** Après avoir lu le ou les textes (selon la condition à laquelle ils avaient été assignés), il était demandé aux participants de répondre à une liste de questions sur une échelle de 11 points (de 0 à 10, les légendes de chaque extrémité variant en fonction de la question). Les questions étaient présentées dans un ordre aléatoire.
- 18 Quatre questions visaient à mesurer les *attitudes réactives* (négatives) des participants (leur colère, leur dégoût, leur haine, et à quel point ils trouvaient Peter Watson antipathique), tandis que quatre autres visaient à mesurer leurs *attitudes empathiques* (leur compassion, pitié, sympathie et à quel point ils

trouvaient Peter Watson sympathique). Ces deux scores constituaient nos principales variables d'intérêt. En outre, pour mieux comprendre de quelle façon les participants comprenaient et interprétaient les récits qui leur étaient donnés à lire, nous leur avons aussi posé 5 questions sur la *responsabilité morale* de Peter Watson (ex : à quel point il méritait d'être blâmé, s'il devait être puni), 5 questions sur le *déterminisme* (ex : si, étant donné son passé, il était nécessaire que Peter Watson agisse de cette façon), 5 questions sur le *libre-arbitre* (si Peter Watson avait agi de lui-même ou librement décidé d'agir), 5 questions sur le *discernement moral* de Peter Watson (s'il était capable de distinguer le Bien du Mal) et 5 questions sur sa *santé mentale* (s'il était mentalement bien portant, ou devrait être interné).

19 Outre ces questions, 4 questions contrôles nous permettaient de détecter les participants qui ne prenaient pas la tâche qui leur était demandée au sérieux. Ces questions contrôles étaient des questions de compréhension sur le récit du meurtre.

20 Tous les textes et les questions étaient rédigés en anglais.

2.2. Participants

21 Après exclusion des participants ayant échoué à une question contrôle ou plus ($n=93$), il nous restait 80 participants recrutés via Amazon Mechanical Turk, un site permettant de recruter des volontaires rémunérés pour accomplir diverses tâches en ligne. Chaque participant était payé 0,50\$ pour sa participation. 52 étaient des femmes, 28 des hommes. La moyenne d'âge était 36.8 (écart-type = 13.5). 40 participants étaient assignés à la condition *avec* récit de l'enfance, 40 à la condition *sans*.

2.3. Résultats

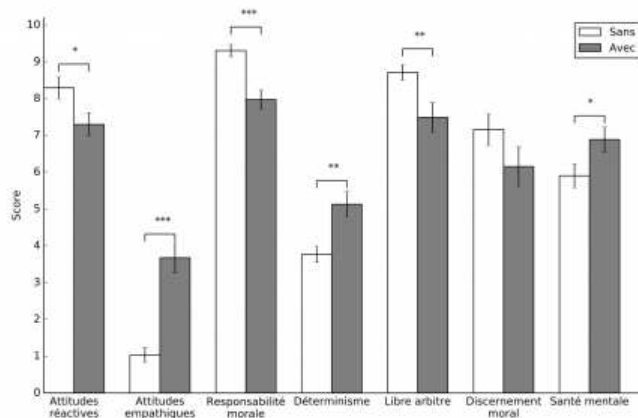


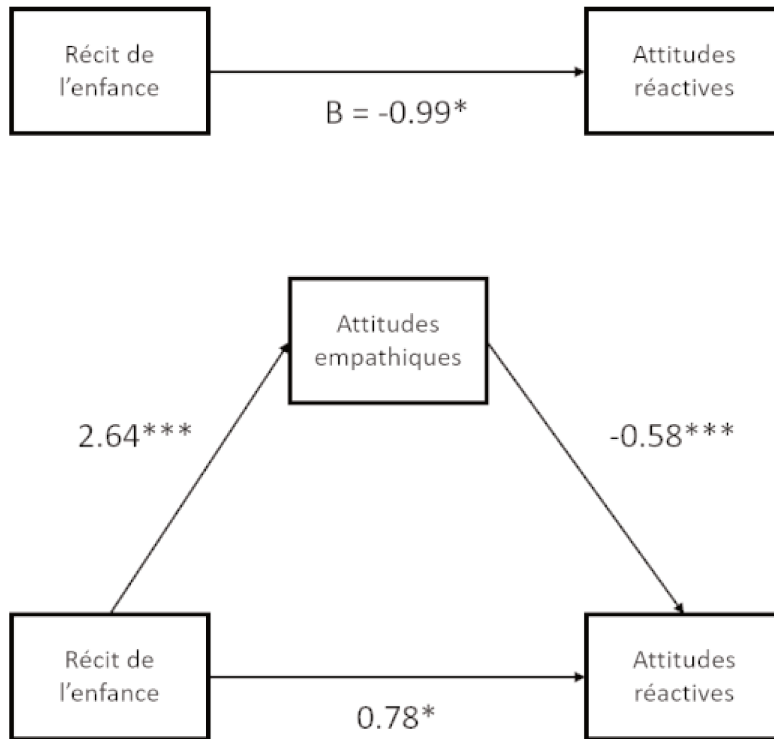
Figure 1. Résultats de la première expérience.

