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Neuroscience Area
Cognitive Neuroscience Curriculum

Investigating the cognitive, computational and neural underpinnings of food choice in healthy individuals

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To mum and dad.

My perennial source of mirth, courage and love.

Contents

Standing upon the shore of all we know

We linger for a moment doubtfully,

Then with a song upon our lips, sail we

Across the harbor bar —no chart to show,

No light to warn of rocks which lie below,

But let us yet forth courageously.

T.S. Eliot

Outline

Choices are quintessential to our lives. Whether we realize it or not, we make thousands of them everyday, shaping our lives deeply. Among the choices we make, choosing what to eat represents one of the most important, as our lives depend on it. Food choice is a complex phenomenon, that is characterized by physiological, affective and cognitive determinants. These dimensions, however, have been studied either separately or jointly but without offering a comprehensive mechanistic approach that could pinpoint which cognitive aspects drive food choice. Most of the literature on the topic stems either from decision-making in cognitive neuroscience (Glimcher and Rustichini, 2004; Krajbich et al., 2012, 2015; Levy and Glimcher, 2011; Mormann et al., 2010; Pearson et al., 2014), considering food only as a special case of a general theory on value-based choice, or comes from experimental psychology and consumer research (Rozin, 1996; Shepherd and Raats, 2006), where it lacks a mechanistic approach to the neurocognitive determinants of food choice.

In my thesis work, I aimed to bridge this gap by showing how we can study food choice combing the two lines of research. This could be done, I believe, by employing a set of different behavioral, neural and computational approaches.

In my first Study I focused on the interaction of a cognitive on a physiological aspect (calories) in food choice, that is, how people understand and judge calories when it comes to choosing different food items. Calories are a fundamental element in driving choice about food, as they give us the energy we need to survive, grow and reproduce. But still little is known about the cognitive processes underlying their evaluation. In fact, it has been shown that the energy density (calorie content) of a food can bias the estimation of a portion size (Frobisher and Maxwell, 2003; Japur and Diez-Garcia, 2010), and vice versa (Wansink and Kim, 2005). However, we still do not know whether calories are considered as an absolute (total in a portion. Caloric Content, CC) or a relative (related to the type of food. Caloric Density, CD) quantity, which has implication as to the importance of controlling the size of portions in meals to contrast overeating (Rozin et al., 2011). I hypothesized that the type of food would be more important than the total amount of calories in a portion in determining how calories are understood, giving rise to known problems in estimating portion size.

In my second Study, I wanted to investigate the neurocognitive mechanism of the interplay between a physiological (calories) and a cognitive-affective aspect (perception of risk). Safety concerns about food represent a powerful factor shaping food choice (Rosati and Saba, 2004), but little is known about how people choose food when it is at risk of being contaminated, with no knowledge about how different aspects of risk and reward (calories) interact with each other. I hypothesized that risk would drive the choice with participants choosing conservatively the least risky options, with a possible exception represented by food with higher CD. What the results show is that overall participants were risk averse, while high calorie foods managed to partially counteract this tendency, i.e., some of them were chosen. Deactivation of the right anterior insula, a risk prediction error area (Preuschoff et al., 2008), as well as activation of the pre-SMA, implicated in working memory (d'Esposito et al., 1998; Pessoa et al., 2002; Petit et al., 1998), supported the idea that perceived differences in calories among the items made the task easier when it comes to risk evaluation.

In my third Study, I wanted to investigate how a physiological element like hunger would impact on two components, one physiological (calorie) and one affective (preference) using a computational approach. While there is a wealth of research on the effects of hunger on food choice (Frank et al., 2010; Hoefling and Strack, 2010; Piech et al., 2010; Read and Van Leeuwen, 1998; Reisenman, 2014; Siep et al., 2009), we still lack a mechanistic approach that could help us examining the effects of hunger on calorie and preference at the same time. I hypothesized that hunger would make calories more important in determining choice, while satiety would, on the other hand, prioritize the role of preference in determining the pattern of choices. Using a drift-diffusion modeling approach I managed to show how hunger has opposite effects on calorie and preference, with participants choosing more high calorie and less preferred items when hungry and low calorie and high preferred items when satiated.

Overall, with this work I aimed to show that the complexity of food choice can be stripped down to three basic dimensions (physiology, affect and cognition) and their interactions and that it is possible to study it, without too much sacrifice in terms of ecological validity, by using a template made of different analytic and quantitative approaches, from behavioral, to computational and neuroimaging.

1. *Introduction*

1.1 Choice

Everyday we choose. It might be trivial to say that you choose what to buy at the grocery store on your way home so that you can cook a decent, satisfying dinner after a day of work. But also the choice of actually going to the store is a decision that rules out other possibilities, such as exercising, ordering out food or enjoying an *aperitivo* with your friends in that place you really like. Some choices are important, like whether you want to buy a house. Others are more trivial, like which brand of toothpaste you buy at the supermarket. However, what makes even trivial choices important is the way they accumulate in patterns that self-repeat without explicit deliberation, i.e., habits, which can deeply shape our well-being, health and quality of life (Duhigg, 2012). This is especially true in the case of food choice, as we depend on it to sustain ourselves, although we may scarcely realize it, as most of us in the western world live amidst general abundance (Shepherd, 2001).

1.2 Theoretical perspectives on Choice

Given the role choices play in our everyday life it comes hardly as a surprise that humanity has tried to make sense of them for centuries. This can be nicely described, I believe, as a set of perspectives that allows to tackle this issue from different angles. In my opinion, based on a review of the literature, three of them deserve especially our attention. A philosophical, or speculative, the most dated and long-standing, alongside more recent axiomatic and experimental approaches.

1.2.1 Speculative approach

How the pattern of choices performed by individuals shapes the structure of society and its interaction - as well as its wealth - has been at the core of the interest of the first political economists from the enlightenment onward. It is, for instance, in the works of John Locke (Locke, 1700), Bernard Mandeville (Mandeville, 1795) and Adam Smith (Smith, 1827) that we can find the notion that individuals pursuing their self-interest can, overall, produce an outcome that is better off for everyone. However, this approach, that we can call - hopefully without making offense to too many philosophers - speculative, can be largely considered, as the name suggests, an intellectual endeavor. Using sharp arguments, thought experiments and examples, what these thinkers hoped to show was that we can make sense of how people make choices using rational deliberation. While this is indeed a good first step, addressing the issue without investigating how people *actually* choose offers a poor ground for any theory of choice. In fact, without any room for testing our hypotheses in reality, we fail to provide a theory that can be disputed with evidence (Popper, 1938). The second issue is the lack of a model of how choices are taken and interact with each other, which allows not only to explain but also to predict, both basic tenets of a scientific explanation (Ladyman, 2002). This approach has endured through the centuries and, in fact, although choice can be considered the cornerstone of modern and contemporary social sciences, it is not until recently that the process of making a choice has been studied scientifically.

1.2.2 Axiomatic approach

Once we take a closer look at the process of choice, we immediately realize one central point, namely the notion of preference, which can be considered in its basic logical sense as the hierarchy of values that different items represent for a chooser (Rescher, 1968)[1]. Without it, most choices would be random, as items would not have, by definition, different values for the chooser. As preference - a way to hierarchically order value (Von Wright, 1963) - can be considered largely subjective, the problem of studying it in a quantifiable manner becomes tricky. One successful approach in dealing with this issue can be traced back to the work of a group of economists starting in the 1930s, most notably Kenneth Arrow (Arrow, 1959), Gérard Debreu (Debreu, 1954) and Paul Samuelson

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[1] There are numerous other ways to conceive preference, including in terms of attitudes towards a set of objects or actions (Lichtenstein and Slovic, 2006). However, what I want to stress here is its *ordinal* aspect, that is, the fact that it allows to construct a (subjective) hierarchy of values or actions.

(Samuelson, 1938). Their idea was to rely on a few sets of primitive assumptions about preferences that could be formalized mathematically and used to model choice behavior on a large scale (we can call this approach axiomatic). Their models were strongly normative, with little regard to the empirical work of experimental psychologists, but without doubt have paved the way to study choice more systematically and precisely. Their work impinged on the notion of *revealed preferences* (Samuelson, 1938). If the value of the items for a subject cannot be measured by reading someone's mind, it can be clearly inferred from her pattern of choices, i.e., her behavior. If she prefers an apple to an orange, and grapes to an apple and her behavior is consistent, we can write her preferences as such:

$$grapes > apple > orange$$

This relationship, which embodies the well known logical property of transitivity, was formalized into a fundamental axiom, known as General Axiom of Revealed Preference (*GARP*; Houthakker, 1950). In the same years, developments such as von Neumann and Morgestern work on game theory and expected utility theory (Von Neumann and Morgenstern, 1945) expanded the scope of GARP including further assumptions and lead to a formal and quantitative framework which has been fundamental in neoclassical economics for the years to come. Quantifying utility, in particular, helped solving the problem of giving an actual value to the options for a decision-maker [2]. The core

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[2] A thorough review of value theory in economics and philosophy goes beyond the central scope of the present thesis. For a clear survey of the field, I recommend the Stanford Ency-

assumptions of this model of human behavior, the so-called *homo economicus* were laid in those years.

This axiomatic approach has been extremely popular for its quantitative rigor and simplicity. In fact a great improvement over the speculative approach is represented by the quantitative dimension, which allowed to make predictions and provide a formal way to conceive rationality. The epistemological bases of this approach are discussed by Milton Friedman in his work on positive economics (Friedman, 1953) and his idea suggests that it does not matter how individuals behave in reality, as long as their aggregate behavior can be usefully accounted for by the higher-level (macroeconomic) theories. This conception maintained (a sort of philosophical instrumentalism; Guala, 2006) that individuals behave *as if* they are maximizing their utility functions, obeying the central axioms of the *homo economicus* conception.

Although we can argue that the axiomatic approach has been an improvement over the previous speculative approach, there are still a number of limitations in the face of determining how people do choose in real life. First, it admittedly lacks a mechanism[3] that would explain how choices are made, both at the neurological level (how choices are implemented by the brain) and the cognitive level (which are the representations at stake?). Second, although predictions were possible, they were largely ignored, not only at the individual level - which was not the focus of economists anyways - but also the aggregate

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clopedia of Philosophy (SEP) page on the topic: Schroeder (2016) as well as the excellent book on economic thought by Blaug (1997). For our purposes we will just consider utility as a way to measure the value of an item for a decision-maker.

[3] The notion of mechanism (Machamer et al., 2000) as an explanatory device has been extensively explored in philosophy of science. For a good introduction to the debate I recommend Marraffa and Paternoster (2013).

level, where it was just assumed that people would behave in a rational way (Friedman, 1962). After all, the axioms were considered to be reasonable assumptions about behavior that did not needed to be scrutinized or be put to test (Samuelson, 1966).

1.2.3 Empirical approach

1.2.3.1 Behavioral Economics

As empirical evidence on real choices started to accumulate, it became more and more clear that the set of assumptions that were held at the core of the axiomatic approach used so far had to be, at best, revised. Pioneering work in the '50s by Maurice Allais on risky choices (Allais, 1953) and Herbert Simon on the behavior of business managers (Simon, 1955), among others, highlighted the limits of human rationality and brought to the foreground a wealth of systematic biases in reasoning. A systematic approach to the study of human decision-making can be found in the work of Daniel Kahneman and Amos Tversky (Kahneman and Tversky, 1979). In their work they integrated ideas from experimental and cognitive psychology, such as the concept of mental representations (e.g., Tversky and Kahneman, 1985). They emphasized the role of heuristics, that is rule-of-thumb shortcuts to decisions that do not need complete information. In particular, their work on the effect of how information is presented on decisions - i.e., framing - is worthy of mention. To give an example, consider you are faced with the following dilemma (asian disease problem; Tversky and Kahneman, 1985):

> *Imagine that your country is preparing for the outbreak of an unusual disease, which is expected to kill 600 people. Two alternative programs to combat the disease have been proposed. Assume that the exact scientific estimate of the consequences of the programs are as follows:*
>
> *If Program A is adopted, 200 people will be saved.*
>
> *If Program B is adopted, there is a 1/3 probability that 600 people will be saved, and 2/3 probability that no people will be saved.*

Most people, but not all, will pick program A here. After all the prospect of saving 200 people is appealing, right? However, imagine you were presented the choice a little differently, like this (as it was the case of half of the participants of the original experiment):

> *If Program A is adopted 400 people will die.*
>
> *If Program B is adopted there is 1/3 probability that nobody will die, and 2/3 probability that 600 people will die.*

The two scenarios presented have the same, identical, consequences, only *framed* differently, in the first case in terms of gains and in the second case in terms of losses. The effect of this simple difference in presenting the information is striking: in the original experiment Tversky and Kahneman found 72% of their participants favoured option A if the dilemma was framed in terms of gains, while this percentage dropped to roughly 22% if the dilemma was presented in terms of losses (with, conversely, 78% participants accepting option B in the loss framing, Tversky and Kahneman (1985)).

This example shows that the set of assumptions of the axiomatic approach had to be revised, to incorporate heuristics and cognitive distortions (i.e., biases) that affect decision-making. Moreover, they demonstrated that the way in which information is framed matters when making choices [4].

Notwithstanding the success of this new, empirical, approach to study decision-making (prospect theory and the heuristics and biases research program Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), whose most important contribution to the study of choices is the use of actual laboratory experiments, we can still find some limitations. First, while mathematically solid, this approach falls short of providing a mechanistic account of how choice is implemented. Indeed, it provides only a formal way - i.e., utility maximization or some form of cost optimization - to predict how people would choose given a set of preferences, reasoning and information constraints, with limited attention to computational models (Gigerenzer et al., 1999; Vranas, 2000), unlike other empirical approaches to decision-making (e.g., Gigerenzer and Brighton, 2009), but similar to the aforementioned axiomatic approach (Von Neumann and Morgenstern, 1945). Second, preferences are exogenously determined [5], that is they are assumed to be given (i.e., external) to the choice process, and not varying in time, for instance, even following a mere change in physiological state, such as being tired or hungry (e.g., Bossaerts and Mu-

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[4] This aspect will be relevant in my work presented here (see chapters 2 and 3).

[5] This is a common assumption in Rational Choice Theory (Green and Fox, 2007), a fairly widespread theory about human behavior in microeconomics.

rawski, 2015; Dietrich and List, 2013). In order to address these issues, some economists felt the need to turn to the emerging tools of neuroscience and investigate whether biological constraints of choice models would help face these issues, shedding light onto the mechanisms at play in decision-making.

1.2.3.2 Neuroeconomics and Decision Neuroscience

This convergence between neuroscience and economics took years to fully develop and give birth to a new discipline: Neuroeconomics (Glimcher and Rustichini, 2004). At its core is the idea of decisions as algorithm-based processes in which information is elaborated. If neurons do process information, then it is clear that hypotheses on mental processes happening during decision-making can be tested relying on neural data, i.e., a mechanistic approach. Neuroimaging tools such as functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) have managed to capture the interest of behavioral economists for their potential in uncovering the underlying processes of decision-making, how they unfold in the brain and how their outcomes can be manipulated, in real time. A larger and clearer picture on how we do make decisions, learn and adapt in a changing environment started to emerge (Rangel et al. (2008), Figure 1.1), together with models of learning originally developed in animals, such as reinforcement learning (see Sutton and Barto, 1998).

Some successes of this approach include the discovery and subsequent manipulation of utility values that are hypothesized in the axiomatic ap-

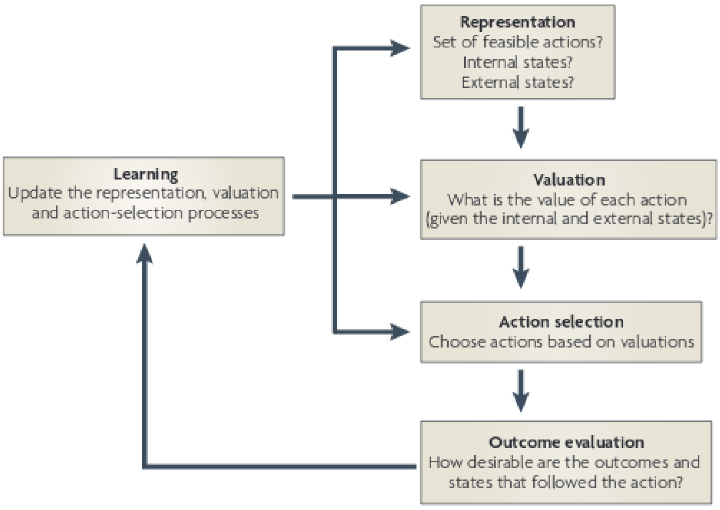

Figure 1.1: Decision-making flow-chart. Adapted from Rangel et al., 2008.
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proach (Padoa-Schioppa and Assad, 2006; Platt and Glimcher, 1999; Rolls and Grabenhorst, 2008, e.g.,), and helping discriminate between different valuation models (Levy and Glimcher, 2011; Padoa-Schioppa, 2011, e.g.,). Furthermore significant amendments to classical utility theories have been proposed. These include the discovery that, under particular circumstances, choices under risk are better explained by models where the subjective weighting of risk does not follow expected utility theory predictions (mean-variance models) Christopoulos et al., 2009 rather than utility models. Other examples include the work by Barbaro et al. (2017), who showed that valence can better drive object representation accuracy in the brain when compared to utility.

