
**Neuronal and behavioral correlates of the
influence of contextual cues on value-based
decision making**

- Die neuronalen und behavioralen Korrelate des
Einflusses von kontextuellen Reizen auf das wertebasierte
Entscheidungsverhalten -

Kumulative Arbeit

Inaugural-Dissertation
zur Erlangung der Doktorwürde (Dr. phil)
der Philosophischen Fakultät
der Rheinischen Friedrich-Wilhelms-Universität
zu Bonn

vorgelegt von
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aus Marl
Bonn 2017

Gedruckt mit der Genehmigung der Philosophischen Fakultät
der Rheinischen Friedrich-Wilhelms-Universität Bonn

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Tag der Mündlichen Prüfung: 22.02.2017

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"In any moment of decision the best thing you can do is the right thing, the next best thing is the wrong thing, and the worst thing you can do is nothing."

Theodore Roosevelt (1854 - 1919)

1 Summary

We make a myriad of decisions about goods or options that have different intrinsic values to us every single day of our lives. Choices guided by individual preferences are referred to as “value-based” decisions (Glimcher, 2014). Individuals can make value-based decisions between items in as little as 313 milliseconds (Mormann et al., 2011). If these decisions can be made in such a short time, one could deduce that the algorithm implemented by the brain to compare options and to reach a decision should be fairly simple and straightforward. However, the following chapters will prove otherwise.

In this thesis summary, the concept of value-based decision making will be introduced, including the current understanding of how the brain computes the subjective value of a choice option based on the available attribute space and then engages in a value comparison process. Dietary choices will be presented as a special case of value-based decision making, as feeding decisions are regulated by interacting subsystems, such as the hypothalamic-controlled homeostatic system (Rangel, 2013). It will be highlighted that attention plays a crucial role in the computation of a relative decision value (Krajbich et al., 2010, 2012). Notably, the computation and comparison of stimulus values in goal-directed decisions can be systematically biased if a decision maker fails to take into account relevant attributes (Fehr and Rangel, 2011). Thus, exogenous cues highlighting certain item attributes, such as health consequences, can positively bias choices towards decisions with longer-term benefits via attention (Hare et al., 2011a). I build on this assumption and analyzed how various contextual cues, including salient versus numeric nutrition, social sustainability, and child-directed labels, can affect the behavioral and neural valuation process, preferences, and the motivation to obtain an item.

There is a distinct tradition in the field of neuroeconomics to use computational modeling to better comprehend the computations made by the brain to reach a decision. Accordingly, a special focus of this thesis will be placed on the Drift Diffusion Model, which might be the optimal statistical solution for sequentially comparing the stochastic value signals of options (Bogacz et al., 2006; Fehr and Rangel, 2011; Rangel and Clithero, 2014). Further, Dynamic Causal Modeling will be intro-

duced as a particularly sophisticated Bayesian framework to understand causal connectivity (changes) between brain regions (Friston et al., 2003).

In the four main studies of my doctoral work, I demonstrate that exogenous cues can act as modulators of value. Specifically, I provide evidence that 1) salient vs. numeric nutrition labels alter the valuation of products. The neural mechanism when confronted with “red signaling” resembles the exertion of endogenous self-control. In 2), I analyzed the underlying computational mechanism by which health and taste attributes are integrated using Drift Diffusion Modeling. I provide evidence that taste preferences and health attributes are integrated into an overall value signal and refute the hypothesis that salient labels induce a choice bias irrespective of the item’s features. Further, salient labeling influences the attribute weighting: taste attributes receive less weight, while the sensitivity towards health features increases. I demonstrate that 3) social sustainability signaling increases the subjective value of options, with directed (causal) influence of regions implicated in reward and saliency processing on the ventromedial prefrontal cortex as assessed via Dynamic Causal Modeling. Moreover, I show that 4) child-directed, but not health-directed marketing cues increase subjective liking ratings as well as effort provision for food items of identical composition in children.

In addition to the four main studies, I have completed another study on dietary choice and taste preferences during my doctoral work. The manuscript stemming from this work is not published yet but mentioned due to its relevance to the overall topic of investigation. In the additional study, I show that the hypothalamic peptide oxytocin contributes to consumer decisions by modulating the experienced utility of identical food items. Further, two published review articles are presented due to their overall relevance to the thesis.

The main body of the summary text presented here puts the studies performed during my doctoral work into a broader context. The text is built upon and reviews work from various authors, such as Clithero and Rangel, 2014; Fehr and Rangel, 2011; Kable, 2014; Rangel et al., 2008 as well as Rangel, 2013. For a deeper context and understanding, readers are invited to more closely read the publications mentioned above.

Finally, the obtained study results are critically discussed and future research avenues are proposed.

2 Value-based decision making

Should I buy option A or option B? Should I invest money in a certain stock? Is this the morally correct solution? Is this dissertation any good? Should I eat the healthy apple or the tasty cake? These, or related questions, have to be solved daily by many individuals.

“Man is man because he is free to operate within the framework of his destiny. He is free to deliberate, to make decisions, and to choose between alternatives.” (Martin Luther King Jr., 1929 - 1968)

Although Martin Luther King Jr. based his axiom of being human on decision making, he probably considered decision making as trivial. However, little was known at this point about the neurobiological foundation how the brain deliberates and makes value-based decisions. Even nowadays, the decision process is not well understood and definitely not considered trivial by neuroscientists. Basic questions include: What is the computational code in the brain encoding the values of items in a choice set? How does a decision maker deliberate in order to identify the option with the highest value among various choice options? Why do some choices sometimes seem to be “random” (Glimcher, 2014; Rangel and Clithero, 2014; Rangel and Hare, 2010)? Can we positively influence behavior and well-being by altering the valuation process (Fehr and Rangel, 2011)?

Let us take a closer look at what *value-based decision making* means. According to a popular English dictionary, the words *decision making* refer to the *process* of making choices. Note that this implies that not only choice outcomes (I chose option B) but also the evolvment or formation of the choice is of interest (how I came to the decision to choose option B). *Value* denotes the importance or worth of something for someone, the amount of money that can be received for something, or how useful or important something is (McIntosh and Press, 2013; chain of reasoning based on Brosch and Sander, 2013). The definition clearly signifies that value is one of the most important concepts in human life, as most decisions involve the comparison between options, differing in their subjective value (Brosch and Sander, 2013). More

broadly, value-based decisions occur whenever an animal chooses between options based on the subjective value of the options under consideration (Rangel et al., 2008).

While the study of value and decision making by neurobiologists and psychologists is relatively new, economists have established various formal models and theories of choice behavior during the last centuries, with economic utility providing a principled theoretical construct (Glimcher, 2009). In the 17th century, Pascal and Fermat (1623-1662, edited (2005)) established the mathematical foundation for probability theory, suggesting that rational decision-makers should choose the option with the highest expected value, calculated as the sum of the probability-weighted reward magnitudes (Fox and Poldrack, 2009; Schultz, 2015). Mathematician Bernoulli (1738) proposed a subjective transformation of the objective expected value, which leads to a curvature in the utility function (rather than a linear function as proposed by Pascal). For example, Bernoulli's theory would suggest that 100 € are valued more by a poor person A, compared to person B, who is a millionaire. While Bernoulli assumed a certain form of the utility function, he did not propose certain rules that a decision-maker should fulfill to explicitly test choice behavior (Caplin and Glimcher, 2014). In contrast, expected utility theory (Neumann, 1944) provides axioms to directly test choice behavior. Whenever observable behavior fulfills certain axioms, the decision maker is said to maximize his/her utility. Further refinements of the theory were developed, such as prospect theory (Kahneman and Tversky, 1979, Rangel and Clithero, 2014). Economists (and more recently also neuroscientists) frequently consider utility as an internal metric (Schultz, 2015, 2016), and value as “a common currency that people use to compare different types of goods or experiences on the same scale when deciding between several options” (Brosch and Sander, 2013).

An option also entails certain “action costs”, which denote the “effort or unpleasantness associated with executing an action” (Rangel and Clithero, 2014). For example, an action cost would be the duration and energy requirement for foraging, or provision of effort in exchange for receiving a good. The *net* value is the *action cost* subtracted from the *stimulus value* (Clithero and Rangel, 2014). However, stimulus value computations have received much more attention in the literature compared to action costs. This is mostly because actions costs are often negligible or identical for all options under consideration in laboratory settings, for example, when the action cost to receive an item always entails pressing a lever (Clithero and Rangel,

2014; Rangel and Hare, 2010). I will only focus on stimulus values, in this text also referred to as “subjective values”, or “relative decision values” in case of comparisons between two or more options.

Simple choices involve decisions between a certain number of goods (very often two) with “informational symmetry” (Clithero and Rangel, 2014; Fehr and Rangel, 2011). A typical example is the choice between an apple and an orange (example taken from Clithero and Rangel, 2014). Although these choices do not seem to be earth shattering, they are important from a neuroeconomic perspective: they allow to study the computations and neuronal underpinnings of decisions without (at least at first sight) complicating factors. These choices are for these reasons considered a “test bed” for neuroeconomics, with the hope and assumption that more complex decision problems are solved in a very similar way (Fehr and Rangel, 2011; Rangel and Clithero, 2014). There is increasing evidence that the brain makes simple choices by first computing a subjective value of the considered options, and then comparing these values (Kable and Glimcher, 2009; Lim et al., 2011; Padoa-Schioppa and Assad, 2006; Rangel et al., 2008; Rangel and Hare, 2010), which will be elucidated in more detail in the following sections.

Consider the initial example of deciding between an apple and an orange. How does the probability of choosing an apple vary as a function of the value difference between the apple and the orange (Rangel and Clithero, 2014)? Psychometric functions have been primarily used in perceptual decision making to explore the threshold where stimulus detection becomes random, that is, stimulus detection and failure are equally likely. The x -axis denotes stimulus properties (such as intensity), and the y -axis denotes the proportion of correct responses, ranging from 0 (certain failure) to 1 (certain success, Wichmann and Hill, 2001). In decision making research, the psychometric choice curve can be used in a similar way: When considering the choice between two items, the probability of choosing the left item varies as a function of preference. More specifically, the x -axis denotes the value difference between the options (left minus right), and the y -axis denotes the probability of choosing left over right, ranging from 0 (certain right choice) to 1 (certain left choice). In case of one option, the x -axis denotes the value for the item under consideration, and the y -axis denotes the probability of choosing it (yes vs. no, Rangel and Clithero, 2014); in

the following, the focus will be on two-option-choices, which can be often easily extrapolated to one-option-choices.

Under perfect conditions, the brain could measure the subjective value of the options under consideration and make the “value-maximizing decision” by choosing the left item whenever the value of the left item is higher compared to the right item, and vice versa (Figure 1, red dashed line, Glimcher, 2014; Rangel and Clithero, 2014). However, behavioral evidence as well as theories show and postulate, respectively, that the choice process is stochastic, in that whenever two options have a similar subjective value, the less preferred option is sometimes chosen (Kable and Glimcher, 2009; McFadden, 1974). A large body of data has demonstrated that repeated choices between items varying in underlying subjective value generate a psychometric choice curve consistent with logistic choice models and similar to perceptual psychometric functions (Luce, 2005; McFadden, 1974; Rangel and Clithero, 2014), see Figure 1, blue line. Value-based decisions are stochastic, partly due to the noisy brain representation of the choice options (Enax et al., 2016; Glimcher, 2014; Krajbich et al., 2014). Assuming that value signals are computed “with identical and independently distributed Gaussian noise”, process models, such as the Drift Diffusion Model (DDM), would implement the “optimal statistical solution” (Rangel and Clithero, 2014), that is, sequential likelihood ratio tests for comparing the value signals at every instant t (Bogacz et al., 2006; Fehr and Rangel, 2011; Rangel and Clithero, 2014), see chapter 4.1 for details.