22 Les moyennes de chaque score en fonction de la condition (avant / après le récit de l'enfance) sont présentées en Figure 1². Dans ce qui suit, nous nous concentrons sur nos principales variables d'intérêt.

23 **Attitudes réactives.** L'ajout du récit d'enfance a un effet significatif sur les attitudes réactives des participants (Welch t-test : $t(80) = 2.27$, $p < .05$, $d = 0.51$, 95% CI = [0.12, 1.87]). Comme prévu, les attitudes réactives sont plus basses *avec* (7.30) que *sans* (8.29) le récit de l'enfance.

24 **Attitudes empathiques.** L'ajout du récit d'enfance a aussi un effet significatif sur les attitudes empathiques des participants (Welch t-test : $t(80) = 5.86$, $p < .001$, $d = 1.31$, 95% CI = [1.74, 3.55]). Comme prévu, les attitudes empathiques sont plus élevées *avec* (3.68) que *sans* (1.03) le récit de l'enfance.

- 25 **Les attitudes empathiques comme médiateur.** L'effet du récit de l'enfance sur les attitudes réactives des participants peut-il s'expliquer par son effet sur nos attitudes empathiques ? Pour le déterminer, nous avons procédé à une première analyse de médiation, avec la présence ou non du récit de l'enfance comme variable indépendante, les attitudes réactives comme variable dépendante, et les attitudes empathiques comme médiateur (pour une introduction aux analyses de médiation à la portée des philosophes, voir Rose et Nichols, 2013).
- 26 Les analyses précédentes ont déjà montré que notre variable indépendante (la présence ou non du récit de l'enfance) était un prédicteur significatif de notre variable dépendante (les attitudes réactives) et de notre médiateur (les attitudes empathiques). Une analyse de régression supplémentaire nous permet de constater que notre médiateur (les attitudes empathiques) est un prédicteur significatif des attitudes réactives ($b = -0.58$, $SE = 0.06$, $p < .001$). Pris ensemble, ces trois résultats justifient une analyse de médiation.
- 27 Une autre analyse de régression incluant les attitudes réactives comme variable dépendante et les attitudes empathiques *et* le facteur récit de l'enfance comme prédicteurs permet de constater que, même une fois pris en compte les attitudes empathiques, le facteur récit de l'enfance continue à être un prédicteur significatif des attitudes réactives ($b = 0.78$, $SE = 0.38$, $p = .045$). Si médiation il y a, elle n'est donc pas complète (voir Figure 2).
- 28 Pour finir, un test de Sobel nous permet de déterminer que les attitudes empathiques sont bel et bien un médiateur partiel de l'effet du facteur enfance sur les attitudes réactives ($z = -4.80$, $p < .001$).
- 29 Une chose qu'il convient de noter, cependant, c'est qu'introduire les attitudes empathiques dans le modèle n'annule pas l'effet (direct) du facteur enfance sur les attitudes réactives mais *en change la direction* (de $b = -0.99$ à $b = 0.78$). Autrement dit, nous avons trouvé à l'origine qu'introduire le récit de l'enfance *diminuait* les attitudes réactives. Mais, une fois pris en compte la part de cet effet expliqué par la médiation des attitudes empathiques, on observe qu'introduire le récit de l'enfance *augmente* les attitudes réactives. Autrement dit, il semblerait qu'introduire le récit de l'enfance ne diminue les attitudes réactives *que dans la mesure où il augmente les attitudes empathiques*.



$$\text{Sobel } z = -4.80, p < .001$$

Figure 2. Analyse de médiation avec les attitudes empathiques comme médiateur, le récit de l'enfance comme variable indépendante, et les attitudes réactives comme variable dépendante. Notez que l'introduction des attitudes empathiques dans le modèle change le signe de la relation entre récit de l'enfance et attitudes réactives (de -0.99 à 0.78).