In recent years the idea of biology merely imposing constraints on economics models of decision-making, so typical of neuroeconomics, is being challenged (Bossaerts and Murawski, 2015). This emerging approach, named decision neuroscience puts biology center-stage and proposes that biology offers more than constraints in the implementation of formal models (Shiv et al., 2005) [6]. It can be argued that not only biology, but also experimental psychology and cognitive neuroscience can offer more than simple constraints to economics models of decision-making. This can emerge more clearly if we focus on a special case of decision-making whose complexity and centrality in our lives encompasses a wide range of factors, from physiology to society, such as food choice. In fact, I hope to show that, in spite of its complexity, we can try to break it down along its relevant dimensions with a range of analytic tools, such as behavioral testing, computational modeling and neuroimaging.

1.3 Food Choice

A complex and important model of choice is food choice (Rangel, 2013). Its multifarious nature escapes simple models of choice in that personal, socio-economical and cultural factors all shape the decisions (Mela, 2001; Rozin, 2006; Shepherd and Raats, 2006, Figure 1.2). Food is arguably the fuel that shaped our evolution (Wrangham, 2009), fostering cooperation among males in hunting (Bowles and Gintis, 2004, 2011; Skyrms, 2004) and that feeds our complex brains (Pontzer et al., 2016), as well as shaping complex social practices (Delormier et al., 2009). Food is so important for our survival that convincing evidence of its own peculiar representation in the brain exists (Rumiati and Foroni, 2016). The ecological importance of food choice is paramount as diet-related diseases, such as obesity, represent an increasing concern for global

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[6] A few examples in this direction are reviewed in Boureau and Dayan (2011) and Pearson et al. (2014).

health (NCD-RisC, 2017), as well as the global effects of food consumption on climate change (McMichael et al., 2007) and environmental sustainability (Pullman et al., 2009).

1.3.1 Relevant dimensions

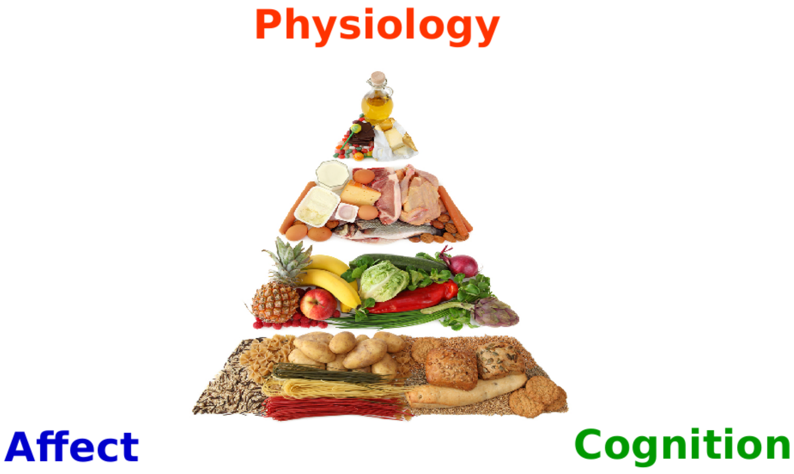

Figure 1.2: Food choice complexity.

There is a vast literature on the topic, and most studies rely on single features that influence food choice. A few ways to organize food choice along a set of key dimensions have been proposed in the literature (e.g., Rozin, 2006; Shepherd and Sparks, 1994). At the center of these models we typically find factors that are related to the food, such as *physiological* aspects (Figure 1.2, top). We can consider these fundamental as they provide the motivational impulse to eat (hunger and energy content). In turn, these physiological elements influence, on a higher level, what the authors call person-related and socio-economic factors. Among these we find the main dimensions of affect (Figure 1.2, bottom left) and cognition (Figure 1.2, bottom right): the first one influencing preferences and attitudes towards food, the second determining how food is categorized.

1.3.1.1 Physiology

Calories and edibility. Physiological aspects are very important when it comes to food as normally they provide the impulse to eat in the first place (Berthoud, 2011). Among these, calories take on a primary role, as they provide the energy that ultimately allows our organism to function. Given the importance of calories, it is no wonder that food with a high quantity of them can have a special representation in the brain. More specifically, foods with high calories have been shown to be processed differently from low-calorie foods, activating reward-related areas such as the ventral striatum and hypothalamus (Killgore et al., 2003). In line with this idea, high calorie foods would also tend to be more craved while on a calorie-restraining diet (Gilhooly et al., 2007). Given the importance of calories as a fuel for the brain and the body, this is not surprising, as extracting information about calories in a reliable way (Toepel et al., 2009) in an uncertain environment represents a clear evolutionary advantage helping secure food for survival and reproduction (Lieberman, 2014).

Furthermore, there is also evidence that not only high-calorie, but transformed food, that is food which thanks to a chemo-physical transformation is able to provide more calories and different nutrients, is categorized differently by our brain (Pergola et al., 2017). Evolutionary speaking, cooked - and hence transformed - food can be thought of as an important element in supporting the growth of our energy-thirsty brains (Pontzer et al., 2016; Wrangham, 2009).

Foods with more easily available calories would also tend to be more salient. Given the importance of vision for mammals and humans in particular, it comes to no particular surprise the importance of color in conveying information about nutrients and edibility (Clydesdale, 1993). The ability to discriminate red-green colors, a characteristic of trichromatic vision, has been shown to be advantageous in foraging ripe fruits and younger leaves, which are normally redder in hue, in many primates species (Dominy and Lucas, 2001; Jacobs, 2009; Lucas et al., 2003; Osorio and Vorobyev, 1996; Regan et al., 2001). This adaptation appears to be preserved in humans. As Foroni et al. (2016) showed, red-colored food items significantly elicit higher arousal than green-colored ones. Green food items were also perceived to be less calorie richer than redder ones, even when calorie content was controlled for.

All in all, calories are important determinants of food choice in that they provide the energy we need to function and reproduce. As a consequence of this, calorie-rich foods are perceived as more salient and have spurred adaptations in perception, such as color signaling, and in motivation, such as increased drive to consume transformed foods. Considering the importance of this life-serving function, it is expected that we have evolved cognitive and bran mechanisms to detect and process calorie information.

Hunger. However, once calories are successfully detected, they would not be ingested by themselves without capitalizing on the motivation to do so. Indeed, hunger and thirst can play this role by prioritizing the choices depending on the state of need of the organism (e.g., proteins; See Griffioen-Roose et al., 2014). As the popular saying goes, hunger can be considered the best spice (Reisenman, 2014). Piech et al. (2010) exemplified this by using a visual target detection task with random food cues and distractors. They found that hunger significantly altered the attentional focus of participants during target detection. As this effect was not present when participants were satiated, it suggests a selective effect of hunger on attentional focus when it comes to food. Along the same line of evidence, di Pellegrino et al. (2010) investigated whether sensory-specific satiety, i.e., decrease in reward value of an item once it has been consumed up to satiety, would affect subjects' attentional focus. As they managed to show using a visual probe task, both pleasantness ratings and focus decreased with sensory-specific satiety for that food, but not for other foods.

As shown by Siep et al. (2009), hunger can modulate brain activity in reward-related areas such as medial OFC, insula, caudatus and putamen while interacting with the calorie content of foods. Indeed, while hungry their participants showed higher activity for high calorie foods in these areas, while when satiated, this happened for low calorie foods. This differential effect of hunger is interesting and is in line with other studies, such as Read and Van Leeuwen (1998), who found that hungry participants would choose more high calorie foods when hungry. Although on satiated participants only, Charbonnier et al. (2015) were also able to find that participants would choose more quickly low calorie than high calorie foods.

Hunger plays indeed such an important role in prioritizing calorie intake that there is evidence suggesting it can override preference for certain foods when others, less preferred, are more readily available (Hoefling and Strack, 2010). Furthermore, hunger does seem to interact with affective elements such as stress. Born et al. (2010) had their fasting subjects perform either a stressful or non-stressful task in two separate sessions in the lab. After the task they had to select their breakfast in the MRI scanner and they were scanned twice, one before and one after food intake. Interestingly, their participants tended, overall, to favor foods that were richer in proteins and carbohydrates when stressed, compared to when they were not stressed. Moreover they found that stress seemed to decrease the reward value of food items, as found in the lower activation of amygdala, hippocampus and cingulate cortex.

Altogether, hunger reflects the need of an organism to obtain calories and promotes behaviors accordingly. It not only affects attention by increasing the focus toward food that can provide needed nutrients but also seems to modulate preferences towards particular foods based on the contextual situation as well as interact with the state of stress and urgency of the organism.

1.3.1.2 Affect

The aforementioned studies seem to suggest that affective aspects constitute an important dimension of food choice. There is, in fact, a wealth of evidence on the effects of mood and emotion on food choice, such as the case of stress or comfort eating (Griffin et al., 1993; Oliver and Wardle, 1999; Oliver et al., 2000; Pool et al., 2015; Zellner et al., 2006). Interestingly, also the converse phenomenon, that is the effects of food choice *on* mood and emotion, has attracted the attention of research in recent years (Gibson, 2006, 2012; Spencer et al., 2017). Most of these effects, however, are related to the actual consumption of food more than the process of choice itself (e.g., Macht et al., 2003).

Preference. Among the different aspects included in the affective dimension, we will address food preference, with a focus on how genetic and environmental aspects shaped its development (Köster, 2009), including early exposure (Garcia et al., 2001; Mennella et al., 2001), and sometimes remarkable stability throughout the years (e.g., Nicklaus et al., 2004). As already mentioned, axiomatic models of decision-making, as well as empirical ones have long considered preferences as exogenous, that is, stable over time. However, evidence is mounting in that not only food preference develops and changes through time, but it can exhibit transitory changes with simple re-exposure or contextual - i.e., framing - effects (Lévy and Köster, 1999; Mojet and Köster, 2002). Other studies have shown that food preferences can also be manipulated in children (Birch and Marlin, 1982; Wardle et al., 2003) through exposure. Mere exposure effects, in fact, (Zajonc, 1968) seems to impact preference formation and choice, with pre-exposed alternatives being either chosen more often (Bird et al., 2012) or considered for a shorter time (Glaholt and Reingold, 2011). This effect has been found and replicated for food items, as well. For instance Fedoroff et al. (1997) found that exposing both unrestrained and restrained eaters to food cues (pizza) had an impact on subsequent food intake on unrestrained eater, while it produced an urge to eat pizza in restrained eaters. Similarly, exposing college students to different drinks significantly impacted their preference ratings on them, with the best ones for drinks that were tasted more (Pliner, 1982). The mere exposure effect, however, does not seem to act equally on items with different valence, with neutral and pleasant items' ratings being influenced while unpleasant not, as shown with chemo-sensory preferences (Delplanque et al., 2015). Food preference can interact with other dimensions such as, for instance, physiological factors. As shown by Spence et al. (2015), for instance, in environments that are rich in high calorie foods, preference seems to be the most important factor in shaping choice. Moreover, while being satiated does not impact preference ratings, hunger seems to lead the choice towards more high calorie food items with a significant alteration of preferences, suggesting a secondary role of affective factors (Finlayson et al., 2007).

Preferences are not born in a vacuum, however. Social norms and habits are a powerful determinants of preferences, especially when social emotions such as shame or disgust can influence practices of food consumption, acting as sort of implicit enforcers of norms without the need of a central authority (Croker et al., 2009; Rozin, 1996). An example of this can be considered the customary eating practices of religions such as islam (*halal*) or judaism (*kosher*) that, although applied in some countries, do not need a central authority to do that (Mukhtar and Mohsin Butt, 2012; Wu et al., 2014).

Taken together, affective processes include a variety of phenomena that influence food choice on different levels. These include motivational aspects (i.e., mood and stress), changes in the importance of different food items for the decision-makers (i.e., preferences) and changes in the context in which foods are consumed as well as the habits governing the eating process (i.e., social norms).

1.3.1.3 Cognition

While physiological and affective factors provide the motivational backbone to the making of food choices, cognitive aspects provide a form of top-down control on them. Wealth, social factors, personal and safety concerns about food can all contribute here. Besides the obvious impact of price on food choice, with lower prices increasing consumption of foods (extensively studied in marketing and economics. See French, 2003; Giskes et al., 2007; Horgen and Brownell, 2002; Steptoe et al., 1995), other relevant cognitive aspects of food choice include dieting and food restraining practices, not only in the general population but also considering special cases such as athletes and restrained eaters. While their reasons might differ and involve different degrees of emotional aspects (e.g., physical shape vs. body image concerns), both populations include a strict control of food choice and intake, with heightened awareness of food composition and health issues (Heaney et al., 2011; Tepper et al., 1997).

How information about food is provided matters as well. In line with the results of framing on choice in general (Tversky and Kahneman, 1985), how the food is labeled seemed to have a significant impact on choice and intake. For instance, Just and Wansink (2014) found that how the portion of food was labeled (either “small” or “large”) influenced consumption and willingness to pay with higher bids and less consumption for foods that were labeled as “large”, regardless of the actual size of the portion. Whether the food is labeled as “healthy” or “tasty” also seems to impact choice, as people would tend to choose more food when the first item they consume is labeled as “healthy” as compared to “tasty” (Finkelstein and Fishbach, 2010). As they authors contend, this might be due to the perception of “healthy” as mandatory and not rewarding. Healthy cues seemed to improve healthy food choices as compared to tasty (and unhealthy) foods as shown by Hare et al. (2011). In their study, they showed that having participants focus on the healthiness of a food as compared to its tastiness influenced their choice pattern towards healthier foods.

How attention is focused, in fact, seems to be crucial in driving choice. Fixation time can be considered as a useful proxy for visual attention, which undergoes both top-down and bottom-up control mechanisms (Orquin and Loose, 2013). Stimulus-driven attention seems to play an important role in driving the choice process, with several studies focus on different aspects that affect the likelihood of choosing an item over others. Indeed saliency (Bialkova and van Trijp, 2011; Orquin et al., 2012; Mormann et al., 2012), surface size (Chandon et al., 2009; Orquin et al., 2012), position (Chandon et al., 2009) and visual clutter (Visschers et al., 2010) all produce noticeable effects in the choice. In line with this idea, Krajbich et al. (2010) investigated whether gaze fixation patterns would influence food choice in healthy participants. Using eye-tracking measures and computational modeling they managed to show a direct relationship between fixation time and choice, with a pattern of accumulation of information towards the option with the more extended fixation time. Moreover, they observed that the last option being fixated was predictive of the actual choice. This model represents an improvement with respect to previous hypotheses about the gaze fixation (e.g., the gaze cascade hypothesis Shimojo et al., 2003). However, while the link between the accumulation of information and choice seems to be backed up by other studies in the literature, the authors' predictions have not been confirmed for what concerns gaze allocation time being a causal factor in determining choice (Nittono and Wada, 2009; Orquin and Loose, 2013). As Orquin and Loose (2013) conclude, in commenting the down-stream effect of attention on decision-making:

> "The observations suggest two underlying processes behind down-stream effects: a soft evidence accumulation process, which leads to higher choice likelihood for longer exposed alternatives, consistent with the mere exposure effect, and a bottom up attention capture process reducing the likelihood of nonattendance, i.e., that the alternative is ignored in the decision process" (Orquin and Loose, 2013, p.201).

Risk. Despite not posing a large threat such as in the past, another undoubtedly important factor determining food choice are safety concerns, such as food poisoning or contamination. Building upon a large literature on dual-processing systems (Epstein, 1994; Evans and Frankish, 2009; Sloman, 1996), some authors have proposed that our brains deal with risky prospects relying on two different mechanisms (Slovic et al., 2005). One, cognitive, brings logic and reason to assess and manage risk (risk as analysis, Slovic et al., 2004). The other, affective, refers to the fast, automatic response to a situation that brings potential danger (risk as feelings, Loewenstein et al., 2001). According to these authors, when it comes to risk, most people would rely on an "affect heuristics", which entails that "people base their judgments of an activity or a technology not only on what they think about it but also on how they feel about it" (Slovic et al., 2004, p.315). According to this theory, "if a general affective view guides perceptions of risk and benefit, providing information about benefit should change perception of risk and *vice versa*"(Slovic et al., 2004, p.315). This is in line with studies finding that, despite risks and benefits being positively correlated in the reality, they tend be negatively so in the way people perceive them (e.g., Alhakami and Slovic, 1994; Fischhoff et al., 1978). We could thus argue that how risk is *framed* influence reactions and evaluation of danger. Indeed, this conjunction of cognitive (framing) and affective (e.g., gut reactions) aspects make risk an important element in decision-making. Food is no exception in this aspect, as understanding the interplay of cognitive and affective elements of risk in the case of food poisoning and contamination can shed light on how these factors are taken into account when making decisions about public safety.

Up to date, most studies in this direction have focused on public perception and awareness of contamination issues (Liu et al., 1998; Rosati and Saba, 2004), but not many on food choice *per se*. Still largely unexplored, however, is the mechanism underlying the decision processes when it comes to food that can be contaminated, as well as how the brain integrates the information concerning hazard and nutritional properties of the food.

All in all, cognitive aspects of food choice mostly focus on how the information about food is elaborated and how this interacts with the other dimensions (i.e., physiology and affect). While framing seems to impact on how foods are perceived in terms of their benefits for the organism (i.e., healthiness), the attentional focus influences how information on foods is acquired and thereby the choice. Moreover, how risky the food is perceived to be for the organism shapes choice by altering preferences and choice patterns.