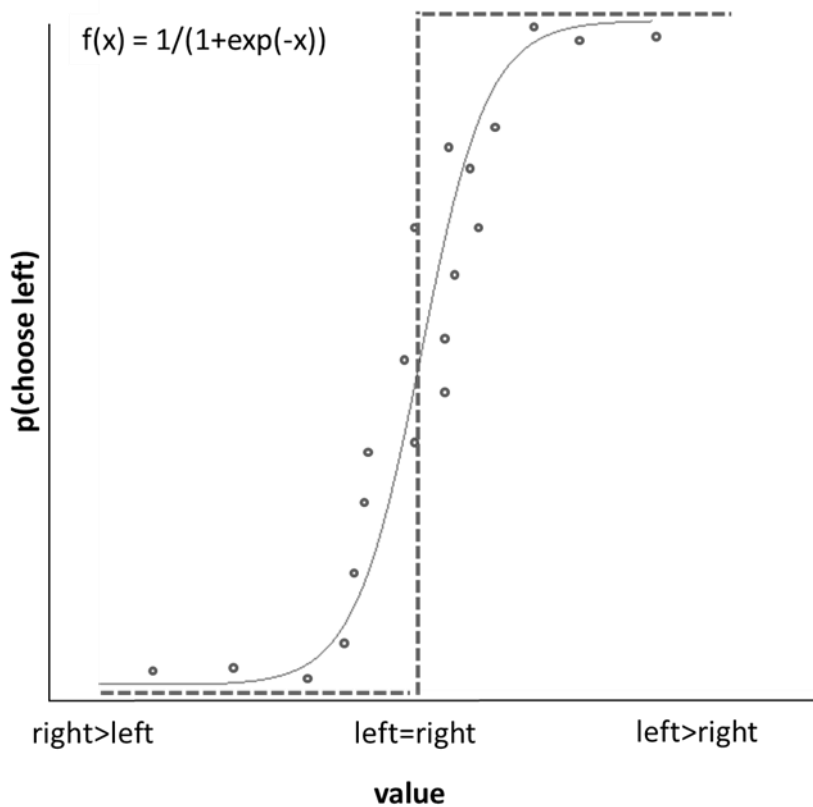


Figure 1: Psychometric choice curve for a choice situation where an individual repeatedly chooses between two options based on his/her underlying subjective values. The x-axis denotes the value difference between two choice options; the y-axis denotes the probability to choose the left item. Previous research has shown that empirical psychometric choice curves are consistent with a logistic regression model, blue line. For illustration, blue points denote individual choice trials between two options varying in their underlying subjective value difference. The dashed red line denotes a “perfect” decision maker, who always identifies the most valuable of the two options.

While classical economic research has traditionally only focused on choice outcomes, value-based decision making research has employed recordings of neural activity, eye movements, and/or reaction times (RTs) to model the process of decision making and underlying latent valuations (Krajbich et al., 2014). For instance, “the time it takes to make decisions” (*i.e.*, RTs) has been shown to be “an informative signal about peoples’ preferences” (Krajbich et al., 2014). In sum, researchers in the field of value-based decision making aim at providing a computational and neurobiological plausible account of the decision making process in order to better understand, or possibly even improve, behavior and well-being (Fehr and Rangel, 2011; Krajbich et al., 2014).

2.1 Framework for studying value-based decision making

Rangel and colleagues (2008) propose that, in general, the computations required for value-based decision making can be divided into five processes, see Figure 2. First, the decision problem representation is composed by identifying internal (*e.g.*, hunger) and external (*e.g.*, availability of food) states and determining potential actions. Secondly, values need to be assigned to the potential actions, depending on the individual's internal and external states. For example, the value of a food item is higher after a certain time of food deprivation (internal state). On the other hand, the value of consuming food may be lower when being chased by a predator (external state). The computed values are an individual's predictions of the benefits resulting from each option. Thirdly, based on the valuation process, a course of action has to be determined. After the decision, the outcomes following the chosen action need to be evaluated. This post-decision evaluation process is highly relevant, as it drives, fifthly, learning processes by updating the predictions that were previously assumed in order to improve decisions in the future. Importantly, this framework is of conceptual nature, and the rigidity of the five sub-processes need to be studied in more detail, for instance the overlap and differentiation between the processes of valuation and action selection (Rangel et al., 2008).

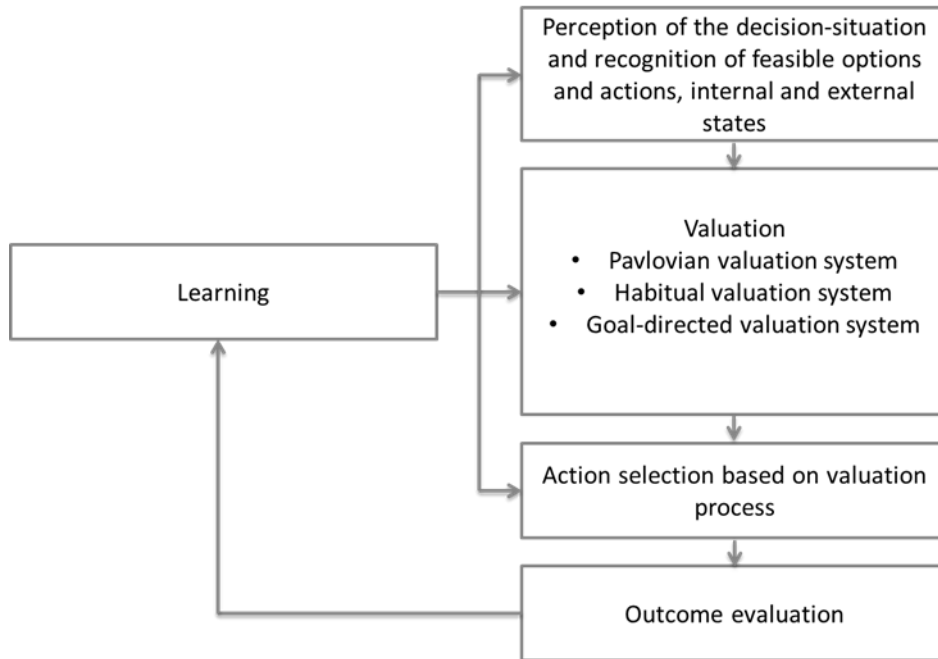


Figure 2: The computations that are thought to be made during decision-making. A decision problem has to be identified, and the actions under consideration need to be evaluated for action selection. After the decision was made, the brain needs to measure how desirable the resulting outcomes are in order drive learning processes and improve future decisions. Adapted from Rangel (2008).

2.2 Valuation systems

The valuation of options is a key component of the decision making process (Grabenhorst and Rolls, 2011). For appropriate decision making, “values have to be reliable predictors of the benefits that are likely to result from the action” (Rangel et al., 2008). Various lines of research propound that the valuation process may be controlled by three types of valuation systems, which differ in flexibility and learning capabilities, and are based on the psychological literature (see Figure 2; based on Rangel, 2008): (a) the relatively automatic (Pavlovian) system, which learns a relation between stimuli and outcomes and activates approach and withdrawal responses, (b) the habitual system, which learns the relation between stimuli and responses (but not outcomes), and (c) the goal-directed valuation system, which learns the relation between responses and outcomes. It is important to note that the existence of three distinct valuation systems is still hypothetical, and most probably oversimplified.

Their exact neural dissociation as well as their common elements are yet to be established (Bouton, 2007; Rangel et al., 2008).

The Pavlovian system (a) assigns values to only a small set of “hard-wired” behaviors, possibly due to the evolutionary advantage of exhibiting these behaviors. An example would be approach behavior in response to food stimuli. In contrast, stimuli or learned cues predicting a negative outcome induce avoidance behaviors. Notably, this system operates in a rather rigid manner, and is insensitive to internal states, such as outcome devaluation (Rangel, 2013; Rangel et al., 2008).

The habit system (b) can assign values to a large number of actions due to reinforcement learning based on trial-and-error. Examples for behaviors controlled by habits include a smoker’s desire to smoke at a particular time of day, or an animal’s tendency to press a lever for rewards in response to a learned cue. The habit system is more flexible than a), but less flexible and sophisticated than c) as it needs sufficient training to learn values (Rangel et al., 2008). Across species, the dorsolateral striatum seems to be crucial for controlling such habitual behaviors. This brain area is closely linked to the motor cortex, possibly to quickly initiate motor actions in response to the learned cues (Daw and O’Doherty, 2014).

The goal-directed system (c, sometimes referred to as a “model-based” system) is more flexible because it dynamically measures action values “by computing action-outcome associations” and estimating the reward value of the outcomes (Rangel et al., 2008). The satisfaction of two requirements is necessary to label an action “goal-directed” (Verschure et al., 2014): First, the individual needs to understand the causal effect between one’s actions and their outcomes given the current context or state. Second, the individual must employ goal representations, that is, representations of action outcomes. This definition entails that the goal-directed valuation system, in contrast to the other two valuation systems, considers an end state that an action should achieve (Verschure et al., 2014). Further, only the goal-directed system would, for instance, include internal states, such as satiety, in the valuation process and update the value of an action when the outcome value changes (Rangel et al., 2008). While habitual systems would choose a value that is on average rewarding, the goal-directed systems is able to pick the optimal action in a trial-wise and context-dependent manner (Rangel and Hare, 2010). However, the goal-directed system may sometimes be in conflict with pre-potent responses driven by a) or b). Activity in the

lateral prefrontal cortex seems to play a key role in deploying cognitive effort to override prepotent responses (Fehr & Rangel, 2011). It is important to note that most of the literature has focused on goal-directed decision making, and the role of, interaction between and integration of several valuation circuits is still in its infancy (Kable and Glimcher, 2009).

As most decisions have consequences, the brain needs to keep track of the outcomes to foster learning processes, as already Mark Twain noted: "*Good decisions come from experience. Experience comes from making bad decisions.*" Experienced utility (that is, the outcome value) signals at the time of outcome occurrence, such as during consumption, are key drivers of learning, and may be different from the computed subjective value signals at the time of choice (Fehr and Rangel, 2011). Consider, for example, an individual who generally likes a certain wine A. At the time of choice between wine A and wine B, he confidently chooses wine A. Upon consumption, however, the decision maker realizes that he does not like the taste of this wine, and therefore, the experienced utility signal during consumption is different from the subjective value signal at the time of choice. The difference in these value signals then drives learning, with higher deviations leading to steeper learning rates (*e.g.*, "reward prediction error" (Schultz et al., 1997)).

2.3 Attribute space in goal-directed value-based decision making

Goal-directed decision making uses much more information resources than the other two valuation systems, and is therefore far more flexible. As mentioned above, some values may be learned over time through reinforcement learning and retrieved whenever necessary, but this cannot account for decision making in response to novel or highly complex stimuli (Rangel and Clithero, 2014). The assumption that decision makers integrate various attributes or dimensions of an option into an overall subjective value signal has been proposed in various domains, such as expected utility theory in economics and prospect theory in psychology (Kable and Glimcher, 2009; Kahneman and Tversky, 1979; Neumann and Morgenstern, 2007; Rangel and Clithero, 2014). Even a very simple choice option, such as an apple, is made up of various attributes, such as sweetness, color and water content (Fehr and Rangel, 2011). Figure 3 (based on Rangel, 2013) summarizes the current understand-

ing of how goal-directed values are computed. The exact attribute space remains unknown, but two distinct types of attributes seem to exist: attributes associated with immediate outcomes (such as a taste reward), as well as more complex attributes (such as the representation of goal states, their utility, future rewards and the current context; Rangel, 2013, Verschure et al., 2014). In detail, it is assumed that each outcome consists of a space of attributes, a value is assigned to each of the attributes based on the attribute's predicted rewarding value by the organism, and then the values are summed to an overall option value according to

$$SV(A) = \sum w_i * a_i (A)$$

Equation 1

Where $SV(A)$ denotes the subjective value of option A, $a_i(A)$ denotes the attribute i of option A, and w denotes the weight of attribute i (Rangel and Clithero, 2014). Thus, the model assumes that the subjective value is the sum of all considered attributes (Bettman et al., 1998; Fehr and Rangel, 2011; Hare et al., 2011a; Rangel and Clithero, 2014). Importantly, the model of stimulus value integration presupposes that the subjective value computed for a particular object depends on the attributes that are assigned a value (and weight) to (Rangel, 2013). This implies that an attribute value and weight can only be summed in the valuation process if the attribute can be taken into account by the brain at the time of choice (Fehr and Rangel, 2011; Rangel and Clithero, 2014) – an important point which will be addressed in more detail in chapter 3. It therefore may be possible (and I show that it is indeed possible) to change the valuation process by making individuals aware of certain attributes, such as nutrition information (see the studies in chapter 5.1 and 5.2).