- 30 **Les attitudes réactives comme médiateur.** Finalement, nous avons exploré la possibilité que l'effet du facteur récit de l'enfance sur les attitudes empathiques puisse être expliqué par son effet sur les attitudes réactives. Comme mentionné, les analyses précédentes ont déjà montré que notre variable indépendante (la présence ou non du récit de l'enfance) était un prédicteur significatif tant des attitudes empathiques que des attitudes réactives. Une analyse de régression supplémentaire nous permet de constater que notre médiateur (les attitudes réactives) est un prédicteur significatif des attitudes empathiques ($b = -0.93$, $SE = 0.10$, $p < .001$). Pris ensemble, ces trois résultats justifient une analyse de médiation.
- 31 Une autre analyse de régression incluant les attitudes empathiques comme variable dépendante et les attitudes réactives *et* le facteur récit de l'enfance comme prédicteurs permet de constater que, même une fois pris en compte les attitudes réactives, le facteur récit de l'enfance continue à être un prédicteur significatif des attitudes réactives ($b = 1.94$, $SE = 0.34$, $p < .001$). Si médiation il y a, elle n'est donc pas complète. De plus, le sens de la relation entre le facteur et la variable dépendante n'est pas affecté par la prise en compte des attitudes réactives.
- 32 Pour finir, un test de Sobel nous permet de déterminer que les attitudes réactives sont bel et bien un médiateur partiel de l'effet du facteur enfance sur les attitudes empathiques ($z = 2.18$, $p < .05$).

2.4. Discussion

- 33 Comme prévu par les philosophes incompatibilistes (comme Kane), nous avons observé qu'introduire le récit de l'enfance malheureuse d'un criminel diminue effectivement nos attitudes réactives à son égard. Le phénomène observé existe donc bel et bien et requiert une explication.
- 34 Néanmoins, conformément aux prédictions de Gary Watson, nous avons aussi observé qu'introduire le récit de l'enfance augmentait nos attitudes empathiques à l'égard du criminel. Plus important encore, il semble que l'effet du récit de l'enfance sur les attitudes réactives soit expliqué par cette augmentation de nos attitudes empathiques. En effet, une fois pris en compte les attitudes empathiques, introduire le récit de l'enfance ne *diminue* plus mais *augmente* nos attitudes réactives envers le criminel.
- 35 Ces résultats vont dans le sens de l'hypothèse de Gary Watson : si introduire le récit de l'enfance diminue nos attitudes réactives, c'est avant tout parce que ce récit nous conduit à voir le criminel comme une victime et à ressentir à son égard de la pitié et de la compassion, des attitudes qui ont du mal à coexister avec des attitudes comme la colère et l'indignation.
- 36 Néanmoins, il est trop tôt pour conclure en faveur d'une hypothèse ou de l'autre. Pour ce faire, nous devons d'abord déterminer *pourquoi* et en vertu de *quelles propriétés* le récit de l'enfance nous conduit à réviser nos attitudes, qu'elles soient réactives ou empathiques.

3. Expérience 2 : déterminisme ou malheur ? Qu'est-ce qui explique l'impact des récits d'enfances sur les attitudes réactives ?

- 37 Les résultats de l'expérience 1 suggèrent que les observations formulées par certains philosophes incompatibilistes sont correctes : prendre connaissance des souffrances qu'a endurées un criminel pendant son enfance peut bel et bien modifier nos attitudes réactives à son égard. La question est à présent : pourquoi ?
- 38 Selon ces mêmes philosophes incompatibilistes (comme Kane), le facteur explicatif est le *déterminisme*. Prendre connaissance de son passé nous rendrait moins sévères à l'égard de Peter Watson parce que nous aurions l'impression que ce même passé *explique* (au moins en partie) les actions de Peter Watson. Cette hypothèse est compatible avec les résultats que nous avons obtenus dans notre première étude : le score de *déterminisme* augmente significativement une fois que les participants ont pris connaissance de l'enfance de Peter Watson.
- 39 Néanmoins, comme nous l'avons vu, il existe une autre hypothèse, avancée par Gary Watson. Selon cette hypothèse, prendre connaissance de l'enfance de Peter Watson diminue nos attitudes réactives à son égard dans la mesure où cela nous conduit à voir Peter Watson non plus comme un criminel, mais comme une *victime*, pour laquelle nous pouvons ressentir de l'*empathie*. Or, comme mentionné précédemment, cette empathie entre en conflit avec les attitudes réactives comme la colère et la haine. Là encore, cette hypothèse est compatible avec les résultats que nous avons obtenus dans notre première étude : le score d'*attitudes empathiques* augmentait significativement après que les participants eurent pris connaissance de l'enfance de Peter Watson.
- 40 Ces deux hypothèses font néanmoins des prédictions différentes. Selon la première hypothèse (appelons-la *l'hypothèse incompatibiliste*), ce qui explique la baisse des attitudes réactives, c'est le sentiment que l'enfance de Peter Watson *explique* et *rend inévitable* le crime qu'il a commis. Selon la seconde hypothèse (appelons-la *l'hypothèse affective*), ce qui explique la baisse des attitudes réactives, c'est le caractère *triste* et *pitoyable* de l'enfance de Peter Watson. Or, il est impossible de départager ces deux hypothèses sur la seule base de notre

première étude, étant donné que notre manipulation (sans récit de l'enfance / avec récit de l'enfance) semble faire varier simultanément ces deux facteurs (le récit de l'enfance conduit en même temps les participants à avoir pitié de Peter Watson et à trouver une explication pour son acte).