1.3.2 Food choice in the lab

I have given in the previous pages a brief overview of the current state of the literature on food choice. While these studies show we have an idea of how different factors interact in shaping food choice, we still lack an overarching picture. One that can benefit from actual models of how the process of food choice unfolds and which psychological and neuroscientific mechanisms it employs, still largely unknown to date despite a not so small amount of knowledge on the phenomenon itself (Shepherd and Raats, 2006). Conceptual models are still the mainstay in the food choice literature (e.g., Furst et al., 1996; Macht, 2008), and the lack of a computational approach, compared to other fields of decision-making (e.g., Rangel et al., 2008) is striking. On top of this, what is also lacking is a way to quantify uncertainty. Given the profound context-based nature of food choice, research on the topic could greatly benefit from approaches assessing model reliability, an important example being Bayesian Statistics (Gelman et al., 2014).

There are, however, a few examples of work using this type of approach. These studies do not focus on food choice *per se*, but only as a specific instance of value-based decision-making, leaving aside most of the complexity that concerns food choice (Krajbich et al., 2015; Mormann et al., 2010; Towal et al., 2013). Mormann et al. (2010) for instance, investigated whether time pressure would affect food choice in a binary forced-choice task according to the predictions of a computational model (drift-diffusion model, Ratcliff, 1978). While they were able to find that a particular version of their model accounted best for the responses under different time pressures, it is clear from their study that food choice was not their main focus. Stimuli, in fact, were not matched for variables of interest but were simply familiar to the participants. However, the use of computational modelling allowed them to track specific task-related variables onto different processes, allowing to quantify the relationship between the two variables.

One of the strengths of these approaches is the use of binary forced-choice paradigms, which allow to tightly control stimulus features, while allowing enough computational power to test complex models of behavior, with some limited sacrifice in terms of generalizability. Another is the fact that they can account for uncertainty, a key aspect in food choices, given the many determinants that simultaneously can affect the process.

1.4 Research Aims

In the effort of characterizing how physiological, affective and cognitive factors shape food choice, I designed three studies. My goal was to uncover some of the neural and computational bases of cognitive mechanisms that are at play when we choose among different foods, by maintaining a central focus on food choice. To achieve this, I used a forced-choice design, a binary food-choice (henceforth, BFC) paradigm that allowed to control for stimulus variables while keeping the analysis computationally tractable and preserve some of the ecological validity of the actual choice. Furthermore, I employed functional magnetic resonance imaging (fMRI) alongside behavioral testing and computational modeling, taking advantage of different levels of explanation (e.g., biological, computational, cognitive, behavioral. Bechtel, 2008, 2009; Craver, 2007).

In Study 1, I investigated the interaction between cognitive and physiological aspects, focusing in particular on how people understand and judge calories. In order to do so I made participants perform a BFC task with foods that differed along the total number of calories (i.e., portion size, caloric content here) and the number of calories specific to that food (i.e., food type, caloric density here) asking them to maximize their calorie intake. I expected this would result in participants not only choosing foods with high calorie density but also bigger portions (higher caloric content) overall. As these two measures have often been conflated in the literature, I hoped to show that both dimensions affect how calories are understood and how they both bias choices.

In Study 2, I aimed at uncovering the neurocognitive basis of a particualr case of food choice, that is risky food choice. Given the interplay between cognitive-affective (contamination risk) and physiological (calorie) aspects, it represents a model of the interaction among the different dimensions of food choice. In Study 2, I expected risk to strongly influence the choice and that participants would forego most of the benefit of gaining calories. At the neural level, I expected the activation of the insula to track risk prediction, while the vmPFC to code for the reward value (i.e. its calories) of the options.

In Study 3, I wanted to address the interplay of hunger, calories and preference using a computational approach that could disentangle the simultaneous and combined contributions of each of these elements to food choice. In order to do so, I employed a drift-diffusion modeling approach to information accumulation in favor of either one or the other option of a within-subject BFC, depending on the features of the food chosen. I expected that participants, while hungry, would choose food relying more on their calories (caloric density), while they would rely more on preference and less on calories in the condition in which they were not fed.

Taken together, with these studies I aim at showing that the neurocognitive bases of food choices include a complex interplay of factors that can be investigated in an experimental setting. On top of this, I aim to demonstrate that the we can propose and test mechanistic models about the process of choice focusing on different, controllable factors, drawing a bridge from value-based decision-making work in cognitive neuroscience and the literature on food perception and choice in consumer research and experimental psychology.

2. *Counting calories*[1]

2.1 Abstract

Calories provide the fuel needed by our brain and body to work. However, to my knowledge, no author has hitherto clarified how people conceive and interpret calories, whether as an absolute (i.e., total number) or a relative (i.e., related to the type of food) quantity. This is important, as calories provide our brains not only with important nutritional information about foods (Nesheim and Nestle, 2012) but also influence our behavior in choosing among different foods. In the present Study, I investigated how this is categorized by asking 23 participants to maximize their caloric intake in a BFC task with food items either differing in the number of total calories (caloric content) or calories x 100g (caloric density). What the results show is that participants tend to understand calories in term of their relative quantity (caloric density), with little regard to the total number of the calories suggesting, in line with other studies (Frobisher and Maxwell, 2003; Japur and Diez-Garcia, 2010),

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[1] A version of this chapter is in preparation for publication: Garlasco P., Corradi-Dell'Acqua C., Foroni F. & Rumiati R.I. The effect of Risk on Food Choice: Understanding the caloric determinants of food choice and the effect of risk of contamination.

that estimates of portion sizes can be biased.

2.2 Introduction

By and large neuroscientists have investigated the perceptual features of food that might guide our choices in everyday life (Verhagen and Engelen, 2006). For instance, the ability to detect food caloric value is of paramount importance because we must be able to modulate our food intake depending on our energetic needs. Several studies succeeded in tracking food processing in the brain as a function of calorie content (e.g., Toepel et al., 2009). However, a possible caveat remains since, to our knowledge, no author has hitherto investigated whether it is the type of food or the total amount of calories in a portion - in other words how calories are framed - that drives the estimation process (e.g., Frank et al., 2010; Killgore et al., 2003; Tang et al., 2014; Toepel et al., 2009).

As some studies showed, portion size - and in particular meal size - can have a biasing influence in estimating the calorie content of a particular food (Wansink and Chandon, 2006), including the known effect of considering a portion smaller when the plate is larger as compared to when the plate is smaller (Figure 2.1,Van Ittersum and Wansink, 2011, named *Delboef* illusion after the eponymous optical illusion Delboeuf, 1865). Also, the calorie content of a food can bias the estimation of the total number of calories of a portion (Japur and Diez-Garcia, 2010), even to the point that increasing a portion of a food leads to higher energy intake through increased consumption (Rolls et al., 2004a,b).

Moreover, while some studies have shown that many factors such as food liking, familiarity, expected satiation (Brogden and Almiron-Roig, 2010), gender, dietary behavior and hunger (Brunstrom et al., 2008) seem to influence portion size estimation, it is unknown whether it is the calories contained in the portion (say a bowl of ice cream vs. a spoon of ice cream) or whether the calories of a certain type of food (that fact that it ice cream or pasta) that would be wrongly estimated.

Understanding which of these two options is preferentially processed, therefore, has implications on how the brain encodes calories, since both ways can be interpreted as a reward (i.e., energy content). Furthermore, we know that cognitive aspects - such as framing (Tversky and Kahneman, 1985) - are relevant in decision-making in general (as explained in section 1.2.3.1) and food choice is no exception, as studies in consumer science (Carels et al., 2007) and cognitive neuroscience (Hare et al., 2011) have shown.

In this Study, we aimed at understanding the relative contribution of two caloric variables - Caloric Content (CC) and Caloric Density (CD) - in making a choice about food. CC is defined as the total amount of calories in a portion (e.g., 160Kcal of chocolate), and CD corresponds to the amount of calories in 100 gr of a particular type of food (e.g., 515Kcal/100g in the case of chocolate) might differently affect food choice. In order to better understand how calories are understood, I decided to ask participants the explicit goal to maximize them. If, notwithstanding the goal, participants would focus more on CD, as I would expect from studies on portion sizes Diliberti et al. (2004); Frobisher and

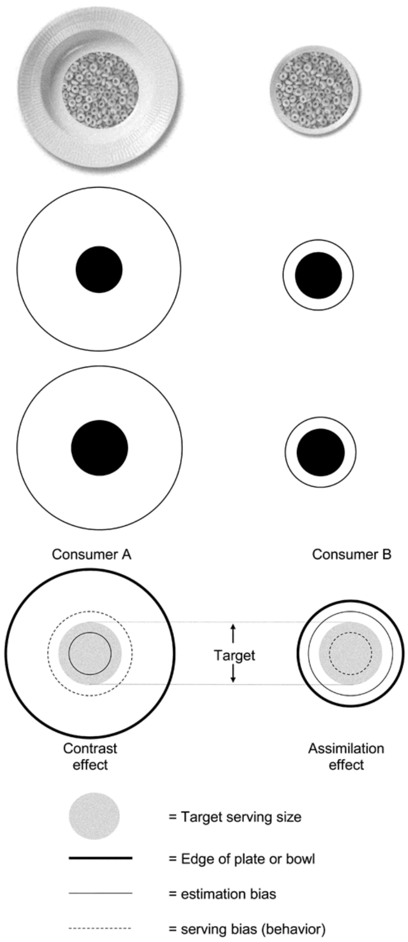

Figure 2.1: The *Delboef* illusion applied to portion size. As you can see for yourself (top Figure) the size of the dish can influence the size of the same portion. Adapted from Van Ittersum and Wansink (2011).

Maxwell (2003), then it would mean that the type of food matters more than the total amount calories, making estimates of the total number of calories of a portion (CC) biased, with significant implications for overeating (Rolls et al., 2002).

2.3 Materials & Methods

2.3.1 Participants

Participants were recruited through internet advertising. Prior to testing, they all provided written informed consent and were informed that they could discontinue the study at any time and upon completion of the experimental tasks. Twenty-eight (16F; Age: 24.38yrs, SD = 3.2) healthy, right-handed, normal body-weight (Body mass Index (BMI): 21.49, SD = 1.95) and normal or corrected-to-normal vision native Italian speakers, participated in the study. All the participants had normal or corrected-to-normal vision, and were controlled for satiety and thirst via pre-test questionnaires. Table 2.1 summarizes the sample features. All participants but five had an omnivorous diet, were non-restrained eaters and had no eating-disorders as assessed via the Restraint-Scale (Ruderman, 1983) and the Eating Disorder Inventory (EDI-3, (Garner, 2004)) post-questionnaires. Therefore, data were analyzed for twenty-three participants.

Participants' information

	Age	Education	BMI
mean	24.38	15.9	21.49
median	24	16	21.49
SD	3.2	2.37	1.95

Table 2.1: Participants' demographic and questionnaires' score. BMI = body mass index; PSQI = Pittsburgh Sleep Quality Index; RS, Restraint Scale.

2.3.2 Stimuli

Forty food images were taken from a purposefully-made database, aimed to be a continuation of the work on FRIDa (Foroni et al., 2013, see Figure 2.2). Half of them (n=20) were depicted high caloric density (HCD: 324Kcal/100g, SD = 130,) foods and the other half (n=20) depicted low caloric density (LCD, 50.85Kcal/100g, SD = 18.25) foods. Within each subset (HCD and LCD), half of the stimuli had high (HCC, 160Kcal) and low caloric content (LCC, 80Kcal), producing four stimuli subsets (HCD-HCC, HCD-LCC, LCD-HCC, LCD-LCC). Food stimuli were matched for variables of interest such as arousal, typicality, hedonic value, familiarity, valence, RGB color and spatial frequency. (Foroni et al., 2013).

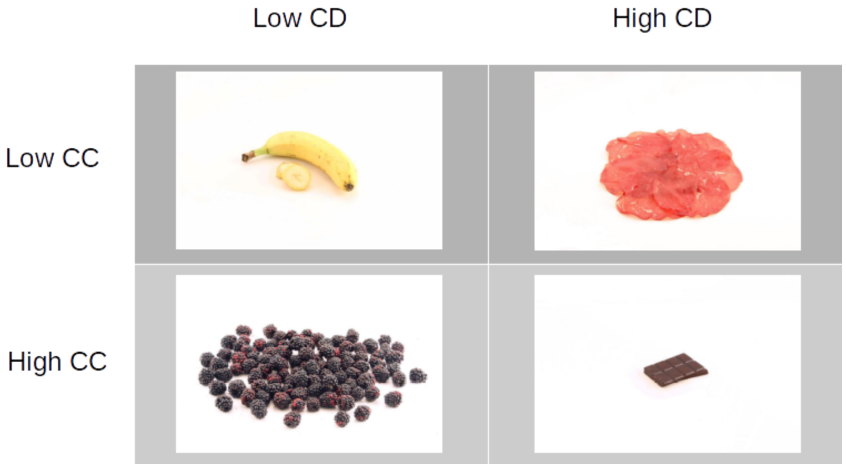

Figure 2.2: An example of selected stimuli. Low caloric density (LCD) foods on the left side and High caloric density (HCD) foods on the right; foods with low caloric content (LCC) in top quadrants and foods with high caloric content (HCC) in bottom quadrants.

2.3.3 Task procedure

To untangle the contribution of either CC or CD in estimating the caloric intake of a given food, a binary decision task (binary food choice, BFC) was implemented. Participants had to choose between pairs of foods with different CC or CD. Participants were instructed to maximize their caloric intake in making their choices. The task was divided in four runs, with breaks in between. A short training phase to help participants to get acquainted with the setup and the stimuli used preceded the experiment.

Each trial was structured as follows: after a small fixation period (1000ms) participants were presented with two food images on the screen. They pressed either the "1" key or the "2" key to choose the left food or the right food respectively. Participants had up to 5s to make their decision. After decision was made, a feedback on the amount of calories gained was provided through a self-filling bar. Participants were instructed to maximize their caloric intake in making their choice (see Figure 2.3). Stimuli were presented electronically using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

In order to identify the contribution of the single feature of interest, we compared the caloric content (CC) and the caloric density (CD), each of which was then divided in two levels: High and Low. In the case of CC, the quantity (i.e., the total number of calories) was either 160Kcal (High) or 80Kcal (Low). Given that different foods could hardly have the same CD, the two CD levels corresponded to a range of values: up to 150Kcal/100g for Low and from 150Kcal to 600Kcal for High, with no values overlapping. These criteria were

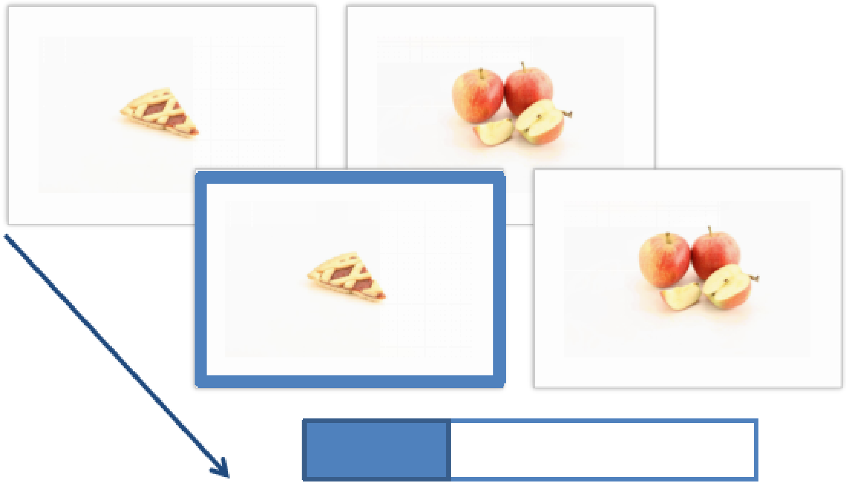

Figure 2.3: An example trial in Study 1.

in line with previous literature (Foroni et al., 2013) and allowed us to distinguish between foods having High CD and Low CD values. While there clearly were differences in the CD *within* the same category (high or low), however, these were considerably smaller as compared to differences *between* categories (Wilcoxon signed-rank test, $W = 36$, $p = 0.002$). All the levels combined produced a factorial design (2x2) with two conditions of two levels each. In diffCD, stimuli had the same CC but different CD; within this condition, half of the trials had high CC while the other half had low CC. Conversely, in diffCC, stimuli had the same CD but different CC; within this condition, half of the trials had high CD while the other half had low CD. Furthermore, Control was included as a control condition in which stimuli were taken from the same "group" - each group represented by a panel in Figure 2.2, giving a total of 4: LCD-LCC, HCD-LCC, LCD-HCC, HCD-HCC - and had the same CD and CC values. This condition was devised to control whether the item choice was balanced, i.e., participants would be choosing randomly between items within the same category. The experiment was divided in four runs with 46 trials each, for a total of 184. diffCD and diffCC consisted of 60 trials each, while the Control condition had 64 trials.