This model also provides a source of inter-individual heterogeneity in preferences, as the attribute space may differ across individuals – either an attribute is valued or weighted in a different way, or an individual cannot compute the attribute value or weight at the time of choice and therefore fails to incorporate it (Fehr and Rangel, 2011). Novel stimuli can be evaluated by assessing known attributes and combining them into a stimulus value signal (Rangel and Clithero, 2014). An important question concerns, which attributes are used for value computations at which

time point. Fehr and Rangel (2011) propose that certain attributes, which are effortlessly computed, are always considered, and other attributes, which require cognitive effort, are not always considered. They propose that whenever “an attribute occurs sooner in time” (such as the taste of a cake, compared to its non-tangible health consequences), “it is more likely to be taken into account”.

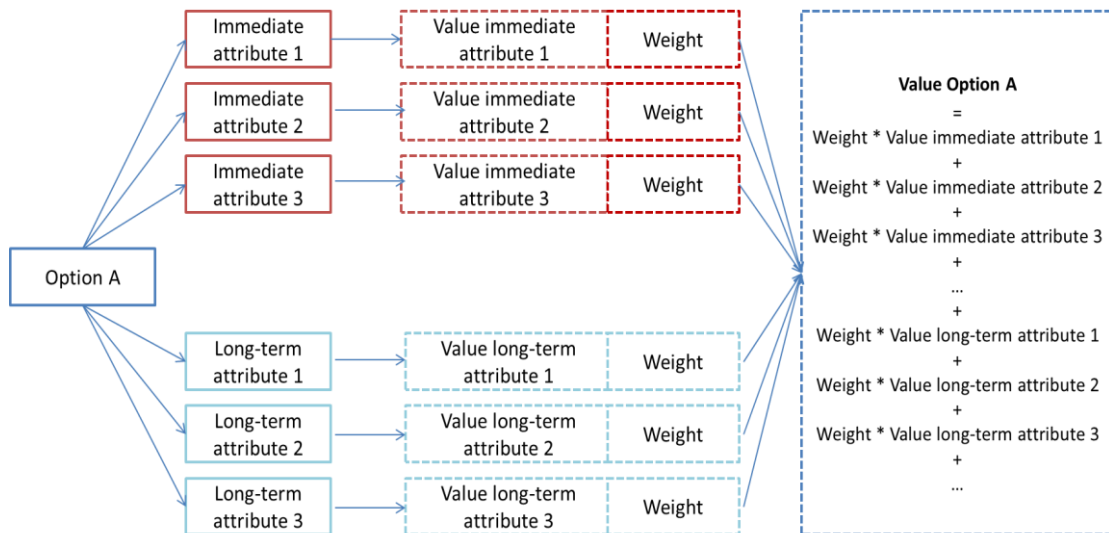


Figure 3: Attribute space of a fictive option A in a goal-directed valuation process: The option can be mapped into a set of attributes that describe it. A value is assigned to each of the attributes. Two classes of attributes are usually assumed, that is, immediate and basic attributes (depicted in orange), such as the sweetness of a food item, as well as abstract attributes (depicted in light blue), such as long-term health or financial consequences. Every attribute is weighted and then summed to an overall subjective value. The actual attribute space used by the goal-directed system has not been identified yet. Crucially, the Pavlovian and habit valuation systems do not take into account long-term attributes. Adapted from Rangel (2013).

On a neural level, the hypothesis of attribute integration was tested by Lim and colleagues (2013). They presented items with two distinct attribute dimensions: the aesthetic quality as well as the semantic meaning of foreign words printed on items. Their research design included two groups, and only the second group learned the semantic meaning of foreign words, hence, they could dissociate areas associated with the value computation of each attribute. Activity in the ventromedial prefrontal cortex (vmPFC) correlated with the overall stimulus value signal (over all considered attributes). Attribute-specific values were computed in distinct cortical areas specialized in the attribute features. Attribute-specific value signals were then passed to the

vmPFC (note, however, that the directionality of connectivity was not tested in this study, Lim et al., 2013).

2.4 Brain circuits involved in goal-directed value-based decision making

Over the last two decades, research in neuroeconomics has mapped the neural underpinnings of value-based decision making (Brosch and Sander, 2013). A vast amount of studies in the domain of value-based decision making employs food items as choice options (Armel et al., 2008; De Martino et al., 2013; Hare et al., 2009, 2011a; Krajbich et al., 2010; Ludwig et al., 2014; Plassmann et al., 2007, 2008), possibly because they are omnipresent reinforcers, which are of importance to most decision makers (as opposed to, for example specific clothing items or stocks).

In a typical neuroimaging experiment in which researchers are interested in identifying brain regions correlating with the subjective value of choice options, that is, brain regions showing activation changes as a function of an item's value, participants view different stimuli and are asked to state their subjective value for an item (such as their willingness-to-pay (WTP) or ratings) or their preference between stimuli (Brosch and Sander, 2013; Krajbich et al., 2010; Linder et al., 2010), see Figure 4. More specifically, for eliciting WTP, an often utilized method is the incentivized Becker-DeGroot-Marschak (BDM) auction (Becker et al., 1964). In a BDM auction, participants are required to state their maximum WTP, and one or several trials is selected after the experiment. The participants receive the product if their WTP was above a number drawn from a predefined distribution. Since only random trials are selected to count, the "optimal strategy for subjects is to treat each decision as if it were the only one" (Hare et al., 2011a). Behavioral value measures are then employed to directly (in case of WTP or ratings) or indirectly (in case of choice data, or weighted ratings) derive a subjective value, which is then used as a parametric regressor in the general linear model (GLM, Brosch and Sander, 2013). If the neural activity is significantly related to the behaviorally derived subjective value measure, this is taken as proof that activity in that region actually encodes the value signal (Fehr and Rangel, 2011; Rangel and Clithero, 2014).

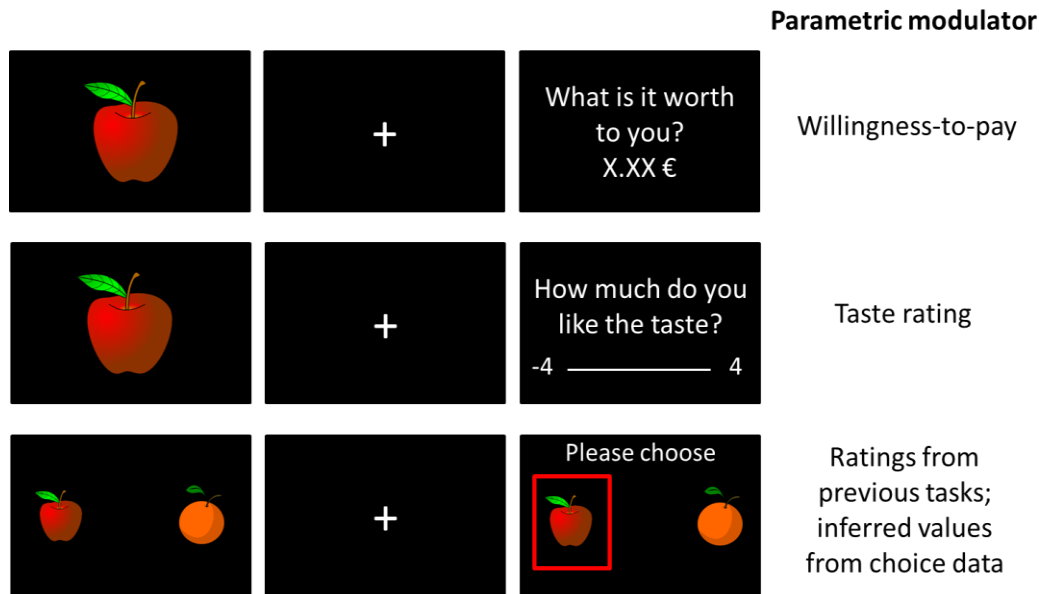


Figure 4: Example experiments for studying value-based decision making. In these experiments, one can investigate regions in which the activity changes as a function of the stated or inferred subjective value. This can be achieved by adding the trial-wise subjective value as a parametric regressor in the General Linear Model; for more detailed task descriptions, see Rangel and Clithero (2014).

The existence of subjective value signals is possibly the “most frequently tested hypothesis”, and the “most systematically replicated finding” in neuroeconomics (Fehr and Rangel, 2011). Converging human functional MRI (fMRI) studies have shown that the blood-oxygen-dependent (BOLD) activity in the vmPFC, ventral striatum, insula and posterior cingulate cortex, among others, reflect how much an individual values an option and which option an individual will choose (Bartra et al., 2013; Brosch and Sander, 2013; Rangel et al., 2008). Importantly, this holds true across stimuli types, such as primary (e.g., food) and secondary (e.g., monetary) rewards (Grabenhorst and Rolls, 2011; Kim et al., 2011), suggesting that these regions indeed encode a “common currency”, which permits the comparison and decision between very different options (Brosch and Sander, 2013). In addition, the vmPFC was shown to integrate different aspects of a choice option, such as expected value, reward outcome, gains and losses (FitzGerald et al., 2009; Grabenhorst and Rolls, 2011; Talmi et al., 2009). Measurement of brain activation in the vmPFC also allows to infer subsequent choices (Levy et al., 2011).

Non-human studies provide converging evidence, for example, monkey neurophysiology studies have found that neurons within the vmPFC encode the value of outcomes (Padoa-Schioppa and Assad, 2006). Monkeys and rats with lesions in this region become insensitive to outcome devaluation (Gallagher et al., 1999; Izquierdo et al., 2004; Machado and Bachevalier, 2007), suggesting that the vmPFC is critical for value-guided, model-based behaviors (Schoenbaum et al., 2011).

Fundamentally, the valuation process is dynamic (Fehr and Rangel, 2011), in that for instance the weight on health-relevant attributes may be higher after being reminded of health consequences, while they may be discounted at increasing hunger levels (Epstein et al., 2003) or during stressful situations (Maier et al., 2015). Strong evidence (next to the study by Lim and colleagues mentioned above) suggests that the vmPFC integrates various attributes into a subjective value signal. For instance, Hare et al. (2009) studied dietary choices that involve self-control. The valuation signal in the vmPFC was shown to incorporate both health and taste attributes in self-controlling individuals, while it only reflected taste attributes in non-controlling individuals. Activity in the dorsolateral-prefrontal cortex (dlPFC) increased when subjects exercised self-control and showed increased functional connectivity to the vmPFC, suggesting that the dlPFC modulates the weight placed on long-term attributes, such as health considerations, during value computations (Hare et al., 2009). In a study investigating charitable decision making, researchers found that the vmPFC again correlated with values assigned to charities, and functional connectivity analyses suggested that the vmPFC integrated inputs from regions important for social cognition (Hare et al., 2010).

Nevertheless, the observed value signals in the vmPFC in the above-mentioned studies are only correlational in nature (and not causal). An important remaining question constitutes whether there is a causal role of the vmPFC in the generation of value signals and the choice process. The only available evidence for a causal role of the vmPFC stems from lesions studies (Rangel and Clithero, 2014). Human lesion studies provide evidence for a strong functional-anatomical specificity in the human frontal cortex, as lesions in the dlPFC are mainly associated with cognitive control deficits, such as deficits in response inhibition and conflict monitoring, while the vmPFC was shown to be required for value-based decision making (Gläscher et al., 2012). More specifically, individuals with lesions within the vmPFC

exhibit inconsistent preference judgments in a simple pairwise choice task (Fellows and Farah, 2007). Targeting the vmPFC using transcranial magnetic stimulation (TMS) is not possible because only surface layers of the human cortex can be stimulated or inhibited with current technology. A seminal study using TMS on the dlPFC in combination with subsequent functional MRI found that TMS decreased activity in both the dlPFC and vmPFC, and diminished the connectivity between them (Baumgartner et al., 2011). Another interesting method to confirm a causal role of the vmPFC in the generation of value signals would be the endogenous alteration of neural activity, for example by down- or up-regulating the vmPFC signal using neurofeedback and observing subsequent choice behavior. If the vmPFC plays a causal role in preference formation and choice, down-regulating activity in the vmPFC should decrease preference judgments and choice probabilities.