41 Départager ces deux hypothèses requiert donc de faire varier la *valence* de l'enfance (positive / négative) et son côté *déterminant* (déterminant / non-déterminant) indépendamment. C'est ce que nous avons tenté de faire dans cette seconde étude.

3.1. Matériel et méthodes

42 Pour faire varier ces facteurs indépendamment, il nous a fallu nous écarter du récit présenté par Gary Watson et utilisé dans notre première étude pour créer nos propres récits. Nous avons ainsi créé 8 scénarios différents (d'environ une page chacun) en faisant varier trois facteurs : la nature plus ou moins *violente* du crime, le caractère *déterminant* de l'enfance, et la *valence* de l'enfance.

43 **Crime.** Le récit utilisé dans notre première étude, et inspiré de l'histoire vraie de Peter Harris, met en scène un crime violent et sanglant. Pour certains, cela pourrait poser un problème, étant donné que certaines recherches suggèrent que les réactions affectives suscitées par la description de tels crimes pourraient biaiser notre évaluation de la responsabilité morale des agents (Nichols et Knobe, 2007 ; mais voir en réponse Feltz et Cova, 2014). Pour explorer l'impact potentiel de cette variable (le caractère violent et direct du crime), nous avons fait varier la nature même du crime. Dans un cas (*crime violent*), le crime décrit était semblable à celui décrit dans notre première étude (le meurtre gratuit d'un jeune homme), dans l'autre (*crime non violent*) le crime était une arnaque financière qui ruinait un jeune homme, le poussant ainsi au suicide.

44 **Déterminisme.** Après le récit du crime, les participants recevaient comme dans notre première étude le récit de l'enfance du criminel. Cette enfance pouvait être soit *déterminante*, soit *non-déterminante*, et ce facteur était manipulé en changeant les valeurs du père du criminel, et le type d'éducation qu'il recevait en conséquence. Ainsi, dans le cas *non-déterminant*, le père était un passionné de musique, qui parlait à ses enfants de musique à tous les repas, les amenait régulièrement au concert, insistait sur l'importance de jouer de la musique, et avait Miles Davis comme idole. Dans le cas *déterminant* pour le *crime violent*, le père était obsédé avec l'idée d'être un 'vrai mec' et un 'gros dur', parlait à ses enfants de la distinction entre les 'forts' et les 'faibles' à tous les repas, les amenait régulièrement à des combats de catch ou à des entraînements de tir, et avait 'The Rock' pour idole. Finalement, dans le cas *déterminant* pour le *crime non violent*, le père était obsédé par l'argent, parlait à ses enfants de l'importance de faire partie des 'gagnants' à chaque repas, les faisait régulièrement regarder des programmes économiques et jouer au *Monopoly*, et avait pour idole Warren Buffett.

45 **Valence.** Finalement, nous avons essayé de faire varier la pitié et la compassion suscitées par le récit d'enfance en manipulant la valence globale. Quand l'enfance était *positive*, le récit d'enfance incluait (i) la description des heureuses vacances que Peter Watson avait l'habitude de passer avec ses grands-parents, et (ii) le temps que son père consacrait à jouer avec Peter Watson. Quand l'enfance était *négative*, le récit d'enfance incluait à la place (i) le récit de la mort de la mère de Peter Watson d'un cancer ovarien alors qu'il avait 10 ans, et (ii) l'alcoolisme de son père, qui l'empêchait de s'occuper de ses enfants pendant de longs moments. Ces modifications étaient faites de façon à laisser aux 8 scénarios une structure de surface identique.

46 Après avoir fourni quelques informations démographiques élémentaires (âge, sexe, langue maternelle), chaque participant recevait l'un des 8 scénarios. Après avoir lu le scénario, les participants répondaient à 37 questions. Ces 37 questions incluaient les 33 déjà utilisées dans la première expérience, plus 4 nouvelles, destinées à mesurer *l'évaluation de l'enfance* comme heureuse ou malheureuse par les participants (s'ils trouvaient que Peter Watson avait eu une enfance malheureuse, ou si celui-ci était souvent heureux quand il était petit). Comme dans la première expérience, ces 37 questions étaient accompagnées de 4 questions contrôles destinées à exclure les participants qui ne jouaient pas le jeu.