2.3.4 Data Analysis

Data were analyzed via a binomial linear mixed model using the statistical package lme4 (Bates et al., 2014). Since not all conditions carried a correct answer (foods having the same CC have, by definition, the same amount of total calories, as in condition diffCD) we chose to use as dependent variable the side of the chosen item (Left vs. Right). As independent variable we split the conditions in the following five levels (summarized in Table 2.2): 1) Condition 3 with foods taken from the same group (given that in this condition participants chose between items of same CC and CD, we expected comparable amount of left/right responses); 2) and 3) conditions with foods from Condition 1 (same CC, different CD), with the item of higher CD located on the left and right sides on the screen, respectively; and 4) and 5) conditions with foods from Condition 2 (same CD, different CC), with items with higher calorie content located on the left and right sides of the screen, respectively. As additional regressors, the model included participants' age, gender and BMI. In the analysis, we considered a significant threshold alpha level of 0.05. All statistical tests were two-tailed.

level	variable
DV	Left vs. Right
1	Control condition
2	diffCD - left
3	diffCD - right
4	diffCC - left
5	diffCC - right

Table 2.2: Study 1 Linear Mixed Model structure. DV = Dependent Variable.

2.4 Results

As indicated by the intercept value (i.e., the Control condition, 0.51, Table 2.3) the experiment was well balanced, as participants chose randomly between items of the same group. Age, gender and BMI did not seem to drive the choice, not reaching significance (see Table 2.3: $p = 0.971, p = 0.588$ and $p = 0.123$, respectively. See also Figure 2.4). Moreover, CD seems to have had an effect on the participant's choice. As it can be seen in Table 2.3 and Figure 2.4, the effect in the case of Condition 1 was significant ($p < 0.001$), as CD contributed to drive the choice either to the left ($0.10, p < 0.001$) or the right ($-0.15, p < 0.001$) with respect to the control condition (intercept, see Figure 2.4). A small effect can be observed also in Condition 2 (Condition 2 L: $-0.07, p = 0.040$) but only on the left and with a large error bar, while in the case of Condition 2 R it was not statistically significant ($0.05, p = 0.072$, see figure 2.4).

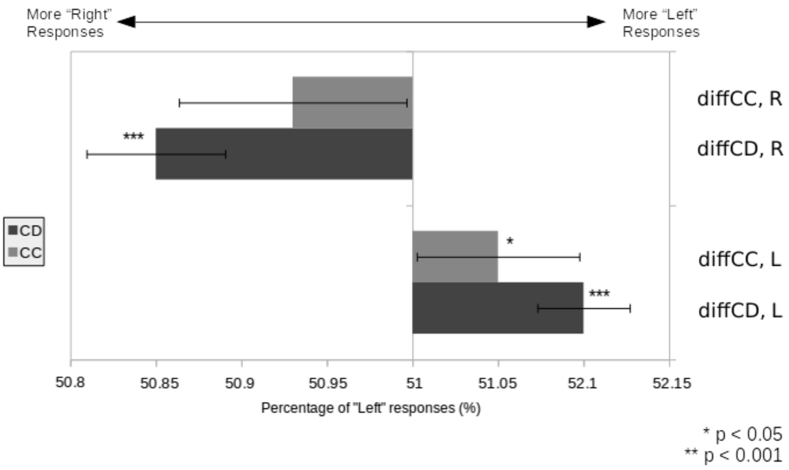

Figure 2.4: Plot of the linear mixed model estimates for fixed effects. In dark gray the Condition 1 and in light gray the estimates for Condition 2. All values are compared against the value of the intercept (Condition 3).

		Model	
	Beta	Confidence Interval (CI)	*p* value
		Fixed Effects	
(Intercept)	0.51	0.44 – 0.98	< **.001**
Age	0.00	0.00 – 0.01	0.791
Gender	−0.01	−0.06 – 0.03	0.588
BMI	−0.01	−0.02 – 0.00	0.123
DiffCC 2, L	0.05	0.00 – 0.10	0.072
DiffCC 2, R	−0.07	−0.15 – 0.00	**0.037**
DiffCD, L	0.10	0.05 – 0.15	< **.001**
DiffCD, R	−0.15	−0.21 – −0.09	< **.001**
		Random Effects	
$N_{subjects}$		23	
Observations		3131	

Table 2.3: Binomial logistic regression predictors for Study 1. The intercept represents the estimate for the Control condition.

2.5 Discussion

In this experiment we investigated how using different notions of calories, i.e., Caloric Content (CC, total number of calories) and Caloric Density (CD, number of calories per 100 grams of food), influenced the participants' understanding of calories and food choice. This was achieved by employing a design in which participants were asked to maximize their caloric intake with binary choices. Stimuli were paired according to their high or low CC, and high or low CD, and controlled for possible confounds such as arousal, valence, typicality, familiarity and perceptual features such as color and spatial frequency. This produced a factorial design plus an additional control condition (Condition 3) in which stimuli were matched for both CC and CD and expected to be randomly chosen.

When asked to maximize their caloric intake, participants chose food based mostly on CD. To our knowledge, our study is the first to show that type of food (CD) but not the total number of calories (CC) matters in the evaluation of the calories of a food. Previous studies have also mostly focused on CD but did not assess whether CC was a confounding factor or not. For instance, in Killgore et al. (2003) study, high and low calorie foods loosely corresponded to what here we called high and low calorie density (CD) foods, and in Tang et al. (2014) CD but not CC was investigated (but see also Frank et al., 2010; Siep et al., 2009; Simmons et al., 2005, for other studies in which CC was not taken into account).

The fact that calories are intended as a relative and not as an absolute quantity seems to be in line with what found by other studies. Japur and Diez-Garcia (2010), for instance, investigated the ability of nutrition students to estimate the size of a portion given pictures of different foods. As the authors report, only a small minority (18.5%) of the estimates was correct (more or less than 10% of the actual quantity). In particular, they found a significant positive correlation ($r = 0.8166$; $p = 0.0002$) between calories (CD, in our case) and portion size estimation. The higher the CD, the more it was overestimated. As the test was performed with nutrition students, one would speculate that lay people would make even bigger mistakes, or perhaps retain a similar bias. This is indeed what has been found in other studies on different populations (e.g., Frobisher and Maxwell, 2003, in adults and children), with the same pattern of overestimation for foods with higher CD. One could argue that these results are not really comparable, as estimating portion size (grams) is different from estimating the total number of calories. However, as some simple algebra shows, the first can be derived from the latter and *vice versa*, using CD:

$$CC(cal) = \frac{portion(g)}{100} * CD(cal/100g)$$

While I do not expect participants to perform this small calculation, I think we can safely assume that our brain might engage in some similar computations, explaining the pattern of results in the present study. In order to test this explanation explicitly, though, further studies targeting directly the estimation process would be needed. Other studies involving food choice and consumption with different portion sizes seem to help explaining our results. For instance, Diliberti et al. (2004) investigated whether people would eat more food by (covertly) increasing on different days of the week the portion of pasta that they consumed regularly in the cafeteria. As their results show, people would tend to consume more calories, as they not only eat all the (larger) pasta, but kept on purchasing the same other foods they would normally buy along it (e.g., main course, dessert). Moreover, when asked whether they found they had consumed more food, the participants were generally unaware of having consumed more calories. Other authors replicated the experiment by giving either medium or large popcorn portions to moviegoers. Even though the portions were so big that nobody managed to finish them, still participants who had the large portion ate 45% more (Wansink and Kim, 2005). Other studies, such as Rolls et al. (2002), found that whether the subjects were either served a plate or had to help themselves from a serving-plate, their consumption increased as the portions increased. These results seem to suggest that portion size can be largely irrelevant to the actual choice and consumption of food[2]. Our study expands this clam by showing that even when the goal is to explicitly trying to maximize the calories the portion does not seem to matter more than the type of food that is chosen. From an evolutionary point of view, one could imagine that our ancestors' brains that were better in estimating calories of the type of food they found (or hunted) would have been selected[3], while CC or the portion size would have mattered less. After all, as the cafeteria studies show, eating more is always the best strategy when food is scarce.

Notwithstanding the implications, as for most studies also this study is not free from limitations. The first one is related to the difference in within-

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[2] And can also explain why we so easily fall prey to the food version of the *Delboeuf* illusion.

[3] Imagine you had the choice to go picking different varieties of nuts but could not get all of them. I bet being able to estimate their CD would far better than trying to put together a total number of calories by using different types of nut.

category variability between CC and CD. As a matter of fact, it is very unlikely to find two different food items with the *same* CD. Indeed, the only case we have here is the one of whole-grain bread and raw ham (see Appendix A). On the contrary, it is easier to find a portion with the same amount of CC, as the total number calories can be, for instance, prescribed in a diet. The fact that CC varied with only two values (80 and 160 Kcal) instead of varying slightly clearly factors a limitation, but it is, I believe, unlikely to alter the results significantly, as the order of magnitude of the mistakes in estimating the size of portions in the aforementioned experiments show (e.g., Frobisher and Maxwell, 2003). A second limitation stems from the fact that it is not always possible to control for all variables of interest when selecting stimuli. All the more so with food images, which are fairly complex visual stimuli. This is the reason why controlling for some low-level variables, such as luminance or contrast (Kohn, 2007), was not done. While it could be argued that controlling for these variables would have rendered the images less ecological it remains the fact that not enough is known about how which neurocognitive process underlies calories estimation to rule out the possible effects of these variables. This is a limitation that is partially related to the construction of the database itself, but also a choice, as it would have implied not being able to control for other variables such as Arousal or Valence, elements which were considered to be more important for the scope of the experiment.

As I hope to have shown, the *framing* of calories - that is whether they are understood as CD or CC - matters when choosing a food item. As the calories appear to be perceived as a relative quantity, the type of food seems to matter more than the total number of calories, whose estimation can to be easily biased and hardly be reliable. Indeed, the fact that CD is mostly used as an estimator for the calorie intake, shows how important it is to control for CC and portions, and this can have a profound impact on calorie consumption and overeating (Rozin et al., 2011). Although this experiment does not evaluate the role of other factors - e.g., affective aspects such as food preference - in shaping food choice, nonetheless it rules out a possible confounding factor that might bias results in experiments evaluating the role of calories in food choice. It will serve as a starting point for the other Studies included in the present thesis.

3. *Contamination and risky food choices*[1]

3.1 Abstract

Every day we choose what to eat and in order to do so we evaluate food items along several dimensions. Due to the complexity of the food-supply chain, food safety might become an issue. Indeed, contamination can occur and this represents a real risk for consumers. Here, we aimed at assessing the neural bases of how the perception of risk contamination alters choice of foods with different CC or CD. To this end, we had 19 healthy participants with normal body mass index (BMI) repeatedly choose among two food items of different caloric content while lying down in the scanner. Analyses were performed using a linear mixed model with binary logistic regression and flexible factorial second-level fMRI analysis. First, we found that with risk probability being equal, participants chose high CD foods more frequently than low CD. This behavior was associated with the right anterior insula (rAI), while activation in the dorsal striatum varied parametrically with risk. The general tendency

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[1] A version of this chapter is in preparation for publication: Garlasco P., Corradi-Dell'Acqua C., Foroni F. & Rumiati R.I. The effect of Risk on Food Choice: Understanding the caloric determinants of food choice and the effect of risk of contamination.

to avoid risk was partially counterbalanced by an increased approach towards foods with high CD, suggesting that this type of food might reduce people's concern toward contamination. The activation of rAI is in line with other studies showing its role in risk perception and prediction errors, while the dorsal striatum has been found to code for reward value suggesting a different perception of the calories of the food. Altogether, these results shed light on the behavioral and neural bases of risk perception in food choice.

3.2 Introduction

As efficiently as our brain seems to extract critical information about food from perceptual cues, food choice requires the acquisition of further information about what we intend to eat. Indeed a food, even a very palatable one, may be poisoned, and therefore eating it may have serious or fatal consequences to our health. Given this, it is not surprising that we are very sensitive to perceptual cues that can indicate that the food we are about to consume is spoiled or poisoned. A bitter taste, sour smell or bluish color indeed provide our brain with cues that can be readily interpreted as a sign of danger and are usually met with a reaction of disgust (Martins and Pliner, 2006; Rozin and Fallon, 1987). Even when none of the perceptual features of food is sufficient to alarm us, ingesting the food is usually sufficient for our brain to evaluate the danger of the item consumed, however at the cost of harming us.

Different is the case where our assessing of the state of the food must rely on other sources of information. Public perception of risk has changed as progress in biotechnology has transformed the way we produce, store and distribute food (Savadori et al., 2004). Like other aspects of communication, risk can also be framed in different ways. And as we have seen in the introduction (section 1.2.3.1), the effects of framing (for instance in terms of gains or losses) can produce large effects[2]. Indeed, based on a pool of 136 studies, Kühberger (1998) analyzed whether framing had an effect on risky choices. What the

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[2] However, this is not always the case. In their review Levin et al. (2002) show that while framing seems to work for attributes and risky choice, results for goals are weak and inconsistent.

author found was that the effect size was low to moderate, with variations depending on the design, instructions and focus of the outcomes (reference point vs. goal). Experimental research on risky choices, however, mostly focuses on monetary gains and losses and, to my knowledge, the research on risk in food choice is scant or not existent (with the exception of work in non-human primates: Platt and Huettel, 2008). On the other hand, most of the research on how we evaluate and discard foods that might be poisoned is primarily focused on public perception of contamination hazards (e.g., Liu et al., 1998; Rosati and Saba, 2004), leaving unexplored the neurocognitive mechanisms underneath the choice process. Indeed, there seems to be no research on the trade-off between calories and contamination in food choice and, in particular, how it is modulated by different types of food (CD) or by the total number of calories (CC).

In this Study, I investigated how food choice interacts with the risk of an averse consequence (i.e., risk of contamination), potentially altering the value of the food item, and the brain mechanisms that may drive the choice. In order to do so, I employed a BFC, building on Study 1. Following the design by Hunt et al. (2012), I decided to pair the food items with discrete probabilities of contamination and use as the reward the CD of the food. Consistently with the literature on framing, I expected that risk would have a general averse effect on the choice. This would imply that participants would rather refrain from choosing a food than risk being poisoned[3]. In fact, I expected participants to try and minimize the poison by choosing the safest option (a strategy

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[3] This highlights an asymmetry between gains and losses. See section 3.5 for a discussion.

known in decision theory as *minimax*, Von Neumann, 1959. A sort of "insurance against the worst case", (Robert, 1994)). On top of this, I expected that if CD influenced the choice, it would be by making high CD items more salient and attractive, and participants would choose at least some of them. This would show that the type of food is an important attribute in determining whether people would perceive it as safe in case of contamination. In line with the results of Study 1, I did not expect to find any effect of CC on the decision patterns. Despite the fact that I could not find any study on risky food decision-making, I expected risk to activate the insula, usually found in prediction-error and risky decision-making (Preuschoff et al., 2008) together with the inferior frontal gyrus (IFG), proposed to code for risky aversion (Christopoulos et al., 2009), thereby extending the results of risky decision-making to a different type of stimulus, i.e., food. Moreover, I would expect to find the activation of the insula, usually tracking the CD of foods (Verhagen and Engelen, 2006). If the "common currency" hypothesis of value-based decision-making is true[4], I would also expect to find an activation in the ventromedial prefrontal cortex (vmPFC), putative hub of the comparison process of options with different values (Levy and Glimcher, 2011).

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[4] This hypothesis states that, in order to decide which item to choose we need to compare its value with others and after the comparison is made select the one with the highest value (Levy and Glimcher, 2011; Rangel et al., 2008).

3.3 Materials & Methods

3.3.1 Participants

Participants were recruited through internet advertising. Prior to testing, they all provided written informed consent and were informed that they could discontinue the study at any time. Nineteen, right-handed, normal body-weight (Age: 25yrs, SD = 3.5, BMI: 22, SD = 1.7, Education: 16.05yrs, SD = 2.78), Italian native-speakers participated in the study. All the participants had normal or corrected-to-normal vision, and were hungry as they were asked to fast before the experiment. All but one had an omnivorous diet, were non-restrained eaters and had no eating-disorders as assessed via the Restraint-Scale(Ruderman, 1983) and the Eating Disorder Inventory (EDI-3, Garner, 2004) post-questionnaires. Therefore the final analysis involved 18 participants. able 3.1 summarizes the sample features.

Participants' information

	Age	Education	BMI
mean	25	16.05	22
median	25	16	22
SD	3.5	2.78	1.7

Table 3.1: Participants' demographic and questionnaires' score. BMI = body mass index; PSQI = Pittsburgh Sleep Quality Index; RS, Restraint Scale.

3.3.2 Stimuli

The 24 stimuli selected for Study 2 were taken from Study 1 and were matched for variables of interest such as arousal, typicality, hedonic value, familiarity, valence, RGB color and spatial frequency. (Foroni et al., 2013). The risk of contamination took six different probability values (0%, 20%, 40%, 60%, 80% and 100%) and each food had an associated value that was consistent within-subjects but randomized between-subjects. The number of probability values chosen represented a trade-off between having enough probability combination while at the same time not increasing too much the number of trials, as the trial length in the fMRI scanner was longer and the time constrained (see section 3.3.3). The conditions were the same of Study 1 (diffCD, diffCC and Control).