While many studies propose a single “core valuation system” (such as the vmPFC), where neocortical and subcortical afferents converge (Hare et al., 2011a; Kable and Glimcher, 2007; Monterosso and Luo, 2010; Plassmann et al., 2007; Rangel and Hare, 2010), other researchers propose a “competition” between, rather than a convergence of, limbic (midbrain dopamine system) and prefrontal structures in decision making (McClure et al., 2004). While much evidence points towards a core valuation system (Kable and Glimcher, 2009), this debate remains unresolved and will be addressed in the overall discussion (chapter 8).

Certainly, goal-directed decision making is complex because individuals have to integrate information from various sources. Nevertheless, Crossley and colleagues (2016) demonstrated that this type of decision making can be performed using a parsimonious system consisting of just two neuron types. The first system reports the external states, such as the availability of foods, while the second encodes the animal’s homeostatic motivational state (Crossley et al., 2016).

As mentioned previously, experienced utility signals at the time of consumption (or more generally when experiencing an outcome) are thought to be different from value signals at the time of choice. Several studies have found experienced utility signals in regions of the vmPFC and nucleus accumbens across goods (Blood and Zatorre, 2001; de Araujo et al., 2003; Rolls et al., 2003; Small et al., 2003). What distinguishes these two signals on a neural level remains to be investigated in future studies.

2.5 Dietary choice as a special case of value-based decision making

Note: This chapter is based on one of my review article and is described in more detail in 6.2. The reasoning follows the structure from Rangel, 2013. For a more detailed view, it is recommended to read these two publications.

Dietary choices, in contrast to many other kinds of decisions, such as financial investments and partner choice, occur very frequently (Wansink and Sobal, 2007). The time, amount and food item we eat depends on various factors, such as physiological states (malnutrition, obesity), psychological states (habitual eating, stress) and external factors (availability of food, marketing). Dietary choices do not only occur very often, they also fulfill a physiological requirement necessary for survival (Rangel, 2013). A variety of subsystems exist to fine-tune energy-intake and expenditure (Saper et al., 2002). Next to a tight hormonal regulation (Morton et al., 2006, 2014; Schwartz et al., 2000), the reward system plays an important role in the regulation of food intake (Berridge, 1996; Berthoud et al., 2011; Volkow et al., 2011). Cognitive control mechanisms determine how much long-term attributes, such as health consequences, are weighted in the decision process (Hare et al., 2009, 2011a; Schonberg et al., 2013). Unfortunately, research in neuroeconomics has mainly focused on processes that are similar across decision contexts, while research in nutrition science has focused on processes that are unique for energy homeostasis; both areas of studies have been rarely combined (Rangel, 2013). Although a vast amount of literature on value-based decision making has been using food items as stimuli, the tight homeostatic regulation and the influence thereof has been largely ignored. Due to the interdependence of homeostatic, reward, and cognitive control mechanisms, the following subchapters will briefly introduce these systems and how they regulate feeding decisions. A multidisciplinary research approach is certainly a fruitful endeavor when studying functional and disrupted energy homeostasis and dietary choice.

2.5.1 *Energy homeostasis*

Energy homeostasis is defined as a stable balance between energy intake and expense (Morton et al., 2014). One of the most important brain regions in the regulation of energy homeostasis is the hypothalamus. Lesions in several hypothalamic re-

gions dramatically affect food intake and body weight, as different metabolic signals converge in this brain region (Abizaid et al., 2006a). Circulating signals, such as the adipocyte hormone leptin, convey information on current energy stores and send a negative feedback signal via the Melanocortin system in the hypothalamic arcuate nucleus (Morton et al., 2006, 2014; Saper et al., 2002; Schwartz et al., 2000). Importantly, receptors for leptin cannot only be found in the hypothalamus, but also in other brain regions, such as the ventral tegmental area, which is part of the dopaminergic reward system. Therefore, homeostatic signals can directly influence the motivation to ingest foods (Hommel et al., 2006). Relating to these findings, it has been shown that gastrointestinal signals as well as nutrients send signals to the hypothalamus, mostly via vagal afferents, and can thereby alter food intake (Morton et al., 2014). Bilateral connections between hypothalamic nuclei and other brain regions, such as the hippocampus and the reward system exist in order to alter motivation, learning and motoric responses (Gao and Horvath, 2007). Thus, the homeostatic system is tightly intertwined with various other regions related to decision making processes.

2.5.2 *Reward system and the reinforcing value of food items*

Imagine you have not eaten for a whole day – would this change your behavior, such as your ability to learn, your patience, and the way you perceive high-caloric food items? As there is a constant interaction between homeostatic systems and other brain regions, this is highly probable. Across species and contexts, the reward system directly influences food intake, most probably in order to ensure survival (Stice et al., 2013). Dopamine is one of the most widely studied neurotransmitters of the reward system, and well-studied in the domain of food intake as well as decision making (Abizaid et al., 2006b; Arias-Carrión et al., 2010; Bassareo and Di Chiara, 1999; Bromberg-Martin et al., 2010; Brozoski et al., 1979; Hernandez and Hoebel, 1988; Hnasko et al., 2004; Rogers, 2011; Schultz, 2010, 2016; Volkow et al., 2011; Winkler et al., 2012). The mesocortical and mesolimbic dopamine systems project from the ventral tegmental area to the frontal cortex and the limbic system, respectively (Volkow et al., 2011). An early study demonstrated that cocaine as well as food intake stimulate dopamine release in the nucleus accumbens, which is part of the ventral striatum (Hernandez and Hoebel, 1988). A human positron emission tomography

(PET) imaging study demonstrated that subjective palatability ratings significantly correlate with the amount of dopamine released in the dorsal putamen and caudate nucleus (Small et al., 2003). Dopamine-deficient mice drastically reduce food intake, their motivation to obtain foods is very low, and they barely react to metabolic signals, such as leptin deficiency (Hnasko et al., 2004; Szczypka et al., 2000). It was shown that the dopaminergic signaling pathway acts downstream the Melanocortin pathway (Gao and Horvath, 2008). In a human study, obese compared to lean individuals exhibit higher activation of the reward system when exposed to high-caloric food cues, but actual consumption of these food items leads to lower reward system activation (Stice et al., 2008). Possibly, obese individuals then compensate with increased food intake (Rothmund et al., 2007; Stice et al., 2008).

Berridge proposed a reward-processing model by distinguishing between liking and wanting elements of a reward. *Liking* relates to the hedonic appraisal of a food reward, and *wanting* describes the motivation to obtain the reward (Berridge, 1996; Berridge and Kringelbach, 2008; Berridge and Robinson, 2003). While *liking* and *wanting* may often be aligned, it is feasible to experimentally distinguish between them, as for example food deprivation influences only food *wanting*, but not food *liking* (Epstein et al., 2003). Neuroscientific evidence suggests that both reward components are processed in distinct brain regions: While the motivation to obtain a reward (the *wanting*) has been associated with the mesolimbic dopamine pathway, *liking* seems to be related to the endogenous opioid circuitry (Berridge and Robinson, 2003). The reinforcing value of a food item can be determined, for instance, by monitoring e.g., the frequency or vigor of motor responses (Bower and Kaufman, 1963; Epstein et al., 2007; Saelens and Epstein, 1996; Temple, 2014). Using such a task, food was shown to be more reinforcing than engaging in sedentary activities, such as playing computer games, in obese participants. In contrast, hedonic liking ratings were not correlated with the reinforcing value of foods and did not differ between obese and lean participants (Saelens and Epstein, 1996). Corroborating evidence proclaims that obesity is not directly associated with heightened liking responses towards food stimuli, but with increased motivation to eat (Mela, 2006). Therefore, measuring both the subjective value (hedonic liking ratings) as well as eliciting the reinforcing value of foods may provide information beyond self-report and may therefore help to better explain dietary choices (see study 5.4).

2.5.3 *A neuroeconomic perspective on food intake*

As alluded to above, the fields of energy homeostasis and neuroeconomics have rarely interacted. Strong evidence points to common mechanisms across decision making domains, including dietary choices (Kable and Glimcher, 2009; Rangel et al., 2008). Relating to the attribute space of value-based decision making (chapter 2.3), a food item can be mapped into basic, immediate attributes, such as the taste of a food item, as well as more abstract, long-term attributes, such as health consequences, which are presumably only considered by healthy eaters. As mentioned above, only the goal-directed valuation system can include abstract attributes, such as long-term health consequences, into the valuation process (Rangel, 2013). Evidence proposes that cognitive control is impaired in obese individuals (Gunstad et al., 2007). Moreover, gray matter volume in the dlPFC was shown to be reduced in obese compared to lean controls (Pannacciulli et al., 2006). The ability to suppress the desire for high-caloric foods may therefore constitute a protective factor for the development of obesity (Wang et al., 2009).

From a neuroeconomic perspective, an “advantageous” decision requires an individual to consider all relevant attributes of an item and correctly value and weight those attributes, including long-term consequences (Rangel, 2013). More specifically, when considering the formula for the computation of a stimulus value, the subjective value computation in dietary choice can be expressed as

$$SV(\text{Food } A) = \sum w_1 * a_{\text{health}} \text{Food } A + w_2 * a_{\text{taste}}(\text{Food } A) + w_i * a_i(\text{Food } A)$$

1. \nexists health
2. $a_{\text{health}} < a_{\text{taste}}$
3. $w_1 < w_2$

Equation 2

where \nexists denotes the absence of health attribute considerations. In conditions of overweight and obesity, which are not due to primary homeostatic dysregulation or monogenetic defects, the neuroeconomic perspective assumes that at least one of the three assumptions needs to be fulfilled: health attributes are

not considered (1.), the value for taste attributes is higher than for health attributes (2.), or the weight on taste attributes is higher than for taste attributes (3.). Note that 2.) and 3.) can interact. Therefore, a failed dieting attempt is seen as a consequence of decisions that do not properly consider, weight or value long-term consequences (Rangel, 2013). Equation 2 makes no assumptions on the underlying process, and does not explicitly distinguish between liking and wanting components of the taste reward.

Environmental factors are important for the development of obesity (Sampey et al., 2011), and interact with the decision making circuitry (Rangel, 2013). Due to the omnipresence of high-caloric food items in most industrialized nations, goal-directed decisions are harder to make, as 1.) automatic behaviors are, as the name suggests, automatically activated in response to food cues, and the goal-directed valuation system needs to override the automatic tendencies; and 2.) the probability that the goal-directed valuation system fails is higher in the presence of distractors and stress, both omnipresent in today's lifestyle (Rangel, 2013). More specifically, stress decreases self-control in goal-directed food decisions by altering the value computation process (Equation 2) towards increased weight on taste attributes, and decreased weight on health attributes (Maier et al., 2015). Further, the influence of automatic valuation systems (such as habitual valuation) increases under higher cognitive load (Mann and Ward, 2007). The excessive consumption of high-caloric foods may affect different levels of feeding regulation (based on Rangel, 2013). On the one hand, the intake of high-caloric foods may disturb the homeostatic system (Clegg et al., 2005; Lustig et al., 2004), and may additionally negatively influence cognitive processing and increase the reactivity to rewards (Kanoski et al., 2007). Impairments of cognitive control may further impede goal-directed choices (Rangel, 2013).

In sum, homeostatic, reward and cognitive control mechanisms tightly interact and depend on each other. As it is assumed that valuation systems work dynamically, valuation processes can be altered. Therefore, modulators of value will be discussed in the following chapter.