3.2. Participants

47 Après exclusion de 287 participants ayant échoué à une question contrôle ou plus, ou bien ayant déjà participé à une autre de nos études, il nous est resté 320 participants recrutés via Amazon Mechanical Turk (40 participants par condition). Chaque participant était payé 0.50\$ pour sa participation. 189 étaient des femmes, 131 des hommes. La moyenne d'âge était 36.6 (écart-type = 12.1).

3.3. Résultats

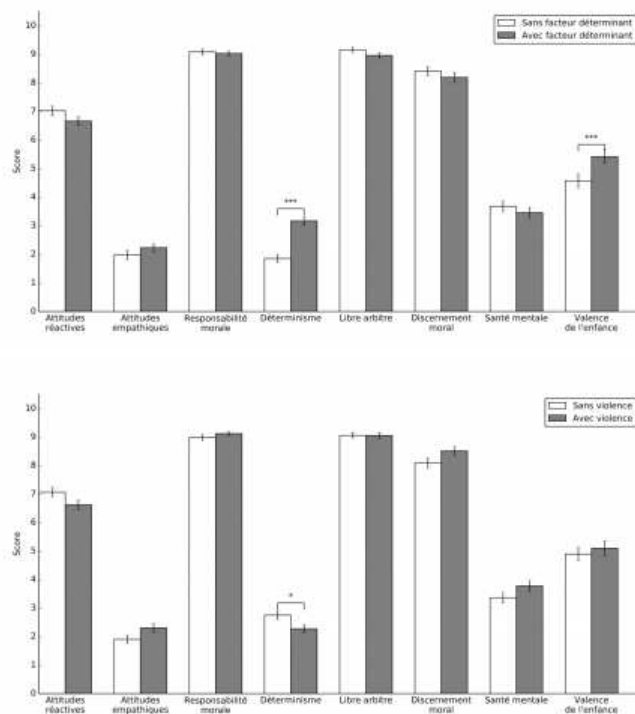


Figure 3. Résultats de la deuxième expérience.

48 L'effet des différents facteurs sur les différents scores est résumé en Figure 3³.

49 **Succès de la manipulation.** Avant d'analyser l'effet de nos trois facteurs sur nos variables d'intérêt, nous avons voulu nous assurer que notre manipulation était un succès. En effet, notre but premier était de modifier en parallèle le côté déterminant de l'enfance et la valence de l'enfance. Pour cela, nous avons analysé l'effet des facteurs *valence* et *déterminant* sur deux variables censées mesurer leur effet : *l'évaluation de l'enfance* et le *déterminisme*.

50 Dans un premier temps, nous avons conduit une ANOVA à deux facteurs (*valence*, *déterminant*) sur les scores d'*évaluation de l'enfance*. Les résultats indiquent un effet significatif du facteur *valence* ($F(1, 316) = 480.37, p < .001, \eta_p^2 = .60$), mais aussi un effet significatif du facteur *déterminant* ($F(1, 316) = 14.35, p < .001, \eta_p^2 = .04$). Dans un second temps, nous avons conduit une ANOVA à deux facteurs (*valence*, *déterminant*) sur les scores de *déterminisme*.

Les résultats indiquent un effet significatif du facteur *valence* ($F(1, 316) = 19.81$, $p < .001$, $\eta_p^2 = .06$), mais aussi un effet significatif du facteur *déterminant* ($F(1, 316) = 41.74$, $p < .001$, $\eta_p^2 = .12$).

51 Autrement dit, nous avons échoué à manipuler de façon parfaitement parallèle la valence de l'enfance et son côté déterminant. Comparée à une enfance à valence *négative*, une enfance à valence *positive* obtient des scores d'*évaluation de l'enfance* plus élevés (comme on pouvait s'y attendre), mais aussi des scores de *déterminisme* moins élevés (comme si les participants considéraient qu'une enfance négative a plus de chances de pousser au crime). Heureusement, dans ce cas précis, la différence de taille entre les deux effets est conséquente ($\eta_p^2 = .60$ pour l'évaluation de l'enfance, contre $\eta_p^2 = .06$ pour le déterminisme), ce qui suggère que le facteur *valence* manipule principalement l'évaluation de l'enfance.

52 De même, comparée à une enfance *non-déterminante*, une enfance *déterminante* obtient des scores de *déterminisme* plus élevés (comme on pouvait s'y attendre), mais aussi des scores d'*évaluation de l'enfance* moins élevés (ce qui suggère que les participants considéraient les enfances déterminantes comme moins heureuses). Dans ce cas précis, l'écart de taille entre les deux effets est plus resserré ($\eta_p^2 = .04$ pour l'évaluation de l'enfance, contre $\eta_p^2 = .12$ pour le déterminisme), ce qui devient problématique.