3.3.3 Task procedure

Participants arrived at the venue 20 minutes before the experiment and were asked to fill-in two pre-experimental questionnaires to control for their state of hunger and their handedness. Hence each participant's expectation was framed by reading one of three written stories about a realistic natural disaster altering the state of the cultivations and food supply, and subsequently answered different questions about how to cope in such a circumstance (e.g., "Which food would you avoid in these situations?"). This kind of framing has been shown to be effective in significantly altering consumer's behavior in circumstances of scarcity and hopefully would work in case of danger, where food would be scarce (see Shah et al., 2015). Hence, participants were instructed about the task which was the same as in Experiment 1 (see also Hunt et al., 2012). They were presented with pairs of food items, with the respective associated probability of contamination (risk) displayed underneath the image. Participants had to choose one of the two foods in order to maximize their caloric intake while minimizing the amount of poisoned food they could get. Participants had up to 4s to make their choice, a time window that a separated pilot study (n = 6) showed was long-enough in order to decide. In case they did not succeed to choose on time, no food item was selected for that trial. A feedback bar was displayed after each trial, increasing only in case of a safe-food choice with an amount correspondent to the calories of the chosen food. A choice was considered safe depending on the probability of the food being contaminated (e.g., a food having 40% risk probability would be safe in 60% of the cases). Every time the bar reached the end point it eventually got back to start, adding bonus food gained, which was given as snack bars to the participant after the experiment was completed. In order for the incentive to be effective, participants were asked to abstain from eating for 90 minutes before the experiment (Killgore et al., 2003). As in Study 1, stimuli were presented electronically using the E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA).

Each participant had a total of 198 trials (72 for diffCD, 60 per diffCC, plus 66 for Control condition) to perform, divided into 66 trials per run. Each run lasted approximately 12-13 minutes with a total scanning time of approximately 50 minutes per participant. After the experiment, participants were asked to fill three different questionnaires: a restraint-scale, an eating disorder inventory, and a questionnaire about the preference for the food stimuli used, including liking and frequency of consumption.

3.3.4 Scanning parameters

Scanning occurred on the premises of Azienda Ospedaliero-Universitaria "Santa Maria della Misericordia" in Udine from May to July 2015. The scanner used was a Philips Magneton Achieva 3T. TR was set to 2s, TE to 35ms with a FOV of 230x230x136 and a FA of 90°. Voxel size was 3mm x 3.59mm x 4mm. An MPRAGE sequence was performed after the functional runs in order to acquire high-resolution T1-weighted anatomical images for coregistration.

3.3.5 Behavioral data analysis

Unless otherwise mentioned, the analysis of participants' choices was the same as in Study 1. The only difference in the model consisted in the addition of the difference in Risk of the two options as factor, parameterized in 11 levels (from -100 to +100), corresponding to the difference between the risk of the left food and that of the right food. As an example, if a banana on the left had a 40% probability of being contaminated and a chocolate bar had a 80% probability, the difference would be $40 - 80 = -40$.

3.3.6 fMRI data analysis

Functional data were analyzed using SPM12. Preprocessing steps included motion-correction algorithms with an exclusion criterion of 1mm of head motion in any direction (no participant exceeded it). Subsequently, data were preprocessed with high-pass filtering (128 s) and then co-registered to the anatomical T1 image. Images were resliced to 3x3x3 mm using sync interpolation and then normalized to Montreal Neurological Institute (MNI) space. Smoothing was performed with a Gaussian kernel filter (full width half maximum (FWHM) = 8). Preprocessed data were subsequently fitted into a General Linear Model (GLM) using as regressors all the conditions of interest (diffCD, diffCC and Control) and motion-related regressors were included to rule out any effect of motion on the data. For each condition its time derivative was additionally modeled. Additionally, two regressors were added for the activity related to the feedback, one for safe choices (Safe) and one for not safe choices (Unsafe). A last parametric set of regressors was used to keep track of risk in each condition. I modeled the moment of the choice as well as the feedback phase. A flexible factorial model was performed on the first-level betas and planned second-level t-tests of contrasts of interest were subsequently assessed. Namely, I was interested in disentangling the effect of varying CC or CD on risk performance. To do so, I contrasted separately the calorie conditions (diffCC > diffCD, diffCD > diffCC) and each of them against the control condition (diffCD > Control, Control > diffCC, diffCD > Control, Control > diffCD). The effect of risk was computed in two different ways. First, I assessed the difference between the risky options, by using the absolute value of the difference between the two options (Risk Abs_diff). The absolute value was used to keep track of the difference between the two risk values regardless of which one was eventually chosen. Second, to assess the contribution of the general level of risk involved in the choice, I also computed the risk as the mean of the two options, regardless of their difference (Risk Mean). This is consistent with the view that the difference between two risky prospects is not evaluated in the same way whether the risk is high or low (e.g., Christopoulos et al., 2009; Kahneman and Tversky, 1979; Tversky and Kahneman, 1985). All statistical parametric maps were corrected for multiple comparisons using a FWE-cluster correction (Friston et al., 1994)[5].

3.4 Results

3.4.1 Behavioral. Averse effect of risk, small effect of CD.

As it is shown in Table 3.2, participants performed at chance level in the control condition (0.53), suggesting that the control was effective. As expected, no effect of age, gender or BMI on performance was observed. Furthermore, the effect of liking and frequency of consumption was not significant (see Table 3.2 and Figure 3.1). As expected, risk seemed to induce a general averse effect on

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[5] Previous studies have confirmed that this type of cluster correction, combined with a smoothing kernel of 8mm, produces a percentage of false positives below 5% (Flandin and Friston, 2016).

the pattern of choices (-0.6, SD $= 0.3$, $p < 0.001$), confirming the hypothesis that participants become generally risk averse when the mere possibility of contamination is at stake. Interestingly, both a main effect and an interaction were present in the case of diffCD ($-0.05, p = 0.019$; $0.1, p = 0.040$) while this was not true for diffCC, suggesting that the CD, that is the type of food, might exert a different effect in counteracting the general effect of risk.

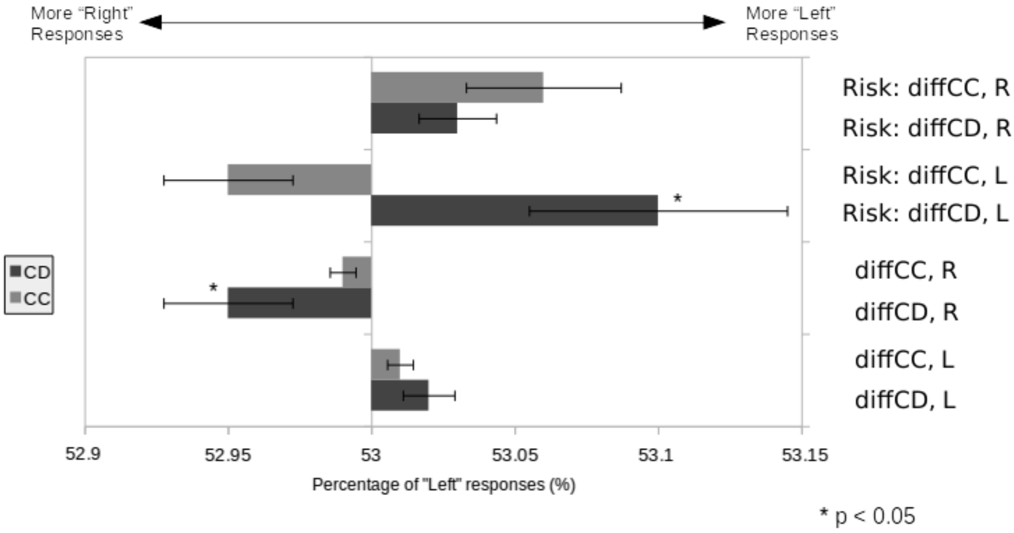

Figure 3.1: Plot of the linear mixed model estimates for fixed effects. In dark gray the diffCD and in light gray the estimates for diffCC. All values are compared against the value of the intercept (Condition 3).

	Model		
	Beta	Confidence Interval (CI)	*p* value
	Fixed Effects		
(Intercept)	0.53	0.49 – 0.57	< **.001**
Age	0.00	−0.00 – 0.02	0.521
Gender	0.02	−0.07 – 0.11	0.691
BMI	0.00	−0.02 – 0.02	0.941
Liking	0.04	−0.03 – 0.11	0.247
Consumption	−0.01	−0.08 – 0.05	0.703
diffCC, L	0.01	−0.03 – 0.05	0.630
diffCC, R	−0.01	−0.05 – 0.04	0.760
diffCD, L	0.02	−0.03 – 0.06	0.446
diffCD, R	−0.05	−0.09 – −0.01	**0.019**
Risk	0.53	0.49 – 0.57	< **.001**
Risk: diffCC, L	−0.05	−0.15 – 0.06	0.411
Risk: diffCC, R	0.06	−0.05 – 0.16	0.320
Risk: diffCD, L	0.10	0.00 – 0.20	**0.040**
Risk: diffCD, R	0.03	−0.07 – 0.12	0.603
	Random Effects		
N_{subjects}	18		
Observations	3462		

Table 3.2: Binomial logistic regression predictors for Study 2. The intercept represents the estimate for the Control condition.

3.4.2 fMRI. Right anterior insula and pre-SMA activation.

The second level flexible factorial analysis allowed to contrast the effect of the different conditions of interest through planned post-hoc t-test contrasts. Most notably, I tested whether differences existed between the caloric conditions (1 and 2) and the control condition. The only contrast that yielded a robust, FWE-cluster corrected ($p < 0.05$) activation was when contrasting the trials where CC was varied and CD kept constant (diffCC), against the trials where CD was varied and CC kept constant (diffCD). As apparent in Table 3.3 and Figure 3.2, two extensive clusters around the right insula and the pre-SMA were more active for diffCC when compared with diffCD.

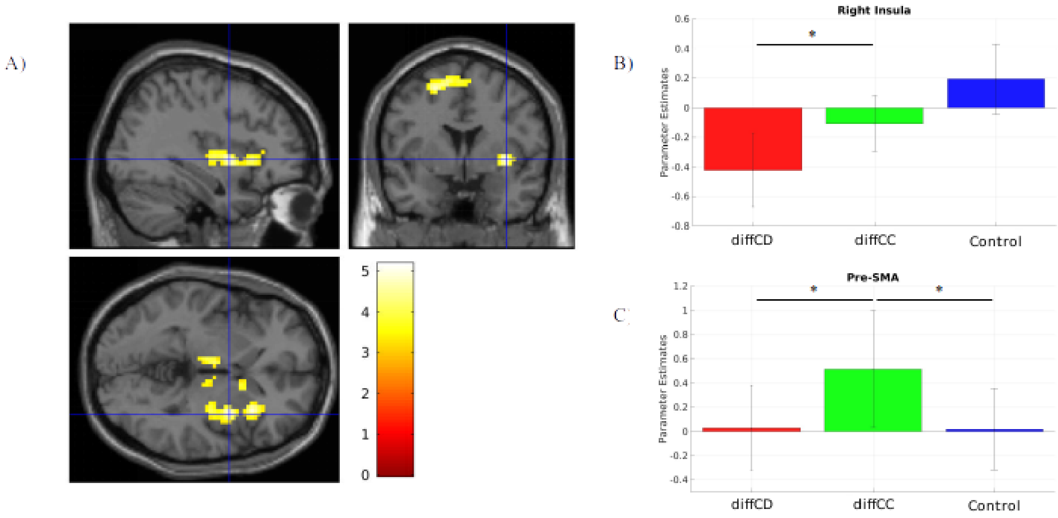

Figure 3.2: diffCC > diffCD contrast activation for the second-level flexible factorial analysis. A) You can see highlighted the clusters around the right insula (anterior and posterior) and the pre-SMA (in the sagittal image) as well as their parameter estimates (B and C).

	Cluster size	**Coordinates (MNI)**	**T value (peak)**	**Area**
diffCC > diffCD	269	36, 2, -1	5.17	Right Insula
	133	-21, 2, 56	4.77	Pre-SMA

Table 3.3: Regions that showed higher activation while contrasting diffCC > diffCD.

	Cluster size	**Coordinates (MNI)**	**T value (peak)**	**Area**
diffCD > Control	251	18, -25, -7	4.94	Dorsal Striatum
	183	57, -7, 41	4.25	Pre-motor cortex
	104	-42,-10, 26	3.95	Ventral pred-motor

Table 3.4: Absolute Risk: Regions that showed higher activation while contrasting diffCD > Control.

3.4.2.1 Absolute risk difference. Risk-related activation in dorsal striatum and pre-motor cortex.

When parametrized using the absolute difference between the two options, risk survived the multiple comparison correction (FWE cluster size) when contrasting diffCC against the control condition. Four clusters of activation were found in the Dorsal Striatum, pre-motor cortex (PMC), corpus callosum and ventral pre-motor cortex (vPMC, see Figure 3.3 and Table 3.4).

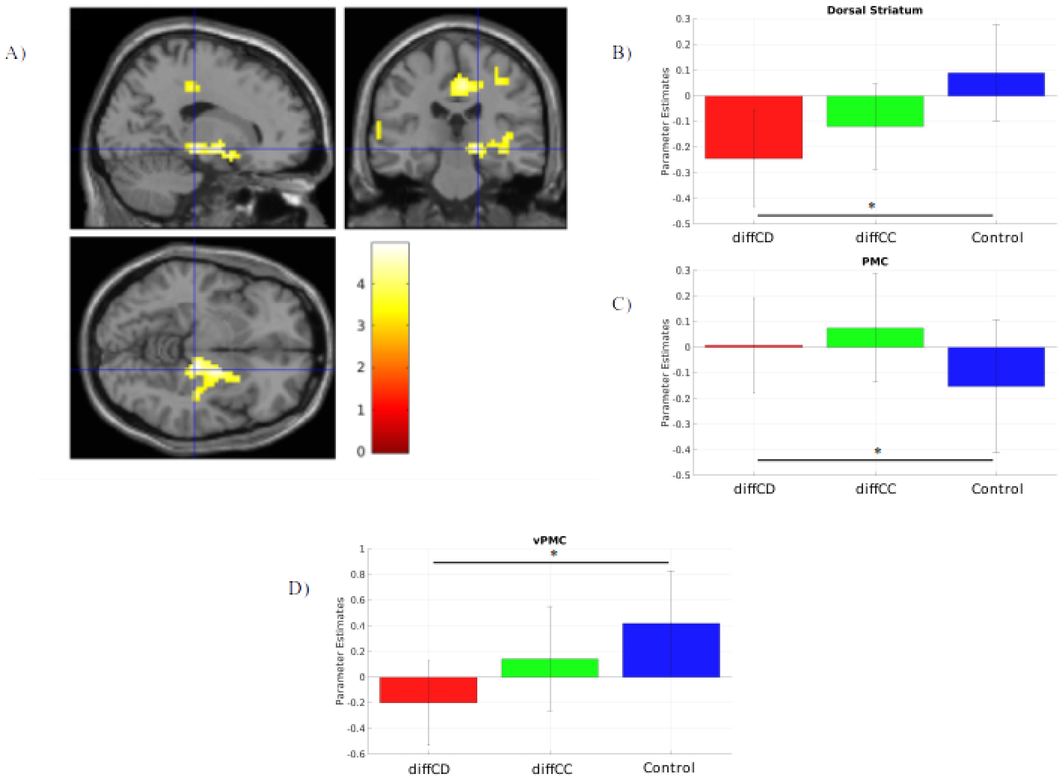

Figure 3.3: diffCD > Control contrast activation in the parametrized Absolute Risk for the second-level flexible factorial analysis. A) The highlighted clusters are around the dorsal striatum and the premotor cortex as well as their parameter estimates (B and C).

3.4.2.2 Mean of the two risks. Risk-related activation in left PCC.

When parametrized using the absolute difference between the two options, risk survived the multiple comparison correction (FWE cluster size) in the diffCD > Control contrast. A significant activation cluster was found in the posterior cingulate area (see Figure 3.4 and Table 3.5). This area has been found to be positively correlated to the perception of physical risk (Qin and Han, 2009) and its activation supports our behavioral finding that risk is perceived differently in the CD and control conditions.

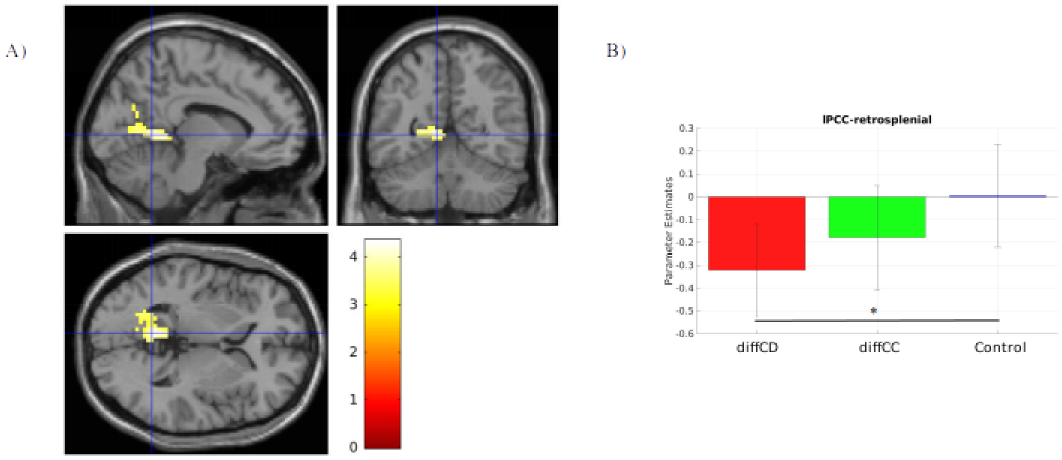

Figure 3.4: diffCD > Control contrast activation in the parametrized Mean Risk for the second-level flexible factorial analysis. A) You can see highlighted the cluster in the left PCC as well as their parameter estimates (B and C).