3 Modulators of value in decision making

If you can choose between 10 € today and 100 € in a year, which offer would you choose? Would your choice change if the delayed offer was only 10.01 € in a year? Imagine you taste a new product, which you have never consumed before. Somebody then tells you that the product surely tastes “rich and delicious”. In another instant, the same product is described as containing a vast amount of “monosodium glutamate” (Grabenhorst et al., 2008). Would these verbal descriptions change your subjective evaluation of the desirability of the taste experience? In the following section, modulators of value and valuation will be addressed, namely delay, visual attention as well as contextual variables. Naturally, a myriad of other value modulators exist, such as risk and uncertainty (Fellows and Farah, 2007; Johnson and Busemeyer, 2010; Kahneman and Tversky, 1979; Levy et al., 2010), but their discourse is out of the scope of this dissertation summary.

As noted above, the model of stimulus value integration described in chapter 2.3 and 2.5.3 provides sources for differences in valuation. Differences in valuation processes may be due to inter-individual differences, such as the weighting of long-term features (Fehr and Rangel, 2011; Hare et al., 2009), or due to environmental factors, such as the salience of an attribute or alternative. Specifically, public policy interventions that aim at nudging people towards healthier lifestyles may change the degree that certain attributes are employed in the computation of a decision value, thereby promoting healthy eating habits (Fehr and Rangel, 2011; Hawkes et al., 2015), see study 5.1 and 5.2.

3.1 Intertemporal choice and self-control

Note: This sub-chapter loosely follows the structure proposed in Kable, 2014. For more details and examples, the original book chapter should be considered.

The majority of decisions entail future consequences (Kable, 2014). For instance, choosing a chocolate bar now may be highly rewarding, but may also have longer-term health consequences when consumed on a regular basis. Likewise,

choosing to purchase a house or a car can have long-term consequences, such as financial gaps. Delay discounting, also known as temporal discounting or intertemporal choice, refers to the process of choosing between an immediate, relatively small option and a larger, but delayed option (Kable, 2014). A consistent finding across modalities and species is that delayed outcomes are discounted compared to immediate outcomes (Frederick et al., 2002; Green et al., 2005; Kable, 2014). In other words, the subjective value of a reward is smaller when it is available at a later point in time. For each individual, it is possible to infer a discount function from choice data, measuring how “the subjective value of an outcome changes as a function of the delay” (Kable, 2014). Much research has been devoted to characterize the model with which decision makers discount future rewards, and the most widely used model is the hyperbolic discount model (Kable, 2014; Kable and Glimcher, 2007; Peters and Büchel, 2009). More specifically, delayed outcomes are assumed to be discounted according to

$$SV = \frac{A}{(1 + kD)}$$

Equation 3

where SV is the subjective value, A is the offer received immediately, k is the individual discount rate, and D is the delay (Kable, 2014). Support for hyperbolic discounting stems from human (Frederick et al., 2002; Green et al., 1994; Soman et al., 2005) and non-human literature (Kim et al., 2008; Richards et al., 1997). Secondary reinforcers, such as money are discounted with smaller discount rates compared to primary reinforcers, such as food (Odum et al., 2006; Reuben et al., 2010; Tsukayama and Duckworth, 2010).

Intertemporal choices have been employed to understand impulsive behavior (Ainslie, 1975), and individual differences in discounting are often assumed to be measures of impatience (Kable, 2014). The individual discount parameter k is relatively stable across time, which indicates that delay discounting is a person’s stable trait (Kishinevsky et al., 2012; Peters and Büchel, 2009; Weber and Huettel, 2008).

BOLD activity in the vmPFC, ventral striatum and posterior cingulate cortex correlate with the subjective value of the delayed reward, estimated from the hyperbolic discount function (Kable, 2014; Kable and Glimcher, 2007). Importantly, neural activity in the vmPFC could be related to individual k -values: in subjects with higher k -values (presumably more impulsive subjects), compared to more patient subjects, neural activity in the vmPFC decreased more steeply at higher delays. This again suggests a “common currency” of subjective value when making choices, taking into account delay and reward magnitude (Kable and Glimcher, 2007), which has been confirmed in follow-up studies of intertemporal choices (Ballard and Knutson, 2009; Peters and Büchel, 2009; Pine et al., 2009), as well as in a variety of other choice domains, such as risk (Levy et al., 2010), and food (Hare et al., 2009, 2011a).

Generally, behaviors that are considered “self-controlled often involve choosing delayed rewards over immediate ones” (Kable, 2014). Thus, the concept of delay discounting is tightly intertwined with aspects of self-control. To give an illustration, a dieter that resists the urge to consume a tasty, high-caloric snack product prioritizes future rewards, or long-term goals over short-term rewards. Steeper discount rates (that is, higher k -values) could be associated with self-controlled behaviors (Kable, 2014), such as tobacco consumption (Baker et al., 2003). Choosing sooner, smaller rewards, such as unhealthy food options, may increase the risk for health problems, such as obesity (Stoeckel et al., 2013). Indeed, a positive correlation between BMI and delay discounting has been found (Ikeda et al., 2010), however, whether k -values predispose for certain health problems, or whether they are consequences remains to be studied in the future. Policy-makers frequently want to influence choices and bias individuals towards choosing options with higher long-term rewards (Kable, 2014), for example in the domain of dietary choice, see study 5.1 and 5.2., as well as review 6.1.

Self-control (or “self-regulation”, often employed synonymously) in humans can be defined as any effort to override prepotent responses (Baumeister et al., 1994). In various influential manuscripts, Baumeister *et al.* propose that choice, self-regulation and volition share a common, limited, and renewable resource. The author repeatedly demonstrated that acts of self-control deplete this limited resource (“*ego depletion*”) and subsequently reduce the self’s ability to function, such as exerting self-control (Baumeister, 2002; Baumeister et al., 1998, 2000; Baumeister and Vohs,

2007). Executive functions refer to several top-down processes, such as cognitive flexibility (set shifting), working memory as well as cognitive control and are important to most aspects of life (Diamond, 2013). The inhibition of pre-potent responses is an important facet of cognitive control (Friedman and Miyake, 2004) and seems to have a genetic component (Kumari et al., 2005; Macare et al., 2014) with genetic influences on, for instance, fronto-striatal brain circuits (Kasparbauer et al., 2015). A common mechanism across different executive functions putatively performed by frontal lobe regions, *e.g.*, the dlPFC and superior frontal gyrus (SFG, Badre & Wagner, 2007; Batterink, Yokum, & Stice, 2010; Duncan & Owen, 2000; Hare et al., 2009; M. Watanabe, Hikosaka, Sakagami, & Shirakawa, 2005), have been proposed (Miyake et al., 2000), but see (Anderson et al., 1991; Reitan and Wolfson, 1994; Shallice and Burgess, 1991) for contradicting evidence. In the domain of intertemporal choice, several studies have reported higher activity in the dlPFC when individuals choose the delayed, and not the immediate, reward (McClure et al., 2004). Lower k -values, denoting higher patience, have been associated with greater gray matter volume in lateral prefrontal regions (Bjork et al., 2009). When the dlPFC activity is temporally disrupted, for example using TMS, participants choose the immediate reward more often (Figner et al., 2010). Differences in cognitive abilities, such as intelligence, influence the degree to which the dlPFC is activated, with higher degrees of dlPFC activity in delay discounting tasks leading to less discounting (Shamosh et al., 2008).

The analysis of event-related potentials revealed that in food choice trials requiring self-control, compared to those requiring no self-control, the dlPFC affects dietary self-control via two mechanisms, namely an early top-down attentional filtering, and a later value modulation (Harris et al., 2013). Regions of the lateral prefrontal cortex, such as the dlPFC, are thought to modulate value representation in the vmPFC also in case of intertemporal choice (Kable, 2010, 2014), similar to how self-control is thought to be employed in simple dietary choice (Hare et al., 2009, 2011a). A study on dietary choice found that cognitive reappraisal strategies, such as thinking of the long-term costs of eating unhealthy foods, increased activation in inhibitory control regions and reduced activity in attention-related regions in response to palatable food stimuli (Yokum and Stice, 2013). Hence, lateral prefrontal activity may depend on how attention is deployed among the attributes of an option (Kable, 2014).

Indeed, in a behavioral study, directing attention towards the reward magnitude increases delayed choices, while directing attention to the delay increased immediate choices (Weber et al., 2007).

The neurocomputational model, which is well established in simple choices, has not been sufficiently tested in complex decision situations, such as complex inter-temporal choices. Notwithstanding, evidence suggests that similar computations are at work in complex decisions: subjective values for each decision option are computed by identifying and weighting attributes, compared using a comparator system, and the process is sensitive to attention (Fehr and Rangel, 2011), see chapter 3.2 for how attention modulates valuation. In terms of the stimulus value equation introduced in chapter 2.3, the subjective value for the delayed option only could be given by

$$SV(A) = \sum w_1 * a_{Reward\ Magnitude}(A) + w_2 * a_{Delay}(A) + w_i * a_i(A)$$

Equation 4

and the attribute weights (w_1 and w_2) are conjectured to depend on attention (Weber et al., 2007). Another plausible model would be that the attribute “reward magnitude” is time-dated, so that the attribute receives different weights at different times (Fehr and Rangel, 2011). This would be given by

$$SV(A) = \sum \underset{\substack{\uparrow \\ Delay}}{w_1} * a_{reward\ Magnitude}(A) + w_i * a_i(A)$$

Equation 5

and is closely related to the hyperbolic discount function.

3.2 The modulating role of attention in value computations

Nota Bene is a Latin phrase frequently found in legal documents that is used to direct attention to something of particular importance (Fellmeth and Horwitz, 2009). Attention can be defined as a state of consciously focusing or concentrating on

a subset of available objects or attributes (James, 1890). More specifically, selective visual attention refers to the ability to selectively process relevant, and ignore irrelevant, objects or attributes of interest (Bergen and Julesz, 1983; Braun and Julesz, 1998; de Haan et al., 2008; Itti and Koch, 2001; Nakayama and Mackeben, 1989; Treisman and Gelade, 1980). From a decision making perspective, attention refers to the brain's ability to vary the deployed computational resources depending on circumstances (Fehr and Rangel, 2011). To give an illustration, it would be adaptive if the brain of the reader of the legal document would increase the involvement of regions important for vision, comprehension and executive functioning after reading the words *Nota Bene* in order to focus on the subsequent evidence or attribute. In other circumstances, physical threats should receive higher attention to increase the probability of survival. The ability to adapt the brain's resources depending on requirements is highly useful due to the brain's biological constraints and energy costs (Fehr and Rangel, 2011). Attention can affect a) the computation of the subjective value of a single item by affecting which attributes are considered and how they are valued and weighted and b) the comparison between items.

For a), the computed attention-dependent subjective value can be given by

$$SV(A) = \sum w_i(att) * a_i (A, att)$$

Equation 6

where *att* is a variable describing the attentional state at the time of choice (Fehr and Rangel, 2011).

For b), consider a typical individual in a store choosing between two different food items. Instead of immediately choosing one of those options, the gaze shifts back and forth between the items, until a choice is made, suggesting that attention is important for the computation and comparison of values (Krajbich et al., 2010; Lim et al., 2011). If you see two items of equal preference and fixate only one of the items - are you more likely to choose the fixated item? Research provides evidence that this may be the case. Psychological theories and evidence suggest that the integration process of different stimulus values depends on how attention is deployed among differ-

ent attributes, and the comparison process depends on how attention is deployed among the choice alternatives (Bettman et al., 1998; Busemeyer and Townsend, 1993; Hare et al., 2011a; Shimojo et al., 2003). Shimojo and colleagues (2003) demonstrated that orienting behaviors, such as fixations, are “actively involved in preference formation”. While participants made binary attractiveness ratings, their eye movements were registered. Initially, their gaze was evenly distributed between the two stimuli, but, starting around 800 ms before the response, fixations were biased towards one of the stimuli, which was ultimately chosen (conditional on similar or equal value of the options). Attention, that is, gaze duration, biased preference decisions towards the more attended item (Shimojo et al., 2003). In various follow-up experiments, Rangel and colleagues supported these findings, and created a computational model that formally includes a fixation bias in preference formation (Krajbich et al., 2010, 2012); see Figure 5. The attentional DDM is based on the original version of the DDM (Ratcliff, 1978), see chapter 4.1 for a detailed discourse.