53 En résumé, nous avons échoué à manipuler de façon complètement parallèle et indépendante la valence de l'enfance et son côté déterminant. Nous reviendrons plus bas sur les conséquences de ce problème.

54 **Effet sur les attitudes réactives.** Pour évaluer l'effet de nos trois facteurs sur les attitudes réactives, nous avons conduit une ANOVA à trois facteurs (*nature du crime, déterminant, valence*) sur les scores d'attitudes réactives. Les résultats révèlent un effet marginalement significatif du facteur *nature du crime* ($F(1, 316) = 3.37$, $p = .07$, $\eta_p^2 = .01$), mais pas d'effet du facteur *déterminant* ($F(1, 316) = 2.28$, $p = .13$, $\eta_p^2 = .01$) ni du facteur *valence* ($F(1, 316) = 1.65$, $p = .55$, $\eta_p^2 = .00$).

55 Autrement dit, aucun de nos facteurs n'avait d'effet significatif sur les attitudes réactives.

56 **Effet sur les attitudes empathiques.** Pour évaluer l'effet de nos trois facteurs sur les attitudes réactives, nous avons conduit une ANOVA à trois facteurs (*nature du crime, déterminant, valence*) sur les scores d'attitudes empathiques. Les résultats révèlent un effet marginalement significatif du facteur *nature du crime* ($F(1, 316) = 3.58$, $p = .06$, $\eta_p^2 = .01$), pas d'effet du facteur *déterminant* ($F(1, 316) = 1.41$, $p = .24$, $\eta_p^2 = .00$), et un effet particulièrement significatif du facteur *valence* ($F(1, 316) = 82.52$, $p < .001$, $\eta_p^2 = .07$).

57 Autrement dit, la valence de l'enfance avait un impact sur nos attitudes empathiques, mais pas le côté déterminant de celle-ci.

3.4. Discussion

58 Dans cette seconde étude, notre but était de faire varier en parallèle et indépendamment la valence de l'enfance et le caractère déterminant de l'enfance d'un criminel pour déterminer lequel de ces deux facteurs expliquerait l'effet de l'introduction d'un récit d'enfance sur les attitudes réactives des participants. Cependant, cette tentative s'est heurtée à deux difficultés majeures.

59 La première est que nous n'avons pas réussi à faire varier ces deux facteurs de manière complètement indépendante. En effet, les participants ont considéré qu'une enfance déterminante était plus malheureuse et qu'une enfance malheureuse était aussi plus déterminante. Il risque donc difficile de séparer les deux facteurs.

- 60 La seconde est que nous n'avons tout simplement pas observé d'effet de nos facteurs sur les attitudes réactives, bien que nous ayons observé l'effet attendu de la valence de l'enfance sur l'évaluation de l'enfance. De ce fait, en l'absence d'un tel effet, il est difficile de déterminer ce qui explique l'impact d'un récit d'enfance sur les attitudes réactives.
- 61 Que nous n'ayons pas observé d'effet peut s'expliquer de deux façons : la première est que notre manipulation du facteur pertinent (quel qu'il soit) n'ait pas été assez puissante (au sens statistique) dans notre seconde étude. Notons toutefois que notre manipulation du déterminisme (par le facteur déterminant) semble dans le même ordre de grandeur que celle observée dans la première étude (une différence de 1.36 dans la première étude, contre une différence de 1.32 dans la deuxième). En revanche, notre manipulation des attitudes empathiques par le facteur évaluation de l'enfance était beaucoup plus petite que la différence observée entre les deux conditions de la première étude (une différence de 2.65 dans la première étude, contre une différence de 1.02 dans la deuxième). Cela suggère que, si l'absence d'effet est dû à un effet trop faible de notre manipulation, c'est du côté de la manipulation des attitudes empathiques qu'il faut chercher.
- 62 L'autre solution est bien entendu que ni le côté déterminant de l'enfance, ni sa valence et les attitudes empathiques qu'elle inspire n'expliquent l'effet observé dans la première expérience. Dans ce cas, il s'agirait de trouver un autre facteur expliquant l'effet observé dans cette première étude.