	Cluster size	Coordinates (MNI)	T value (peak)	Area
diffCD > Control	167	-9, -55, 2	4.34	Left posterior cingulate - Retrosplenial cortex

Table 3.5: Risk Mean: Regions that showed higher activation while contrasting diffCD > Control.

3.5 Discussion

In this Study, I investigated how the perception of risk contamination affects human choices about foods with different calories. To assess the effect of risk, I introduced a probability of contamination associated with each stimulus (counterbalanced between subjects) ranging from 0%, safe, to 100%, poisoned. This event-related fMRI design allowed to disentangle the contribution of different brain areas to the processing of risk probability as well as its interaction with the caloric value (either CC or CD) of the food items.

In addition to an expected general averse effect of risk, I also found both a main effect for diffCD and an interaction of risk with diffCD. This supports the idea, in agreement with other studies (see e.g., Frank et al., 2010; Nummenmaa et al., 2012), that high calorie foods act as powerful rewards not only in obese and overweight but also in individuals with normal BMI. More importantly, the result has been obtained after controlling for the size of the portion (CC), allowing us to attribute it to the effect of caloric density alone. The main finding, however, is that CD seems to exert a partially counteracting effect when associated with the risk of contamination, reducing its averse effect. Importantly, this effect was not found for CC. Figure 3.5 schematizes the view on how food choices are influenced by food characteristics (CC and CD) in the event of food contamination (risk). Risk exerts an effect both directly on choice and indirectly through CD. Moreover, while Study 1 clarified that participants can also judge food calories by relying on CC, with no information about risk of contamination, in Study 2, when risk of contamination is factored in, there is no evidence that CC plays a role.

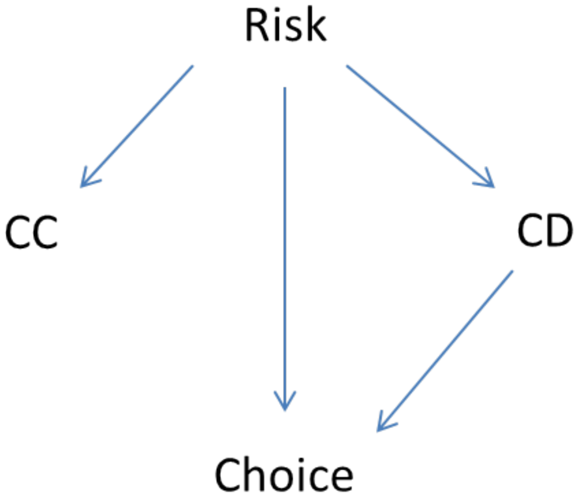

Figure 3.5: A mechanistic model of the effect of Risk, CD and CC on food choice. Risk influences CC, CD and choice; CD in turn influences choice, while CC does not.

The fMRI results were able to distinguish a set of areas that are arguably affected by risk and calories processing. The contrast between diffCD and diffCC highlighted both the right anterior insula (rAI) and the pre-SMA. The activation in these areas should represent the different effect on risk on the two caloric measures of interest (CC and CD). In fact, in the trials of diffCD, where CD was varied, the rAI was deactivated. In other words, rAi is activated more when the absolute calories are tracked rather than when the relative calories (CD) are.

Activation in the anterior insula has consistently been linked to the presentation of food cues in different modalities, including vision (Rolls, 2007; Simmons et al., 2005; Small, 2010). The anterior insula has also been associated with risk prediction and prediction errors (Preuschoff et al., 2008; Rao et al., 2008). I suggest that a lowered activation in the rAI might be related to the reduced risk perception of CD. A hypothetical mechanistic explanation considers the putative role of anterior insula in representing not only risk but risk prediction error (Preuschoff et al., 2008), with the purpose to help the organism to adapt and learn fast the risk of an option with constant updating, while comparing the real outcome with the predicted one and using the error to fine-tune the evaluation process to the new stimuli. The difference in activation when comparing choices in diffCD and diffCC suggests that risk might be perceived more correctly, and updated accordingly, when two foods differ in CC (diffCC) than when they differ in CD (diffCD). On the other hand, pre-SMA activation has been found in association with action decision and preparation, especially when participants made their choice under time pressure (Forstmann et al., 2008), as well as with working memory tasks (d'Esposito et al., 1998; Pessoa et al., 2002; Petit et al., 1998). This might imply that making decisions in diffCC was more demanding than in the diffCD, and that this extra processing effort was due to the presence of risk. Taken together, the deactivation of rAI and activation of pre-SMA suggest that risky decisions about foods equal in total number of calories (i.e., same CC) but different in caloric density (i.e., High CD vs. Low CD) are easier to make. I hypothesize that the brain pays less attention to the probability of contamination here, with the task being easier (lower pre-SMA activation) and less risky (deactivation of rAI).

The possibility that risk could have differently been perceived with foods of different CD seems to be consistent with the activation of the dorsal striatum, pre-motor cortex (PMC) and left posterior cingulate (lPC) tracking the absolute difference of the risk and its mean. The dorsal striatum has been frequently found to be involved in reward computation and anticipation (e.g., Schur et al., 2009) even in the context of food (Rothemund et al., 2007). Its involvement has also been observed in coding for the magnitude of both actual reward and punishment, particularly for the latter (Delgado et al., 2003). Its activation seems to be consistent with the literature on the first representing value of options of negative valence (Balleine et al., 2007). Since risk of contamination is clearly averse, it could be treated as a sort of punishment, and its presence when contrasting CD with the control condition, suggests that, since in the Control condition the calories are similar, it might make the negative outcome more salient, driving the choice away from CD. The activation of PMC and deactivation of dorsal striatum in diffCD – the latter found to be involved in action-contingent learning, especially with appetitive stimuli (O'Doherty et al., 2004) – here might signal the higher difficulty in learning to associate options with high reward to different levels of risk, although this evidence is hard to interpret. Even taking into account the effect of risk as the mean of the two options (Risk Mean) the activation of the left posterior cingulate (lPC) seems to be consistent with its role in tracking subjective physical danger (Qin and Han, 2009), since the higher the overall risk, the higher this risk irrespective of the choice.

What I could not find in the results is the activation of IFG and vmPFC. A possible explanation for the lack of activation in IFG, which should be expected in line with Christopoulos et al. (2009), can be that the contrasts performed did not allow to highlight a general averse effect of risk, as all the conditions I had included risk and, as they were counterbalanced, they probably cancelled out in the averaging process. On the other hand, the lack of activation of vmPFC can be arguably related to the possibility of participants not actually comparing the options in term of their values. This opens the possibility for a different mechanism, one that relies on the probability of contamination as a main factor shaping the choice, with the possible, secondary, contribution of CD to decide whether to choose one item of the other. However, this is mostly speculative, and further studies would be needed to clarify this point.

The Study presented here has many limitations and a few biases. The first bias could derive from the use of few stimuli, affording a reduced variability and generalization of the results. Unfortunately, given the constraints of the fMRI design, the reduced number of stimuli was a compromise, as even adding two more stimuli per group (each with a different probability) would have implied 122 more trials to balance all the comparisons. Another bias could stem from the fact that, as in Study 1, not all the possible confounds were accounted for (see section 2.5). Another limitation can stem from the fact the task demanded to compare two very different things (calories and risk of contamination) and there it is not clear as to what would be the strategy employed to calculate the optimal outcome. One option would be to calculate the expected value (EV, Von Neumann and Morgenstern, 1945), multiplying the calories and the probability of obtaining them (that is, 1 - the probability of the item being contaminated). However, it is not clear how the negative consequence of eating contaminated food could be computed, and this is clearly a limitation in the design. Another limitation is that I used only one framing option. Future studies could investigate whether different framing scenarios could influence the task. One interesting option would be to contrast the risk of contamination framing with a simple mathematical game with probabilities to win food items. The difference in how probabilities are treated in the two cases can provide interesting insights in how the brain handles risk and reward in two very different context and determine what is specific about the perception of food safety.

Taken together, these results confirm that risk of contamination is highly averse: the higher the risk, the more it is considered akin to personal harm (lPC). When the choice involves foods with different caloric density, however, things get more complex. The type of food and arguably its history of positive reinforcement can partially counteract the negative effect of risk, making certain foods look more attractive and therefore perceived as less risky (rAI), hence lowering the cognitive load of the choice (pre-SMA). In this case, the difference between the two foods could be perceived as more salient and risk playing a larger role in discarding the item with lower CD (Dorsal Striatum).

4. *Accumulating information of calorie, hunger, and preference to make food choices*[1]

4.1 Abstract

Decision-making theories have long explained decisions as based on perfectly rational value assignment, the decision strategy of the *homo economicus*. However, decisions based on affectively relevant stimuli, such as food items, hardly follow strictly rational heuristics. Being hungry, the food's caloric content and subjective preferences are known factors to modulate food choices. Yet, how these factors relatively and altogether contribute to the food choice process is still rather unknown. Here, we ask 16 healthy young adults to choose among 800 food image pairs when satiated or hungry. The food items belonged to a low or high-calorie density (CD) subgroups and their preference was assessed

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[1] A version of this chapter is under review in *Cognitive Science*: Garlasco P., Parma V. & Rumiati R.I. Hunger, calories and food preference predict food choice: a computational model.

for each participant. To simultaneously link the hunger state, the CD of the food and their preference to the probability of subsequently choosing each item, we applied a novel computational model, the hierarchical drift diffusion model (HDDM). Results indicated that hunger, preference and calorie all affected the speed of the food choice. The choice was faster towards low CD foods when participants were fed and the food items were highly preferred. Conversely, the choice was faster towards high CD foods when participants were hungry and the foods were less preferred. All in all, these findings confirm the complex nature of food choices and the need for nuanced computational models able to account for multifaceted decision-making and value assessment processes, such as those regarding food.

4.2 Introduction

Accounting for multiple decision factors and ruling out the non-relevant noisy information is argued to depend on a process called Bayesian Causal Inference (Rohe and Noppeney, 2015), which consists in an estimate of the probability of a cue based upon prior information and weighted by the current evidence. Choice models have often capitalized on a family of models called drift-diffusion models (DDM, Ratcliff (1978)). In a Bayesian framework, such models allow to quantify the speed of the decision process based on other factors, such as accuracy (e.g., Cavanagh et al., 2011; Vandekerckhove et al., 2011). The DDM models assume that the subject is accumulating evidence for each of two alternatives (i.e., two food items), until a threshold for a decision (i.e., food choice) is met. Compared to classical frequentist analyses, these models allow to quantify uncertainty based on the data and an informed prior distribution, instead of relying on a theoretical (usually Gaussian) one. Furthermore, they allow for the possibility to consider simultaneously, with different parameters, the speed of the accumulation of information (drift-rate, v) and the point at which the decision is made (threshold/boundary, a), a possible pre-existing bias towards one of the two options (bias, z) and also non-decision related components of the task (non-decision, t). Indeed, this approach favors the joint investigation of critical aspects of the choice, rather than separating them into different models (as the frequentist approach calls for).

A handful of studies has employed DDM to study specifically food choice.

Krajbich et al. (2010) presented participants with food snacks in a BFC and investigated how fixation patterns can contribute to the choice of one of them. Both first gaze direction and total fixation time speeded up the accumulation of information towards one of the two foods, contributing to the final food choice. These data were extended by Towal et al. (2013) who investigated whether and how bottom-up (perceptual salience) and top-down (subjective value) processes influence fixation patterns and food choice. Their results indicate that the fixation patterns modulate choice primarily in accordance with the food item value, but also based on perceptual salience, again confirming a complex interplay between bottom-up and top-down factors underlying even the most basic food choices. Furthermore, Mormann et al. (2010) consider whether limiting the decision time affects the way food items are chosen. They devised a paradigm where subjects chose among pairs of food items randomly assigned according to their subjective preference. Time constraints facilitated the choice of preferred foods but made the subjects make more errors, both elements captured by different model parameters. Still, when instructed to minimize their choice time (Mormann et al., 2011), participants are able to reliably choose preferred food items in BFC with a 73% accuracy in only 404ms on average, implying that food choice can be a quick and reliable decision process.

As evident by this short summary of the literature, the DDM approach on BFC has mostly considered one or two determinants of the decision at a time, failing to address the complex interplay among the determinants contributing to food choice which includes hunger, calories and food preference. Also, to our knowledge, most studies failed to use a clear-cut definition of calories, relying on either caloric density (CD) or fat content. Here, we aim to fill this gap by extending the investigation of the food choice information accumulation patterns to physiological, i.e., hunger and calorie (CD), and subjective, i.e., preference, experiences.

To assess the effect of hunger, calories and food preference on food choice, we employ a series of DDM: one complete model (hunger x preference) and two main effect models (hunger only and preference only). To assess simultaneously the role of hunger and calorie in food choice, we evaluated whether participants chose high and low calorie food in function of their hunger state (hungry/fed) and controlling for preference (high/low). We hypothesized that hunger would affect the boundary position (a), by moving it closer to the starting point of the drift when the subjects are hungry compared to satiated. This would mean reducing the amount of information necessary to make the choice when hungry as compared to when satiated. On the other hand, preference would influence the bias term of the model (z), indicating whether participants tend spontaneously to choose low- or high- calorie foods. We expected participants to choose more rapidly low calorie foods when fed, as found in other studies run in industrialized countries (Charbonnier et al., 2015). At last, we expected the calorie content to influence the speed of information accumulation (i.e, the drift rate, v) in function of hunger. In other words, we expected the drift rate to be greater when participants are hungry then when they are fed. As a control check, we did not expect the non decision parameter t to be any different between the models.

4.3 Materials & Methods

4.3.1 Participants

Participants were recruited through internet advertising. Prior to testing, they all provided written informed consent and were informed that they could discontinue the study at any time. Sixteen healthy (8F; Age: 24.53, SD = 2.85), right-handed, normal weight (BMI: 22.07, SD = 2.44), with normal or corrected-to-normal vision and no eating disorder (assessed through the Eating Disorder Inventory, EDI-3, Garner, 2004) Italian native-speakers participated in two experimental sessions at the same hour but three days apart from each other. Participants were omnivorous and had no dietary restriction. They were all normal weight (BMI, 22.07, SD = 2.44) and unrestrained eaters, according to the Restraint Scale questionnaires scores (RS, mean = 11.07, SD = 5.09, restrainers > 15; Polivy et al., 1988; Nederkoorn et al., 2004). They also exhibited regular sleep patterns and were not sleep deprived. This was assessed using the Pittsburgh Sleeping Quality Index (PSQI, 10.69, SD = 3.13, Buysse et al., 1989; in its validated Italian version, Curcio et al., 2013). Participants had to fast (only water allowed) for the 12 hours before coming to the laboratory. This was done in order for them to be hungry. Fasting time in the literature ranges from 3hrs (Frank et al., 2010) to 18hrs (Siep et al., 2009), with behavioral effects emerging already at its lowest end (i.e., 3hrs). In one session ("hungry" condition) participants had to perform the task without eating, while in the other ("fed" condition) they were offered cereal bars to eat up to satiety before performing the task. They were compensated with €8 per session, €16 in total. Table 4.1 summarizes the sample features. One participant (ID 2) was removed from final analyses given that her responses were on average of 0.6s and could not be deemed accurate.

Participants' information					
	Age	Education	BMI	PSQI	RS
mean	24.53	17.6	22.07	10.67	11.07
median	24	18	22.78	10	10
SD	2.85	1.35	2.44	3.13	5.09

Table 4.1: Participants' demographic and questionnaires' score. BMI = body mass index; PSQI = Pittsburgh Sleep Quality Index; RS, Restraint Scale.

4.3.2 Stimuli

Forty images were selected from a validated database (FRIDa, Foroni et al., 2013). Stimuli were divided in two groups of interest based on their caloric density/100g: twenty of them were low CD (range from 0 to 150 Kcal/100g) and twenty were high CD (range from 300 to 450 Kcal/100g). Within these two groups, ten images were salty and ten were sweet, to account for any sweet tooth or savory preferences, in line with other studies (Mormann et al., 2010, see Table 4.2). Stimuli were matched for variables of interest such as arousal, typicality, familiarity and valence (Foroni et al., 2013).

The use of food pictures instead of actual foods is well supported in the literature. Kringelbach and Rolls (2004) argued that OFC neurons respond more strongly to the visual modality of foods, while Simmons et al. (2005) found that food pictures, similarly to real food, activate areas of the primary gustatory cortex (Right Insula) and areas implicated in reward such as the lateral OFC.

	Low CD	**High CD**
Salty		
Sweet		

Table 4.2: Examples of the stimuli used.

In order to compare high CD vs. low CD foods, food images were paired into four different conditions: condition 1 had stimuli of high vs. high (200 trials), condition 2 stimuli of low vs. low (200 trials), condition 3 and 4 had stimuli with high vs. low and low vs. high (400 trials). The total number of trials per each session, 800, was in line with previous studies (Mormann et al., 2010), and was meant to provide enough data points for the DDM to converge. Stimuli presented were randomly paired using these conditions.