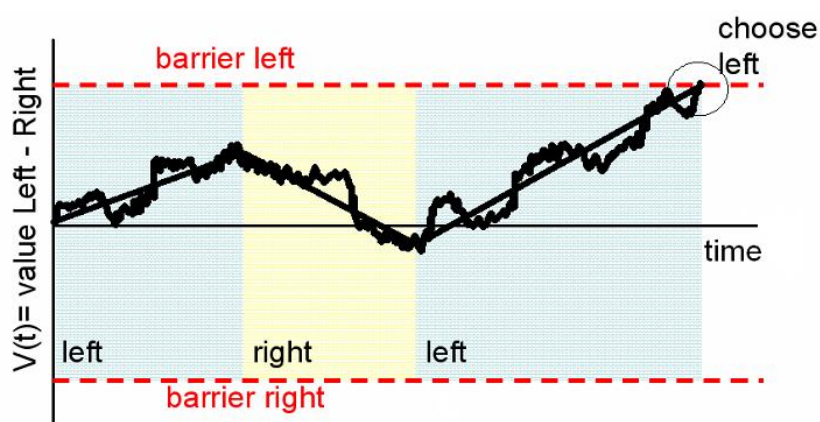


Figure 5: Computational model of the role of attention in the value comparison process. A “relative decision value” evolves over time. Importantly, the slope is biased toward the fixated item. Whenever the decision value reaches one of the barriers, a choice is made. The blue shaded regions denote that the participant is looking to the left, while the yellow shaded region denotes that the participant is looking to the right. From Krajbich et al. (2010).

More specifically, the attentional DDM assumes that a “relative decision value” evolves over time and depends on an individual’s fixations. “The weight θ dis-

counts the value of the unfixated item relative to the fixated item” (Krajbich et al., 2010). Formally, whenever an individual is looking to the left, the relative decision value evolves according to

$$V_t = V_{t-1} + d(u_{left} - \theta u_{right}) + \varepsilon_t$$

Equation 7

and whenever the individual is looking to the right, it evolves according to

$$V_t = V_{t-1} + d(\theta u_{left} - u_{right}) + \varepsilon_t$$

Equation 8

“where V_t is the relative decision value at time t , u_{left} and u_{right} denote the values of the two options, and d is a constant which controls the speed of integration” (Krajbich, 2010). $\theta \in \{0,1\}$ is a parameter reflecting the fixation bias (towards the item that is being fixated), and ε denotes Gaussian noise at time t . Note that whenever $\theta < 1$, a fixation bias is present, and whenever $\theta = 1$, no fixation bias is present (Krajbich et al., 2010). More concretely, the discount parameter θ was shown to be around 0.3 in several experiments (Krajbich et al., 2010, 2015). For a practical example, consider choosing between option A with an underlying subjective value of 4 (arbitrary unit) and option B with an underlying subjective value of 9. According to the model and a discount parameter of $\theta = 0.3$, attention towards option A only discounts option B to

$$0.3 * 9 = 2.7$$

(conditional on the assumption that both items were consciously perceived). Consequently, option A should be chosen, albeit the subjective value for option B is higher. Value differences do not affect which item is fixated first, but the number of fixations, similar to RTs, relate to difficulty – when the value difference is small, the number of fixations per trial until a response is made is higher. The model predicts that one is

more likely to choose an item when one is fixating it. Nevertheless, if the other item is much better, it is possible that the item that is not fixated is chosen. Thus, the authors found that attention cannot “make you like” items that are of much lower value (Krajbich et al., 2010). In an eye tracking study (Enax, Krajbich & Weber, in preparation), I could replicate the observation that fixation duration biases preferences, in that for instance a left-looking bias (that is, the first gaze went more often towards the left item), translated into a left-choice bias. Likewise, whenever the last gaze went to the left item, the probability to choose the left compared to the right item was higher, see Figure 6. Note that the word “attention” in the attentional DDM is used somewhat carelessly as the model does not take into account covert attention, that is, attention shifts in the absence of eye movements (Beauchamp et al., 2001; de Haan et al., 2008; Hunt and Kingstone, 2003; Itti and Koch, 2000; Posner, 1980).

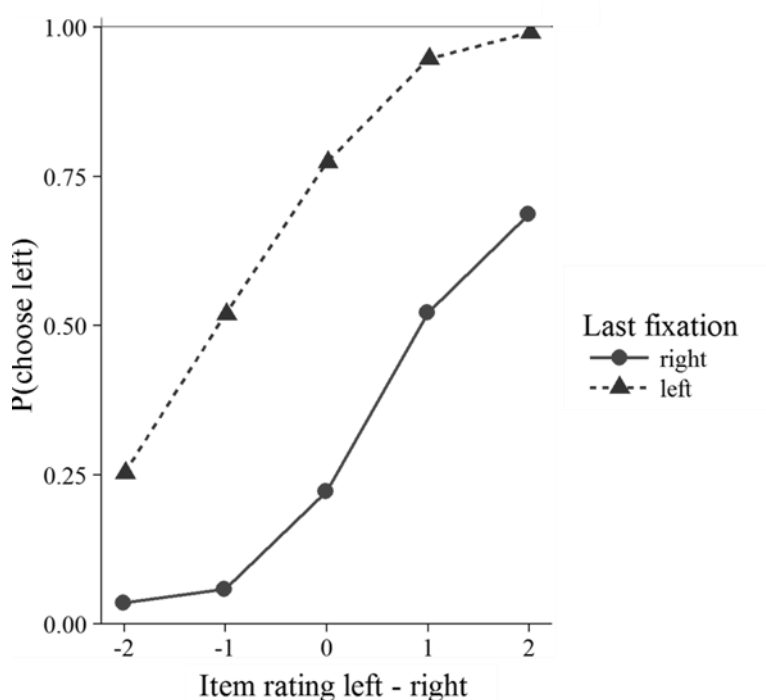


Figure 6: Psychometric choice curve conditional on the location of the last fixation. The data support the idea that fixations influence preferences, in that the probability (P) to choose the left, compared to the right item, was higher when the last gaze went to the left item. Enax et al., unpublished data.

Much of the current debate revolves around the causality of visual fixations (overt attention) on preferences. In a first study, Armel and colleagues (2008) con-

trolled visual attention by manipulating the exposure time of items. In a binary choice paradigm with roughly equally liked items, one of two items was shown for a longer duration compared to the other item. They found that increasing the relative visual attention (by increasing exposure duration of one of the items) increased the probability of choosing the item with the higher exposure duration. In case of aversive items, longer exposure duration decreased choice probabilities, suggesting that attention acts as a value “amplifier” (Armel et al., 2008). Nevertheless, the effect sizes were at most modest, and future research analyzing the causal role of attention on choices is certainly necessary, particularly by influencing attention in a more subtle way.

On a neural level, Lim and colleagues (2011) showed that attention modulates value signals. They found that the vmPFC and ventral striatum encoded value signals that were fixation-dependent (Lim et al., 2011). In addition to the attentional DDM, other process models, such as Decision Field Theory, also assume that attention on attributes of the choice options influences choices (Busemeyer and Townsend, 1993).

3.3 The influence of contextual variables in the valuation process

The computational model outlined in the previous subchapter makes stark predictions how contextual variables should affect the choice process. For example, time pressure was shown to speed up decision, but also increased choice mistakes. These behavioral findings could be explained by changes in two key parameters of the model, namely a decreased decision barrier height (see Figure 5) and increased noise in the slope of the choice process (Milosavljevic et al., 2010). Thus, the quality of decisions changes with contextual factors.

As visual saliency (such as the color or brightness of a package, also referred to as “bottom-up saliency”) influences fixation location and duration (Itti and Koch, 2001; Mannan et al., 2009), saliency may induce a choice bias. Indeed, a study demonstrated that at rapid decision speeds, saliency influenced choices to a higher degree than actual preferences, and this bias increased under cognitive load, and was highest when items were roughly equally preferred (Milosavljevic et al., 2012). For instance, the physical proximity of rewards affects choices (Fehr and Rangel, 2011; Mischel, 1974; Mischel and Moore, 1973).

Multidisciplinary evidence has demonstrated that higher-level cognitive concepts are important influencing factors on subjective value computations and experienced utility during consumption. Expectancies can be raised by various external cues, such as packaging information or pricing (Chandon and Wansink, 2007; Lee et al., 2006; Plassmann et al., 2008; Shiv et al., 2005). In a reference-dependent utility model, the reference points are fully based on expectations based on prior experiences, which influence outcome valuation (Kőszegi and Rabin, 2006). The seminal studies on the effect of expectations on various behavioral outcomes were conducted in the medical domain: the term “placebo effect” was employed to refer to the analgesic responses due to a treatment with an inert substance (treatment success could thus only be attributed to the expectation that medication will improve symptom severity, Beecher, 1955). The term “Marketing Placebo Effect” (MPE) has been coined to refer to changes of the experienced value of otherwise identical products presented with a certain marketing cue (Plassmann and Wager, 2014). The seminal study on MPEs by Allison and Uhl (1964) showed that brand knowledge strongly influenced subjective taste evaluations of identical beverages (Allison and Uhl, 1964). Likewise, prices are cues signaling the quality of a product and influencing the taste experience (Goldstein et al., 2008; Plassmann et al., 2008). Follow-up studies have replicated this effect across contexts, product domains and modalities (Chandon and Wansink, 2007; Wansink et al., 2007; Wright et al., 2013). Moreover, marketing effects influence various behavioral outcomes, above and beyond the subjective taste experience. Shiv and colleagues (2005) demonstrated that prices of an energy drink influenced the performance in a complex puzzle task, with higher pricing leading to better achievement in the task (Shiv et al., 2005).

Whilst the main focus of existing literature on MPEs has been on the effect of contextual cues on observable behavior, a seminal study has demonstrated that marketing cues do not merely generate a bias in behavioral responses, but concurrently influence neural signatures of outcome valuation. More specifically, a higher price (of an identical wine) did not only change the reported utility ratings, it also increased activation in the vmPFC, which correlated with the subjective value (Plassmann et al., 2008). Correspondingly, Grabenhorst and colleagues (2008) demonstrated that linguistic contextual information, such as “rich and delicious taste” versus “monosodium glutamate” altered taste evaluations as well as activity in the vmPFC, demonstrat-

ing that valuation processes can be effectively influenced by top-down processes (Grabenhorst et al., 2008). In a study by Crum and colleagues (2011), participants received an identical milkshake twice, once framed as high-caloric, and once as low-fat. The authors measured ghrelin levels; ghrelin levels are suppressed whenever sufficient energy is consumed (Murphy et al., 2006). Interestingly, ghrelin levels were influenced by expectations, in that ghrelin levels in the high-calorie condition steeply declined after food consumption, which usually reduces appetite, while ghrelin levels remained flat in the low-calorie condition (Crum et al., 2011), underlining the tight interaction between homeostatic systems and the decision making circuitry. However, which signaling molecules lie at the core of the effect of contextual variables on value computations and experienced utility during consumption remains rather unknown, for a first step, see study 7.1.

3.4 Using contextual cues to promote healthier dietary choices

If attention plays such a crucial role in the valuation process, could we utilize this information to improve choices? Nudging can be defined as an aspect of the choice architecture that alters people's choices and subsequent wellbeing without compulsion, to improve "decisions about health, wealth and happiness" (Thaler and Sunstein, 2008).

As mentioned above, corroborating evidence suggests that stimulus values are computed by determining values and weights for an item's attributes. All attributes are then integrated into an overall subjective value (Rangel, 2013). The attribute integration process is thought to depend on the attention that is deployed among the attribute characteristics (Hare et al., 2011a). The attentional DDM suggests that visual saliency can interact with the comparator process and influence choices (Krajbich et al., 2010). Thus, attention can be shifted towards certain cues (e.g., nutrition labels), which should bias choices towards the attended option or attribute if the value is positive (with opposite effects if its value is negative, Fehr and Rangel, 2011). In case of dietary choice, the weighting of health (long-term) and taste (short-term) aspects is of importance. For example, if individuals put a large weight on short-term attributes, this may come at the expense of possible negative long-term health consequences.