4. Conclusion

- 63 À l'issue de ces deux études, quelles conclusions pouvons-nous tirer sur l'objection incompatibiliste à l'argument de Strawson et, plus généralement, sur le lien entre attitudes réactives et perception du déterminisme ?
- 64 Dans l'ensemble, nos résultats semblent aller contre l'hypothèse déterministe de Kane et en faveur de l'hypothèse affective de Watson. En effet, l'hypothèse affective de Watson postulait l'enchaînement causal suivant : (i) la nature malheureuse et difficile de l'enfance suscite des attitudes empathiques, et (ii) l'augmentation des attitudes empathiques suscite à son tour une diminution des attitudes réactives. Les résultats de la première étape confirment la seconde partie de ce modèle : si prendre connaissance de l'enfance d'un criminel nous conduit à revoir nos attitudes réactives à la baisse, c'est précisément dans la mesure où cela nous conduit à ressentir plus de sympathie et de compassion pour le criminel. Quant à notre seconde étude, elle semble confirmer la première partie de ce modèle : une enfance plus malheureuse (mais pas plus déterminante) nous conduit à ressentir plus de pitié pour le criminel. Ainsi, pris ensemble, les résultats de nos deux études semblent confirmer le modèle de Watson, et l'idée selon laquelle prendre connaissance de l'enfance d'un criminel ne diminue pas nos attitudes réactives parce qu'elle nous conduit à le voir plus *déterminé*, mais tout simplement parce qu'elle nous conduit à avoir *pitié* de lui.
- 65 Cependant, montrer que l'hypothèse de Watson fonctionne ne suffit pas à rejeter définitivement l'idée de Kane et de ses collègues. En effet, les deux hypothèses ne sont pas strictement exclusives : il se pourrait que les deux soient simultanément vraies, et que l'enfance d'un criminel affecte nos attitudes réactives *à la fois* parce qu'elle nous conduit à avoir pitié de lui *et* parce qu'elle nous conduit à le voir plus déterminé. Autrement dit, prouver la vérité de l'hypothèse affective de Watson ne suffit pas à prouver la fausseté de l'hypothèse incompatibiliste.
- 66 Contre l'hypothèse incompatibiliste, nous pourrions souligner que notre seconde étude n'a trouvé aucun effet de la manipulation du côté déterminant de l'enfance. Cela fournit quelque raison de penser que les incompatibilistes ont tort de penser

que la perception du déterminisme peut avoir un effet sur les attitudes réactives. Cependant, cet argument se heurte à deux limites. La première est que ne pas observer d'effet ne suffit pas à conclure immédiatement à l'absence d'effet : il se peut que nous ayons joué de malchance, ou que notre manipulation ne soit pas assez puissante pour faire apparaître l'effet. La seconde est que notre deuxième étude a échoué à observer un effet de l'enfance sur les attitudes réactives *tout court*, qu'il s'agisse d'un effet de sa valence, ou de son côté déterminant. Étant donné que nous avons échoué à observer cet effet (attesté par les résultats de notre première étude), il serait imprudent de conclure que cet effet n'est pas dû au côté déterminant de l'enfance.

67 Ainsi, avant de conclure que l'effet du récit de l'enfance sur les attitudes réactives n'est pas dû (au moins en partie) à son côté déterminant, il nous faut parvenir à mettre sur pied une étude dans laquelle (i) nous parvenons à observer l'effet du récit d'enfance sur les attitudes réactives, et (ii) nous observons que le côté déterminant de l'enfance n'explique pas cet effet. Cela nous conduit alors à nous demander pourquoi nous n'avons pas observé d'effet du récit de l'enfance sur les attitudes réactives dans notre deuxième étude. Comme indiqué dans la discussion de cette étude, le problème ne semble pas venir de notre manipulation du déterminisme : les écarts observés dans les scores de déterminisme sont aussi grands dans notre deuxième que dans notre première étude. Bien plutôt, le problème semble venir des écarts dans les attitudes empathiques : bien que notre manipulation de la valence de l'enfance ait été hautement efficace, cela semble avoir eu un impact très limité sur les attitudes empathiques. Si l'effet du récit de l'enfance sur les attitudes réactives est bel et bien médié par son effet sur les attitudes empathiques (comme suggéré par notre première étude), cela pourrait expliquer l'absence d'effet dans notre deuxième étude.

68 Mais comment mieux manipuler les attitudes empathiques ? Ce que nous apprennent les résultats de notre deuxième étude, c'est que le simple fait d'avoir une enfance *triste* ne suffit pas à inspirer beaucoup d'attitudes empathiques. Certes, nos participants ressentaient plus de pitié pour les criminels qui avaient une enfance triste que pour les criminels qui avaient une enfance heureuse, mais cette pitié restait largement en deçà de celle inspirée par le récit de l'enfance présenté dans notre première étude. Une possibilité (suggérée par la citation de Watson présentée en introduction) est que ce n'est pas tant le côté *triste* de l'enfance d'un criminel qui suscite la pitié, que son statut de *victime* (de coups et blessures, de mauvais traitements, etc.). Ainsi, il suffirait de modifier nos récits d'enfance triste pour faire du criminel une *victime*, et nous serions en mesure de manipuler les attitudes empathiques plus efficacement.