4.3.3 Task procedure

As already mentioned, participants were asked to come to the lab at a predetermined time (either 8:30, 9:30 or 10:30 in the morning). Before they began the experiment, they were offered water and cereal snack bars in the "fed" and water only in the "hungry" condition. The order of the "hungry" and "fed" conditions was counterbalanced across participants. Eventually, they had to fill questionnaires on sleeping habits (PSQI) as well as rate their hunger, thirst and tiredness on a 10-point visual analog scale (VAS). The ratings confirmed that our manipulation between sessions was effective (hunger, $p < 0.05$; thirst, $p = 0.58$, tiredness, $p = 0.25$).

After this, participants performed the BFC task sitting in front of a computer. Stimuli were presented on a LCD screen (60 Hz) located approximately 80cm from the participant using PsychoPy2 (Peirce, 2007)

The task was a food BFC, whereby they were shown pairs of food images and they had to pick the one they preferred (see Figure 4.1) pressing either the "z" key for left food or the "m" for right food (this was done to allow enough physical space between the two keys). Before each trial, participants had to fixate a cross for a random interval between 1 and 2 seconds. Participants had a maximum of 3 seconds to make their choices, more than enough as shown by published literature (e.g., Mormann et al., 2010). After this amount of time was elapsed without a key press, the response was considered null. Reaction times were measured as the time difference between the onset of the images and the button press. The task lasted approximately 40 minutes, with three breaks in between.

After the task, participants were asked to rate the food images according to their preference and frequency of consumption. Eventually, they completed the other questionnaires, EDI-3 (Garner, 2004) and Restraint Scale (RS, Ruderman (1983)). Total time of a session was around 1h-1h15'.

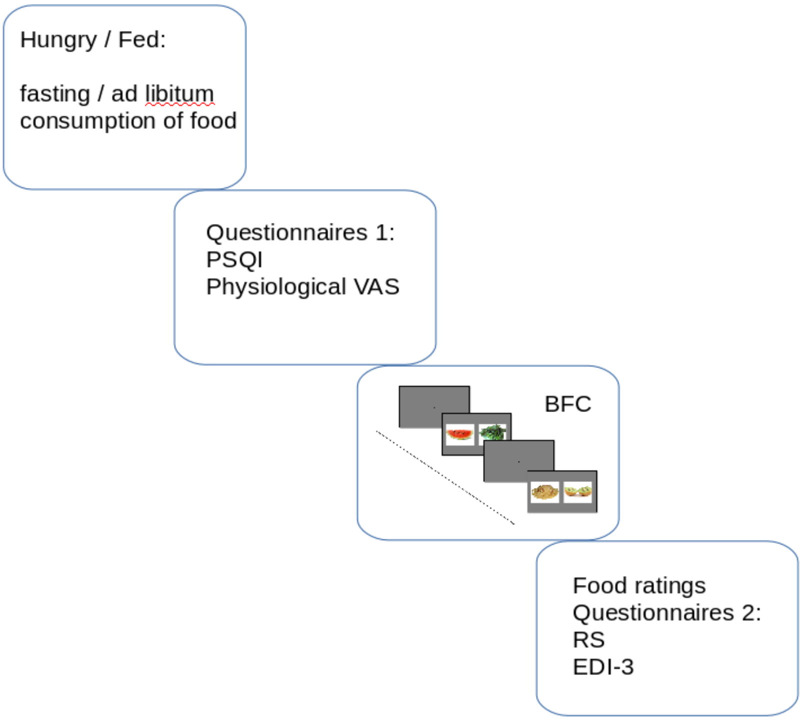

Figure 4.1: The timeline of the procedure of the experiment for each session (fasting/fed).

4.3.4 Data Analysis

4.3.4.1 Descriptives

We quantitatively inspected the BFC RTs distributions to assess whether any participant was either too slow or too fast to be considered reliable. As previously mentioned, one participant was excluded.

4.3.4.2 DDM Analysis

The analysis was performed using a modified Bayesian version of a drift-diffusion model: the Hierarchical Drift Diffusion Model (HDDM). A HDDM employs Bayesian estimation of the model parameters providing a quantification of the reliability of such parameters (Vandekerckhove et al., 2011). Hierarchical Bayesian estimation allows to constrain subject variability to a group-level distribution (Lee and Wagenmakers, 2014; Regenbogen et al., 2016).

Model fitting Data analysis was performed using the *hddm* module for Python3 (Wiecki et al., 2013). In the models, we assumed that the slope of the drift increased linearly with the difference in hunger and preference between the two to-be-chosen food items. The upper boundary represented here high CD foods, while the lower boundary represented low CD foods. A negative average drift (drift-rate) would therefore indicate a higher number of choices for low CD food items, while a positive one just the opposite. The bias, instead, indicated the starting distance from each of the two boundaries. In order to obtain a 2x2 design we split preference ratings into Low Preference (ratings from 1 to 4) and High Preference (ratings from 6 to 10). Hence, we estimated the model a-posteriori distribution of the parameteres by using Monte-Carlo Markov Chain simulation (MCMC) with gradient ascent optimization, drawing 10000 samples and burning the first 1000 to stabilize the model (Regenbogen et al., 2016). To allow for convergence analyses, we repeated the simulations 5 times per model (Wiecki et al., 2013).

Model convergence Convergence of the models was inspected both visually and numerically. We plotted the trace of the models, the auto-correlation and the mean and distribution of the boundary, drift-rate, bias and non-decision time (movement) parameters. A numerical estimate of the convergence used the Gelman-Rubin $\hat{\mathrm{R}}$ statistic (Gelman and Rubin, 1992), with values close to 1 indicating a small difference among the estimates of the different distribution of samples, an index of the reliability of the simulations.

Model testing and comparison In order to assess the reliability in the difference of the parameter estimates, we calculated the difference in mean probabilities of the posterior estimates of the conditions of interest (as done in Cavanagh et al., 2011; Wiecki et al., 2013). Moreover, null hypothesis significant testing was performed with a rmANOVA with two within-factors (Hunger and Preference) and two levels (High and Low). In case of significance, unplanned bonferroni-corrected post-hoc tests were performed accordingly (as in Regenbogen et al., 2016). Model comparison using the DIC (Deviance Information Criterion, particularly suited for hierarchical models: Spiegelhalter et al., 2002) allowed us to compare models including different parameters (e.g., only hunger vs. hunger & preference), holding into account the complexity of the model itself as a penalizing factor. With this criterion, lower values indicate a better fit of the model.Importantly, the values of DIC make sense only relative to each other, so there is meaningless to compare them with DICs from other studies (Gelman et al., 2014; Spiegelhalter et al., 2002).

4.4 Results

4.4.1 Descriptives

The distribution of RT was not normal and right-skewed, as expected, with an overall $mean$ of $0.76s$ and a SD of 0.28 (Kolmorov-Smirnov test, $D = 0.65, p < 0.001$).

Since the preference ratings were fundamental in our design, we evaluated whether hunger changed the rated preference across sessions. Such difference was not significant (Hungry vs. Fed, $p = 0.13$, Wilcoxon signed-rank test), allowing us to safely use the ratings of each respective session in estimating our models.

4.4.2 HDDM

4.4.2.1 Model convergence and comparison

Overall, our models converged satisfactorily. As you can see in Figure 4.2, the auto-correlation of the last hundred trials was close to zero, as you can expect from a Markov-Chain that has converged (Wiecki et al., 2013). This means that the samples are independent draws from the posterior. On the upper left panel, the trace is plotted as a function of the number of iterations. As you can see, the iterations do not stray too far away from the mean of the distribution (which is the point of highest probability of the posterior). The histogram on the right confirms this.

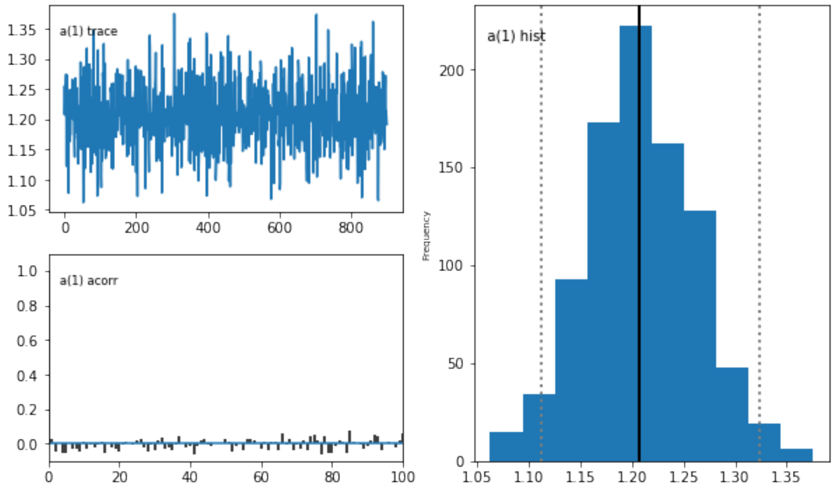

Figure 4.2: Convergence plots for a representative node of the model. On the top left you can see the trace plot, on the bottom left the auto-correlation while on the right the histogram of the estimates.

Moreover, the Gelman-Rubin statistics ($\hat{\mathrm{R}}$) for our models was mostly close to 1, ($mean = 1.0002, SD = 0.0004$, for a total of 164 nodes per model) allowing to infer that different simulations of the same model obtained similar results, which is considered an index of robustness of the estimation itself. Overall, estimated non-decision time (parameter t) lasted approximately 0.42s. This is consistent with our data suggesting that given an average RT of 0.55s, the participants took approximately 0.1s to decide on most images what to choose.

Model comparison included all the three models we run (preference*hunger, preference, hunger). As reported in Table 4.3, the model with preference*hunger was the most reliable model (22710.46), whereas the hunger model was the one with the highest DIC and thus the least reliable (25078.55). Given the lower score of the all factor model, we decided to rely on it to decide in case of incongruities between different models.

Models' DIC	
Model	DIC
preference*hunger	**22710.46**
preference	24029.13
hunger	25078.55

Table 4.3: DIC values for our three HDDM. Lowest values represent a better fit. preference*hunger = model with hunger and preference; preference = model with preference; hunger = model with hunger.

4.4.2.2 Model results

Boundary Contrary to our expectations, the effect of hunger, preference or both factors together on the boundary parameter was close to chance level ($50 - 52\%$, see Table 4.4). A rmANOVA with the two within-factors (Hunger and Preference) and two levels (High and Low) was not significant ($F = 1.06$, $p = 0.36$). Therefore, the decision threshold for the high and low CD food can be considered equidistant.

preference*hunger model boundary results		
	Contrast	Probability
Preference	P(Fed - High Pref > Fed - Low Pref)	51%
	P(Hungry - Low Pref > Hungry - High Pref)	52%
Hunger	P(Hungry - Low Pref > Fed - Low Pref)	51%
	P(Fed - High Pref > Hungry - High Pref)	52%
Interactions	P(Hungry - Low Pref > Fed - High Pref)	51%
	P(Fed - Low Pref > Hungry - High Pref)	51%

Table 4.4: preference*hunger model. Probability difference of posterior estimates for boundary (a)

Drift-rate We found a main effect of hunger on the drift-rate. As it can be seen in Figure 4.3a, participants chose more low CD foods and were overall faster in choosing them when fed as compared to when they were hungry, as it evident from the more negative drift for the fed session (95%). Even preference alone had an effect on the drift-rate, as displayed in Figure 4.3b. Low CD food items seemed to be chosen faster when they were highly preferred (more negative drift), while more slowly when they were less preferred (79%). Including preference*hunger (preference*hunger model), we could find both main effects of hunger and preference, as well as their interaction (Table 4.5, Figure 4.3c). A rmANOVA with the two within-factors (Hunger and Preference) and two levels (High and Low) was in fact significant ($F = 1240.75$, $p < 0.001$). All six post-hoc tests were significant and survived the multiple comparison correction ($p < 0.01$ Bonferroni corrected). As you can see, different sessions seemed to impact on the speed of information processing as well as on the direction of the choice. Decisions taken when fed were overall faster towards low CD foods with a high probability, 98% and 80%, for high and low preference respectively. Interestingly a different pattern was observed when hungry. In this session, participants choose overall more high CD items when they had a low preference (70%), while high preferred items tended to move the decision towards low CD (79%). Interestingly, the interaction between hunger and preference (98%) sped up the accumulation of information in different directions. Towards low CD foods with high preference and being fed and towards high CD foods with low preference and being hungry.

Bias No bias was retrieved in either model (Figure 4.4).

preference*hunger model drift-rate results		
	Contrast	Probability
Preference	P(Fed - Low Pref > Fed - High Pref)	86%
	P(Hungry - Low Pref > Hungry - High Pref)	80%
Hunger	P(Hungry - Low Pref > Fed - Low Pref)	83%
	P(Hungry - High Pref > Fed - High Pref)	88%
Interactions	P(Hungry - Low Pref > Fed - High Pref)	98%
	P(Hungry - High Pref > Fed - Low Pref)	54%
Sign	P(Fed - Low Pref < 0)	80%
	P(Fed - High Pref < 0)	98%
	P(Hungry - Low Pref > 0)	70%
	P(Hungry - High Pref < 0)	79%

Table 4.5: preference*hunger model. Probability difference of posterior estimates for drift-rate (v)

4.5 Discussion

Food choice is a complex decision that requires the assessment of conflicting information (Rangel, 2013). In this study we aimed to investigate food choice by addressing the interplay of physiological, affective and cognitive factors. By using a DDM approach, we assessed how hunger, calorie content and preference shape the accumulation of information patterns in food choice. Having participants fast for 12 hours successfully induced a state of hunger evident in the subjective ratings and the speed of accumulation of information to reach the choice. Conversely, subjective preference for the food items was not modulated by the hunger state.

The results reported here show that choosing high CD or low CD food is equally probable, given that the boundary is equidistant from the starting point and that there is no previous bias towards either choice. The analy-

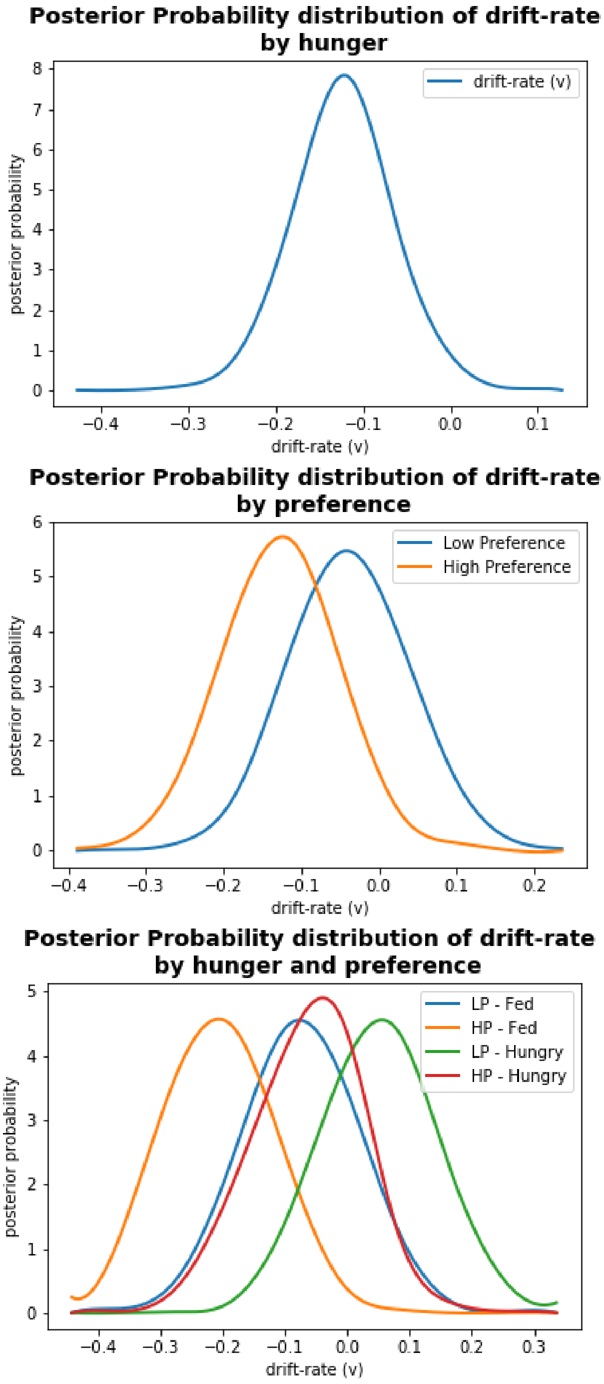

Figure 4.3: Posterior probability distribution of the drift-rate parameters (v). a: preference*hunger model with hunger x preference. b: Main effect model of preference. c: Main effect model of hunger. LP = Low Preference; HP = High Preference.

sis of the posterior parameter distributions of the drift-rates instead showed significant differences in the speed of the decision process. In other words, as evident by the preference*hunger model, the speed was higher towards low CD

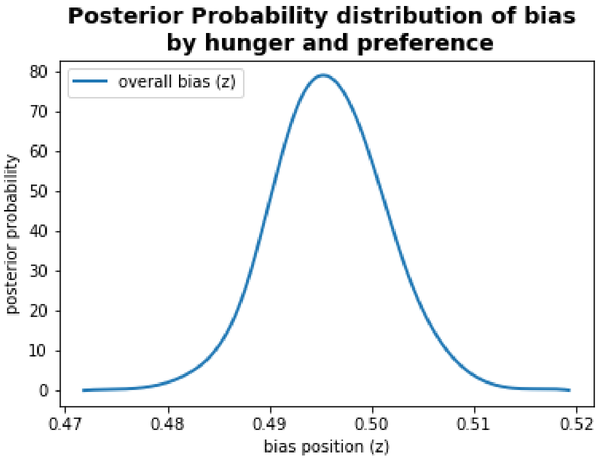

Figure 4.4: Posterior probability distribution of the bias parameter depending on CD for the preference*hunger model (z).

foods when participants were fed and the items were highly preferred, while it was higher towards high CD foods when participants were hungry and the foods were less preferred. This supports the assumption that low CD preferred foods accumulated evidence for the food choice in a faster manner when fed. Whereas, when hungry, accumulation of information was faster for high CD, non preferred foods.