A seminal study suggested that self-control in dietary choice depends on an individual's ability to incorporate both health and taste information into the vmPFC value signal (Hare et al., 2009). In a follow-up study, Hare and colleagues (2011) manipulated the attentional focus in dietary choices by instructing participants to focus on health, taste, or no particular attribute while choosing whether they wanted to eat a food item at the end of the experiment. On a behavioral level, they found that cues directing attention towards health features increased the weight on health attributes in their choices. In addition, healthy choices were correlated with the degree that health ratings reflected the vmPFC value signal. Also, health attention cues increased activity in regions of the dlPFC, which in turn indirectly modulated the vmPFC (Hare et al., 2011a). Thus, attention manipulation towards health cues led to behavioral and neural changes resembling those of endogenous self-control (Hare et al., 2009, 2011a). Naturally, asking participants to direct their attention on choice attributes is not feasible in every-day life. Henceforth, it is of high interest to unravel potential means to improve goal-directed decision making by subtly influencing attribute attention deployment, see studies 5.1 and 5.2. For instance, salient cigarette warnings, compared to text-based information, were shown to increase smoking cessation, possibly due to increased attention on long-term health attributes (Borland et al., 2009; White et al., 2008). The computational model described above would explain this outcome with increased weight on long-term attributes, and possibly decreased weight on short-term rewarding properties of the cigarettes, however, this has not been explicitly tested. As mentioned previously, so-called “nudges” could be used to improve consumer welfare (Thaler and Sunstein, 2008). Various factors, such as framing, attention, and saliency, have been shown to affect choices, but having said that, a unifying model accounting for these effects has not been employed. Most probably, many of the results could be explained by changes of subjective value computations via attention (Fehr and Rangel, 2011).

4 Computational modeling in value-based decision making

The previous chapters already introduced - in passing - various computational models of decision making. Computational models have been used in various domains of psychology, such as perceptual decision making (Ratcliff, 1978), classical conditioning (Rescorla and Wagner, 1972), and other forms of learning (Gluck and Granger, 1993). There is currently also a strong trend in the field of value-based decision making to model the computations required for goal-directed decisions (Pezzulo et al., 2014). Two important models in the field are therefore discussed in more detail in the following subchapters: Drift Diffusion Modeling as a model of stimulus value computation and comparison, as well as Dynamic Causal Modeling as a general computational model for inferring effective connectivity between brain regions. After an introduction of the methods, applications in the field of decision making research are provided.

4.1 Drift Diffusion Modeling

Recall that the standard economic literature has traditionally only used outcomes of decision making, that is, *choice* data, for theory development and hypothesis testing (“revealed preference approach” (Samuelson, 1938)). However, psychologists and neuroeconomists have introduced formal models of the decision making *process*, which has proven to add important insights into the underlying mechanism. For instance, RTs are closely related to preferences (Krajbich et al., 2014).

DDMs are models of decision making that “provide a mathematical framework to understand decisional processes” (Voss et al., 2015) by decomposing choice and reaction time data into distinct parameters that can be used to infer internal psychological processes (Voss et al., 2013a, 2015). Originally, the DDM has been employed in perceptual tasks in which participants decide, for instance, which of two stimuli is brighter, or which of two numbers is larger. The DDM assumes continuous information sampling until sufficient information is gathered for one of the possible

outcomes (Ratcliff, 1978; Ratcliff and Smith, 2004). Response time distributions from the two decision thresholds are used to estimate a predefined parameter set, which may vary in complexity (Voss et al., 2015). The DDM offers an alternative to classical RT and choice analysis as parameter estimates can be employed to infer underlying cognitive processes (Metin et al., 2013; Philiastides and Ratcliff, 2013; Ratcliff and Smith, 2004; Voss et al., 2013a).

In detail, the process of information sampling can be described by “a Wiener diffusion process” with a slope (i.e., drift (v), Voss et al., 2015) towards one of the boundaries and Gaussian noise (see Figure 7). The drift rate parameter is frequently “interpreted as the speed of information uptake” (Voss et al., 2015). “The better the quality of evidence, the larger the drift rate toward the appropriate decision boundary, and the faster and more accurate the response” (Philiastides and Ratcliff, 2013). The two thresholds (“barriers”) at 0 and a represent the two alternative outcomes of the decision process; $|a|$ denotes “the amount of information that separates both possible decisional outcomes” (Voss et al., 2015). Larger threshold separation leads to longer decision times but fewer errors (Metin et al., 2013; Voss et al., 2015). If one decisional outcome is preferred, the starting point (z) is positioned further, *i.e.*, biased, to one of the boundaries. Thus, if the starting point z is closer to one of the two thresholds, less information is needed to reach a decision (Voss et al., 2015). Extra-decisional processes, such as task preparation and stimulus encoding that take place *before* the comparison and decision phase, as well as motor execution *after* the decision process are mapped onto a single parameter, the non-decision component t_0 (note the difference to the parameter v , which relates to the processes *during* the comparison and decision phase and depends on the quality of evidence).

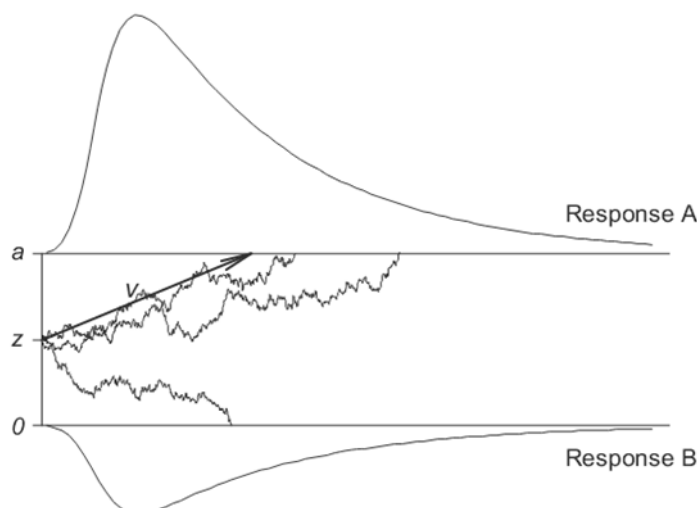


Figure 7: Simplified version of the Drift Diffusion Model: At the beginning of a trial, the information accumulation process starts at a starting point (z) and runs over time with a mean slope (drift, v), until a barrier (a , or 0) is hit. Reaction time distributions are presented above and below the decision thresholds. For simplicity, the non-decision time (t_0) before and after the diffusion process is not shown. From Voss et al. (2013).

While most DDM research has been done in the domain of perceptual decision making (Heekeren et al., 2008; Ratcliff and Smith, 2004; Voss et al., 2004), recent studies have used the information accumulation process models to analyze economic decisions (Busemeyer and Townsend, 1993; Hare et al., 2011b; Krajbich et al., 2010, 2015; Milosavljevic et al., 2010; Towal et al., 2013). Various lines of research propose that using RTs along with choice data can improve preference predictions (Krajbich et al., 2014, 2015).

Perceptual DDM tasks usually rely on stimuli that are stochastic in nature (such as different brightness levels). In contrast, in value-based decision-making, the noisy brain representation of the choice options is thought to lead to stochastic choices (Glimcher, 2014; Krajbich et al., 2014). While perceptual decision making requires very similar stimuli in order to compare different experimental tasks, economic decisions are based on value comparisons as a “common currency” (Brosch & Sander, 2013). For example, the DDM fit to a food choice experiment could quite accurately predict choices and RTs in social-preference experiments (Krajbich et al., 2015).

In a refinement of the original DDM, the economic decision DDM assumes that every decision involves a dynamic computation of a relative decision value (*RDV*) variable (Fehr & Rangel, 2011).

In detail, when a decision maker has to decide between two options x and y , “the decision maker observes value signals x_t and y_t , randomly drawn from two distributions with means u_x and u_y ” (Krajbich et al., 2014). At time t , the individual observes value signals and updates her *RDV*. The *RDV* evolves over time (see Figure 9). Note that this model assumes that the decision maker cannot instantly access his/her preferences, but repeatedly samples from normal distributions and applies a sequential likelihood ratio test (Krajbich et al., 2014). Because of the stochasticity of choice, there is the probability that individuals choose an option of lower subjective value (Fehr and Rangel, 2011). Choice “mistakes” result from too little samples, distributions lying very close together (choice difficulty, see Figure 8), or lower barriers (for example due to a speed instruction).

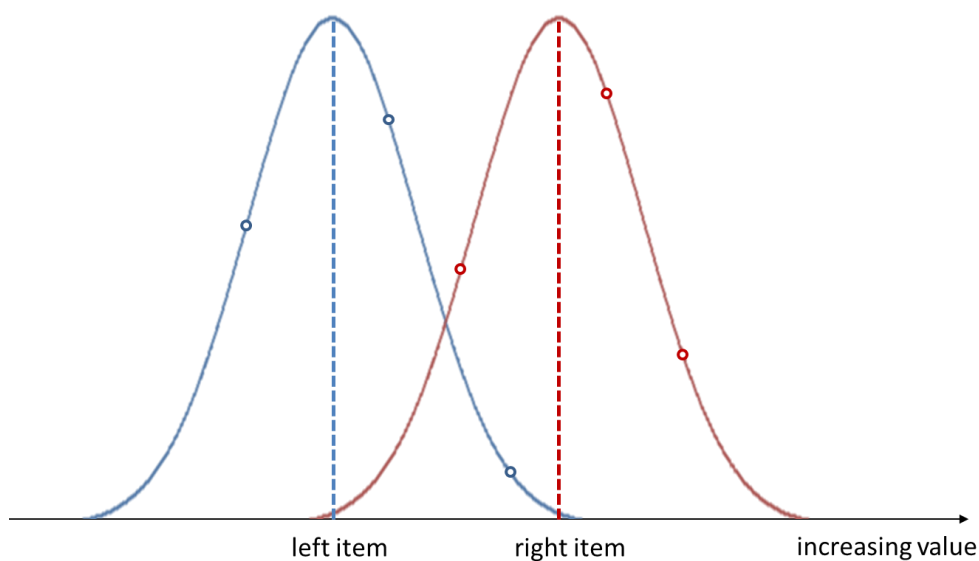


Figure 8: The DDM in economic decision making assumes that decision makers cannot immediately access his/her preferences, but randomly sample from normal distributions around the true value signal. Here, it is assumed that the dotted lines are the true value signals, and the decision maker samples three times from each distribution (dots). Note that if the decision maker only samples once from each distribution, for example the right-most dot of the blue distribution, and the left-most dot of the red distribution, the outcome will be a “mistake” – that is, the left item will be chosen over the right item, although the right item is preferred.

In detail, the RDV, assuming that signals are drawn from normal distributions, evolves over time according to

$$RDV_t = RDV_{t-1} + d(u_x - u_y) + \varepsilon_t$$

Equation 9

where d is a parameter governing the speed of accumulation of the RDV . Trivially, the average rate at which evidence is accumulated relies upon on the difference in subjective value between the two options under consideration (Krajbich et al., 2014, 2015). Thus, when the absolute value difference is large, the RDV evolves with a steeper slope, compared to small value differences; see Figure 9. “Difficult” decisions, that is, decisions between roughly equally liked items (or decisions between equal amounts of moving dots in both directions in case of a perceptual Random Dot Motion task, for example), result in longer RTs.