69 Il y a cependant un problème : si nos récits d'enfance triste n'incluaient pas de mauvais traitements dans notre deuxième étude, ce n'était pas un hasard, mais une décision délibérée de notre part. En effet, inclure des mauvais traitements dans les récits d'enfance triste aurait sûrement pour effet d'augmenter plus efficacement les attitudes empathiques, mais cela aurait probablement pour effet supplémentaire d'augmenter leur côté déterminant. En effet, les mauvais traitements semblent perçus par nombre de participants comme un facteur susceptibles de causer des comportements violents dans l'avenir. Or, le but de notre deuxième étude était précisément de manipuler les attitudes empathiques et le côté déterminant de l'enfance de manière *indépendante*.

70 En somme, distinguer l'effet du côté déterminant de l'enfance de celui des attitudes empathiques sur les attitudes réactives n'est pas une mince affaire. De nombreuses difficultés méthodologiques doivent encore être surmontées. Néanmoins, en attendant d'y parvenir, il nous semble que nos résultats, même s'ils ne permettent aucune conclusion définitive, devraient encourager les

incompatibilistes au scepticisme. En effet, étant donné que (i) nous n'avons trouvé aucun résultat en faveur de leur hypothèse, et (ii) que nos résultats confirment l'hypothèse de Watson, qui fournit une explication alternative à l'effet du récit de l'enfance sur les attitudes réactives, il semble que les raisons de soutenir l'hypothèse incompatibiliste sont, en l'état, assez faibles.

Remerciements. *Nous remercions les participants du groupe de travail sur le libre-arbitre du Collège de France, en particulier Jean-Baptiste Guillon et Cyrille Michon pour leurs commentaires détaillés et leur invitation. Nous remercions l'Institut Jean-Nicod (financement SOPHA 2015), le Département d'Etudes Cognitives de l'Ecole Normale Supérieure, l'Agence Nationale de la Recherche (ANR-10-LABX-0087 IEC, ANR-10-IDEX-0001-02 PSL*, et crédits restants ANR-07-JCJC-0070) et le NCCR en Sciences Affectives, financé par le Fonds National Suisse (n° 51NF40-104897).*

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Notes

1. Le texte complet des scénarios et des questions est trop long pour être présenté en intégralité dans ce chapitre. Néanmoins, l'intégralité de nos stimuli est disponible en ligne sur le *Open Science Framework*, à l'adresse suivante : <https://osf.io/8882t/>. De plus, une traduction française des extraits de journaux utilisés par Watson et dont nous nous sommes inspirés dans la première étude peut être trouvée chez Watson (2012).

2. Pour s'assurer de la validité de nos scores, nous avons réalisé le calcul d'un α de Cronbach qui compare la variance des items qui ont été agrégés pour former un score avec la variance du score lui-même. La formule utilisée est :

$$\alpha = [n / (n - 1)] \cdot [1 - (\sum_{i \in [1, n]} \sigma^2(x_i)) / \sigma^2(X)]$$

avec X , le score de n items qui est évalué, $\sigma^2(x_i)$, la variance de l'item $x_i \in X$, et $\sigma^2(X)$ la variance du score X . Il est habituellement accepté qu'un α égal ou supérieur à 0.70 indique que le score est valide.

Les α obtenus sont les suivants : attitudes réactives : 0.70, attitudes empathiques 0.84, responsabilité morale : 0.75, déterminisme : 0.59, libre arbitre : 0.87, discernement moral : 0.94, santé mentale : 0.72.

3. Les α de Cronbach obtenus lors de l'expérience 2 sont les suivants : attitudes réactives : 0.73, attitudes empathiques 0.81, responsabilité morale : 0.72, déterminisme : 0.75, libre arbitre : 0.82, discernement moral : 0.91, santé mentale : 0.86, valence : 0.94.

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Référence électronique du chapitre

NIOCHE, Aurélien ; ÉGRÉ, Paul ; et COVA, Florian. *Les attitudes réactives et le déterminisme : une étude expérimentale* In : *Le libre arbitre : Perspectives contemporaines* [en ligne]. Paris : Collège de France, 2017 (généré le 09 août 2018). Disponible sur Internet : <<http://books.openedition.org/cdf/4981>>. ISBN : 9782722604797. DOI : 10.4000/books.cdf.4981.

Référence électronique du livre

GUILLON, Jean-Baptiste (dir.). *Le libre arbitre : Perspectives contemporaines*. Nouvelle édition [en ligne]. Paris : Collège de France, 2017 (généré le 09 août 2018). Disponible sur Internet : <<http://books.openedition.org/cdf/4937>>. ISBN : 9782722604797. DOI : 10.4000/books.cdf.4937.

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