Here, we demonstrate for the first time that there is a complex interplay of factors in food choice with effects going in different directions - i.e., hunger, caloric content and preference - which the HDDM approach allows us to disentangle and to point to specific aspects of the decision process.

In line with Charbonnier et al. (2015), our participants chose more often low CD than high CD foods. The authors hypothesized that this was owed to the fed state of their participants, which we confirm here by looking at the differences in the accumulation of information patterns for low CD and high CD foods when fed but not when hungry. Considering that there was no initial bias towards either food category based on CD, it can be argued that the physiological state of hunger is responsible for this food choice pattern. At the neural level, as suggested by Siep et al. (2009), these different patterns of accumulation of information may be underlined by a greater activation in the right insula and medial orbitofrontal and ventromedial pre-frontal cortex for high CD foods when hungry. This would be in line with the role of orbitofrontal cortex in representing value-based decision alternatives, as previously contended (see Levy and Glimcher, 2011). An attempt to all together consider hunger, preference and calorie can be found in the work by Finlayson et al. (2007), who used food fat content as a proxy for CD. One of their main results is that hunger unbalanced the choices of participants towards highly fat foods (which can be equated to the high CD food items in our design). On the other hand, while being satiated they were driven towards their preferred food irrespective of calories. In contrast with their results, in our study, hunger did not seem to affect our preference ratings. In spite of this, in our sample the analysis of the posterior drift-rates let emerge an effect of preference on the choice of low and high CD foods. This discrepancy in the subjective ratings may be due to a methodological reason. When controlling for arousal, typicality, familiarity and valence of the food images, the preference range may be constrained, therefore reducing variability irrespective of hunger states (Foroni et al., 2013). Furthermore, in line with Bielser et al. (2016), our data suggest that liked foods tend to be chosen more often than non-liked food, even though such pattern is not extremely skewed, due to a general preference for the the food items presented. Such intuitive result confirms that liked items require lower decision times (Kahnt et al., 2014), even when the choice is forced among two alternatives (Bielser et al., 2016).

All in all, the present findings extend the investigation of food choice which has been mostly addressed via the analysis of self-report questionnaires or behaviorally via frequentist statistical approaches which allow only for the evaluation of one relevant factor at a time. Conversely, applying a computational HDDM approach by simultaneously considering the effect of hunger, preference and calorie on food choice, allows us to overcome this shortcoming. Our results show that the food choice process deviates from the *homo economicus* assumptions, in allowing the choice not to be uniquely determined by fixed - i.e., exogenous - preferences but demonstrating that the real food choices are malleable to changes in physiological and subjective states. Hereby we contend that this approach is a strong candidate for the assessment of the complexities of food choice, contributing to a nuanced view of value-based decision in a unified framework (see Krajbich et al., 2015). The importance of being able to experimentally model nuanced food value-based decisions seems to be reflected at the neural level by greater activation in a network of regions known to process salience-related information and cognitive control processes (Menon and Uddin, 2010; Mitchell, 2011), including the insula, the dorsolateral pre-frontal cortex, and the ventromedial pre-frontal cortex.

One might argue that the data are based on fictional food choices since they were only mediated by food items that people visually inspected but were never able to eat. If on the one hand this represents a limitation of the current study, it extends a flourishing literature demonstrating that visual features maximally contribute to ecological food choices (see Foroni et al., 2013, 2016; Levy and Glimcher, 2011). On the other hand a future extension of the present work would consider the use of real food choices would significantly modulate the accumulation of information patterns hereby found.

To conclude, I showed that food choices are complex decision processes that require the assessment of conflicting information, including one's hunger state, the calories of the food item and the subjective preference for those items. Furthermore, by capitalizing on the HDDM approach, this work sheds light on how to nuanced computation models represent the next frontiers in understanding multifaceted decision-making and value assessment processes, such as those regarding food. The present work is to be included among the efforts toward simultaneously understanding the computational basis of decision-making in the context of the systems that serve as homeostatic regulators of feeding (Rangel, 2013). Given the complexity of the phenomenon, I believe that this approach can help understand the contribution of factors not considered in this study, such as socio-economical ones, food attitudes, pathological behaviors towards food (e.g., obesity and anorexia) and sensory features of foods.

5. *General Discussion*

In this thesis I aimed to present you a template for the investigation of food choice employing a set of different techniques, namely behavioral, computational and neuroimaging analyses. Food choice is in fact a complex, multifactorial, phenomenon and, to be studied, it needs to be broken down into its main components, to investigate their interaction in different contexts. After I introduced you to its main dimensions (physiology, affect and cognition), I guided you through a set of studies aimed at investigating each of these dimensions as well as how they interact, to deepen our understanding of how food choice are made.

In order to achieve the main goal, I tried to convey the idea that it is possible to study food choice in an experimental setting without extremely sacrificing its ecological and contextual validity. This has been done by trying, on the one hand, to harness the ideas and concepts of decision-making research in neuroscience (Levy and Glimcher, 2011) and experimental psychology (Köster, 2003). This included a paradigm, BFC, which represents a good compromise between ecology and rigor, alongside more control on confounding variables and the stimuli employed, through the use of databases. On the other hand, this has been done by focusing on the specific dimensions of food choice (physiology, affect and cognition) studied in the vast, sometimes qualitative, research of food choice in ecological contexts of consumer research (Grunert, 2002).

In **chapter 2** I showed that even with a theoretically simple physiological variable such as calories, there are cognitive aspects that can change the way they are understood altering choice behavior. As already pointed out, calories represent a very important feature of food, as they provide nutrients for our brains and bodies. However, many studies in the literature do not seem to distinguish between two important ways of counting calories, and therefore energy intake. One is a relative way and relies on the type of food (calories x quantity), that we called caloric density (CD), the other one is absolute and counts the total number of calories in a given portion of food, and we called it caloric content (CC). In the BFC task, participants chose foods that were combined along these two dimensions. As they were instructed to maximize the calories, if they were to act according to some sort of utility maximization principle (as the *homo economicus* would predict) they would try to maximize CC, as this value represents the total calories they could get. However, this was not the case, as participants chose mostly relying on CD. This pointed to a possible bias in understanding how calorie are counted, as participants would rely on the type of food to evaluate how many calories they have in front of them, making how big is the portion secondary. This is a relevant point, since relying on the relative number of calories of the food has been shown to produce biased estimates of portion and meal size. As argued in **chapter 2**, this has been shown to cause significant overeating, mostly without peoples' awareness (Rolls et al., 2002, 2004b,a; Diliberti et al., 2004).

After focusing on a powerful motivational factor in driving food choice and consumption, namely calories, and how this is cognitively interpreted, I wanted to investigate how a powerful motivational factor in controlling intake, namely food safety, would impact food choice. In **chapter 3** I investigated how the risk of a food being contaminated would affect the participants' food choices between two options. Building on the design of Study 1, I devised a BFC which included food images with different CC and CD as well varying probabilities of contamination (from 0% to 100%). Here, the task was to maximize calories while minimizing risk. I expected participants to try to avoid poisoned food as much as possible, that is choosing the lowest risk. Such goal may be achieved by implementing a *minimax* strategy (Von Neumann, 1959). However, I doubted that participants would rely only on this conservative and rational behavior and still choose more caloric items than you would expect given this strategy. The results showed that this was the case. In fact the effect of risk was partially diminished but, in line with Study 1, by relying on CD, and not on CC. That is, the type of food seemed to make a difference in driving the choice, while the total number of calories did not, which is what you might have expected if participants had simply calculated the number of calories they needed, pointing to a different mechanism. The fMRI results supported this idea, with the deactivation of the rAI and activation of pre-SMA in diffCD compared to diffCC and Control, respectively, highlighted differences in the demands of the task as well as the role of risk.

After having found that there is an interplay between cognitive and affective components, I decided to test how a physiological component might impact on the affective dimension. In **chapter 4**, I investigated whether hunger would impact choice of food items based on preference. As the food images chosen for the BFC varied along the CD dimension, I expected calories to impact on preference as well. The results showed that hunger impacted choice patterns significantly. As our HDDM results show, while hungry, participants tended to focus more on the items' CD, with the accumulation of information for the high CD choice being faster for less preferred items. On the other hand, while satiated, participants seemed to rely more on preference, as the information accumulated more rapidly towards the more preferred and low CD food items.

5.1 Food choice in the lab (revised)

Food choice, as thoroughly explained in this work, is a complex and context-dependent phenomenon. This seems at odds with studying it in a very controlled environment such as a laboratory. While I agree in principle with this remark, I still think most of the elements of food choice can be studied in a laboratory with proper care. Although it is arguably very difficult to reproduce the context of a meal at home or food shopping in a supermarket[1], we can approximate some of the features of the decision process that actually take place in these context while, at the same time, taking advantage of the control that a laboratory setting allows in order to reduce the noise in favor of

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[1] One example in this direction exists, i.e. the “Restaurant of the Future” in Wageningen University, but indeed represents a *unicum* in the food choice line of research.

the signal. For instance, my participants had to choose among food pictures instead of real food. While it is not the same, lacking the smell and texture, many studies have shown that primate and human food selection relies mostly on vision (Laska et al., 2007; Linné et al., 2002), and that the sight of food can elicit a wide range of physiological, cognitive and emotional responses that are related to food consumption (van der Laan et al., 2011). So, I would argue, as long as it is food choice and not food intake that it is investigated, using pictures represents an acceptable solution.

Employing a BFC can face similar criticisms. One might argue, in fact, that everyday choices are seldom, if ever, binary. The typical choice among different food items in a supermarket scaffolding is a representative example. The same goes, in most cases, for a menu in a restaurant. However, real-world equivalents of BFC are present and often encountered. Think, for instance, about having lunch in a canteen. Here choices can be binary (e.g., pasta vs. rice, chicken vs. frittata) and hunger does have an impact. If you compare the same person on different days, on the first being hungry while on the second not, there you have a real world scenario which is not too dissimilar from study presented in **chapter 4**. However, the limitations of a BFC should be acknowledged, and in fact it would be interesting to replicate and extend the studies here to multiple forced-choice paradigms (simulating a choice from a restaurant menu, for instance). There are already studies that extend the DDM approach to multiple choice tasks (Krajbich and Rangel, 2011; Towal et al., 2013). Interestingly, one of their conclusions is that, although the effect is smaller, it is likely that the same computational model that works for binary choices can extend to ternary and other simple purchasing decisions (Krajbich et al., 2012). However, these studies still face the same limitations of previous works in the same line (the aforementioned poor control of food-specific variables). Nonetheless, this is a promising line of research, and the constant improvement of computational modeling (Wiecki et al., 2013) offers hope to make tasks more "manageable", such as, for instance, reducing the number of trials needed for the model to converge[2].

5.2 Calories do matter

Among other relevant variables in food choice that one could have focused on (e.g., price, availability, color, etc...), we chose calories. Why? As pointed out in the introduction, calories provide the fuel that our brains and bodies require to function. The need to metabolize a lot of calories in a reliable and efficient way is one of the goals that have shaped the evolution of our digestive apparatus (Wrangham, 2009). However, one might question why focusing on calories and not on more specific variables. After all, we do not seem to spend much time consciously monitoring our energy intake, relying mostly on non-conscious feeding mechanisms, such as hormonal regulation (e.g., ghrelin, Wren et al., 2001) to guide our eating behavior. Moreover, although different nutrients seem to have a differential impact on motivational aspects of eating (e.g., craving for sugars but not for proteins), we did not investigate the effects of *macronutrients* such as proteins, fats or carbohydrates in influencing food

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[2] Which, right now, is fairly high, as seen in **chapter 4**, and poses serious limitation in extending DDM to, for instance, fMRI.

choice. Is the relative balance of macronutrients important for food choice? If so, does it overshadow the role of calorie tracking?

This question is not new and, for what concerns weight management, the answer would seem to be: not much. In their widely cited study, Kinsell et al. (1964) had their obese patients undergo the same liquid-formula diet totaling the same number of calories but with widely varying macronutrient compositions (fat from 12 to 83 %, protein from 14 to 36% and carbohydrates from 3 to 64 %). Their results showed that all obese patients lost weight at a constant rate, no matter the relative composition of the diet. What matters, it seemed, was just the number of calories. A 2001 review of several types of diets, found that calorie balance was a major determinant of weight loss, and that all diets were effective, regardless of their composition, provided they restricted calorie intake to max 1500 per day (Freedman et al., 2001). A more recent year-long clinical trial conducted by Gardner et al. (2007) comparing different low-fat, high-fat and low-carbohydrate diets in roughly 300 overweight women found the high fat diet more effective. However, the researchers note that the difference was highest after six months and progressively reduced and it would have likely waned if the study lasted longer. What these studies seem to point out is that:

> The source of the calories may make a small difference in weight maintenance or loss, but it appears to be much less important than the ability to resist pressures to overeat calories in general.(Nesheim and Nestle, 2012, p.172).

This reasoning goes into the same line as recent policies that try to address the problem by actually acting on the calorie-rich environment in which we live, on the one hand by increasing general awareness of calories with compulsory calorie labeling [3], on the other by pressuring the food industry into reducing portion sizes [4] which, as we have seen in **chapter 2**, often influence calorie estimation on a par with the type of food itself.

5.3 Bayes in the plate. New approaches to study food choices

Analogously to what is happening to the study of decision-making, it is probably time to study food choice more rigorously. The development of quantitative and computational models in cognitive neuroscience has reached the stage where they can be successfully applied to more complex and multifarious phenomena than what they used to in the beginning (i.e., memory retrieval or perceptual decision-making for the DDMs, Heekeren et al. (2008); Ratcliff (1978)). The framework provided by Bayesian statistics, which provides estimates of the uncertainty of models, and Dynamic Causal Inference, allows modelling to take into account more than single factors of interest (such as calorie and hunger) but also more complex socio-economical and personal variables and investigate how these factors act together to shape the choice

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[3] Such as with the initiatives of the food and drug administration (FDA) in the US, which is trying to improve package labeling by requiring chain restaurants and vending machines to provide nutrient information about the food they offer (Food et al., 2014).

[4] This is what happened, for instance, in New York City, where mayor Michael Bloomsberg banned large sugary drinks for consumption (Grynbaum, 2012).

process. This can capitalize on DDMs or race models (such as Linear Ballistic Accumulators) in allowing to track how the accumulation of information in favor of one out two or more options unfolds, depending on variables that map psychological or neural processes. Interesting in this direction is the work by Krajbich and colleagues, who use DDMs alongside eye-tracking and neuroimaging data (Krajbich and Smith, 2015) to investigate the effects of attention and gaze fixation on food choice. Indeed neuroimaging data can be included into the computational model (see Wiecki's group work with EEG and deep-brain stimulation, DBS, Cavanagh et al., 2011), accounting for the variation and the process underlying it as it influences the outcome. I believe applying these methods to ask interesting and relevant questions about food choice and how the bran implements them is important, as the large availability of food in rich countries, the rising of obesity, climate and environmental concerns pose significant issues to our well-being and survival of our species.

5.4 Epilogue

All in all, the results of the studies presented here show that it is possible to study food choice tackling its different relevant dimensions and their interplay. This can be done by using a framework that allows different questions to be asked, while accounting for possible confounds and some limited sacrifice in terms of its ecological validity. I have tried to achieve this by using a carefully controlled task (BFC) and stimuli, alongside the use of a multitude of statistical (such as linear mixed models, drift-diffusion models) and technical (behavioral, neuroimaging) approaches.

To convey this message I focused my attention on a few relevant dimensions and their interplay. I believe the studies here managed to show that: a) calories matter, and that we consider them as a relative quantity, focusing mostly on the type of food (CD) with less regard to the total quantity (CC), which has implications in terms of how much we eat; b) food safety produces risk aversion, especially when it is framed in quantitative terms, but allows some room to evaluate calories in terms of their CD. The fMRI results show that the interplay of risk and CD seems to be tracked by the activity of the right anterior insula and the pre-SMA, suggesting that risk is processed and as a result of such elaboration, weights are assigned to different probabilities depending on CD. c) hunger (and lack thereof) influence choice by acting differently on either preference or calories, and this effect can be nicely captured by a computational model (HDDM) that tracks how the information is accumulated during the trial in favor of the different options.

Overall, the studies presented here provide a template to map a multi-factorial, complex and context-dependent phenomenon such as food choice. However, this is just a tiny step in the direction towards a more rigorous and ecological investigation of how we actually choose food on a daily basis. Given the stakes, though, I believe it is a good idea to walk this way.

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