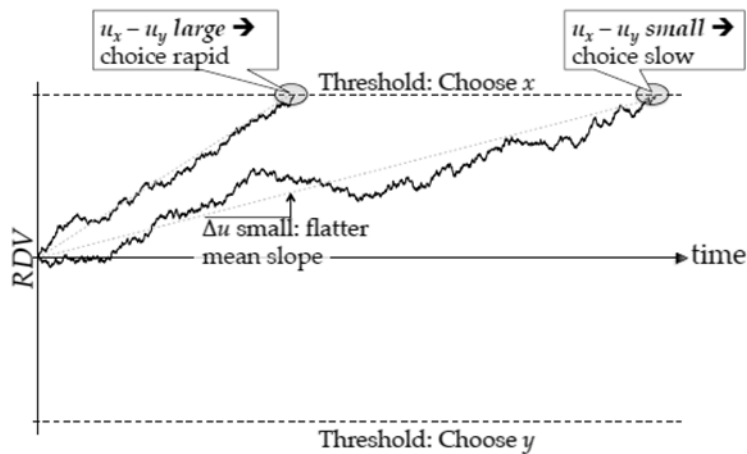


Figure 9: The relative decision value (RDV) evolves over time until one of two decision thresholds is reached. The slope is dependent on the value differences of item x and y (u_x and u_y). From Krajbich et al. (2014).

Note that from a classical economic perspective, decisions between items of equal value should be very fast, as time is a valuable resource and both options are equally utility-maximizing. Empirical evidence and the model demonstrates, and pre-

dicts, respectively, the opposite (Krajbich et al., 2014). The DDM could be fit to a vast-amount of perceptual and value-based decision-tasks (Fehr and Rangel, 2011; Krajbich et al., 2015; Metin et al., 2013; Milosavljevic et al., 2010; Philiastides et al., 2010; Philiastides and Ratcliff, 2013; Rangel and Hare, 2010; Ratcliff and Smith, 2004; Schmitz and Voss, 2012; Voss et al., 2004, 2013a, 2013b).

Functional MRI and non-human electrophysiology data suggest that the computations described by the DDM are similar to the way the brain computes and compares value signals (Basten et al., 2010; Hare et al., 2011b; Heekeren et al., 2008; Philiastides et al., 2006). Further refinements of the DDM include the multi-alternative DDM (Krajbich and Rangel, 2011), the attentional DDM (Krajbich et al., 2010, 2012), see chapter 3.2, and the neural DDM (Hare et al., 2011b).

4.1.1 Applications of DDM in value-based decision making

As outlined above, the DDM implies a suboptimal use of time, as decisions between items of equal value take the longest although both items are equally utility-maximizing. In one study, researchers analyzed whether it is possible to improve this suboptimal use of time by imposing a time limit on individuals' choices. In a block without time limit, participants could take as much time as they wanted for each choice, but had to complete 100 choices in 150 seconds. Unreached choices led to random draws of choices. In a time-limit block, participants were asked to choose as quickly as possible whenever a choice took too long. If participants did not reach a decision within half a second after the onset of the prompt, the choice was drawn randomly. The time limit improved participants' final choice surplus compared to no time limit, that is, the mean difference in value between the chosen and worst option on the screen (this difference is naturally higher when random, instead of preference-based, choices are made). The authors concluded that "DDMs yield new empirically validated insights into the potential sub-optimality of decision makers, which "can be mitigated with novel policy interventions" (Krajbich et al., 2014). In a similar line of research, participants were asked to make value-based decisions under low and high time pressure. The researchers found that the distance between the two decision thresholds (a), that is, the amount of information a participant requires before initiating a response, significantly decreased under time pressure (Milosavljevic et al., 2010), which is in line with results in perceptual decision making tasks (Ratcliff and

McKoon, 2008; Voss et al., 2004). Philiastides & Ratcliff (2013) used brand labels of modulators of value in binary decisions between products. In two blocks, products were presented either with a brand label, or without one. In the block without labels, participants chose based on their subjective values. However, branding biased subjects' decisions towards the more-preferred brand, which could be explained by changes in drift rate only. The study suggests that information on brands and subjective preferences are integrated into an value signal in the decision making process (Philiastides and Ratcliff, 2013).

4.2 Dynamic Causal Modeling

Dynamic causal modeling (DCM) is a biologically plausible Bayesian framework “for inferring hidden”, that is, unobserved, “neuronal states from measurements of brain activity” (Stephan et al., 2009). In a standard mass univariate functional neuroimaging analysis, one can use statistical parametric maps (SPMs) to localize differences in brain activity between, *e.g.*, different tasks, conditions or populations (Friston et al., 1991). More specifically, one can use experimental manipulations (for example different tasks or a pharmacological intervention) to attribute significant regional or focal activations to the processes (sensorimotor or cognitive) manipulated in task A compared to task B, or under pharmaceutical A versus B (Friston et al., 1994). This method only allows the analysis of direct experimental effects on each voxel, without permitting connections between nodes and their modulation (Friston et al., 2003). Psycho-Physiological Interaction (PPI) analysis, a type of functional connectivity analysis, is used to investigate “task-specific changes in the relationship between activity in different brain areas” using regression analysis (O’Reilly et al., 2012). For example, one could analyze the statistical dependency between a region of interest and the rest of the brain during task A compared to task B. Importantly, PPI analysis does not make inferences on the direction of information flow (if region A influences region B, or region B influences region A, or both, or whether the influence is mediated via another region; O’Reilly et al., 2012).

In contrast to functional connectivity analyses, DCM allows inferring effective connectivity, that is, a causal relationship between brain areas, for example, whether activity in region A causally influences activity in region B, or whether ex-

perimental task A modulates the connectivity between brain region A and brain region B. In DCM, the brain is regarded “as a deterministic nonlinear dynamic system”, which is subject to experimental “inputs and produces outputs” (Penny et al., 2011). More specifically, the input, that is, the experimental manipulation, is regarded as “perturbation of neuronal dynamics”, which is distributed through coupled nodes (Penny et al., 2011). Thus, exogenous experimental stimuli evoke brain responses, which can influence network nodes: Inputs can a) influence state variables (neuronal activity) directly, or b) influence the coupling between nodes (Marreiros et al., 2010, Stephan et al., 2007). An example for a direct influence would be visual stimulation, while an example for an indirect influence would be attention (Friston et al., 2003).

To this end, a dynamic input-state-output model is employed. The inputs are usually explanatory variables (from a conventional design matrix as used in classical univariate fMRI analyses). The outputs are hemodynamic responses in the considered brain regions. DCM uses a forward model of how brain regions respond to experimental inputs (as neuronal activity cannot be directly measured using fMRI and is therefore inferred, Friston et al., 2003), see Figure 10.

Neuronal dynamics in nodes (z) are transformed into BOLD signals (y) via a hemodynamic response function (λ); DCM uses this forward model to estimate parameters at a neuronal level, with the aim to maximize the similarity between predicted and estimated BOLD signal (Stephan et al., 2009). Given the neural state equation (see Figure 10), that is, the change in neural systems, the neural parameters can be expressed as partial derivatives of the endogenous connectivity (A-Matrix), modulatory input (B-Matrix) and direct input (C-Matrix, Friston et al., 2003; Marreiros et al., 2008). It is important to note that “DCM does not assume temporal precedence” as a necessity for causality, as “the lag between neuronal activity and BOLD activation can theoretically vary across brain regions” (Ballard et al., 2011).

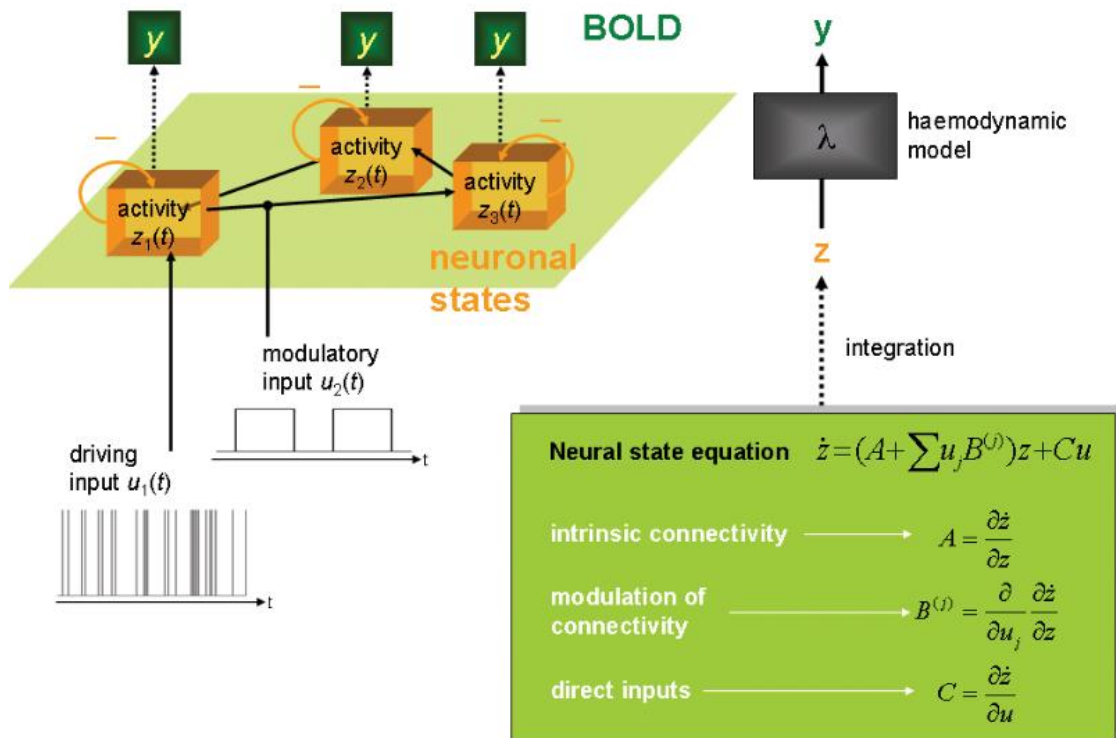


Figure 10. Summary of the state equation used in DCM: The dynamics of the brain system consisting of various nodes cannot be directly observed (orange boxes) and are “determined by experimental manipulations”. Driving inputs, such as visual stimulation, elicit local responses, which are propagated through the system according to intrinsic connections. These in turn can be altered by modulatory inputs, such as changes in task or attention. The integration of the state equation (green box) produces predicted neural dynamics (z), “which enter a model of the hemodynamic response (λ) to give predicted BOLD responses” (y , “hemodynamic forward model”). From SPM 8 Manual, Ashburner et al. (2010).

A ubiquitous question in any modeling approach is which model to select - in most modeling approaches, the decision is not solely made by comparing the relative fit of the alternative models, but also by accounting for the relative complexity, that is, the number of free parameters of the models (Ashburner et al., 2010). While more parameters improve model fit, the generalizability of a model often quite drastically decreases. Bayesian model selection (BMS) is employed for determining the most likely model among competing hypotheses about the mechanisms generating the observed data. “BMS is based on model evidence, which is the probability of obtaining a particular model, given the data” (Rosa et al., 2012). A model space with n nodes has $2^{n \times n}$ permutations of connections that can be turned on or off, which can be addi-

tionally modulated by experimental inputs (Friston and Penny, 2011; Rosa et al., 2012). DCM analyses with several nodes and only few prior hypotheses about the nature of the network hence lead to a combinatorial mass of all plausible models; estimating all possible models in model space is for this reason computationally expensive (Hillebrandt et al., 2013). In a relatively novel, more explorative model selection procedure, that is, “post-hoc” Dynamic Causal Model selection, it is possible to determine the best model out of all possible connection structures. Because only a single model is estimated, this procedure drastically reduces computation time, allowing to search huge model spaces (Rosa et al., 2012).

Post-hoc DCM can be performed in three steps (based on the appendix in Enax et al., 2015b, see original appendix for additional details):

a. Eigenvariate extraction

In a first step, one needs to extract each participant’s principal eigenvariate (preferably around an individual’s local maximum activation closest to the peak voxel identified in a second level group analyses) of at least two regions of interest (nodes) within a specific radius at a specific, relatively liberal, predefined threshold. Whenever no supra-threshold voxels in one or more of the nodes can be extracted, the participant has to be excluded from further analyses

b. Specification of model space and estimation

Driving input and, if applicable, modulatory input, is specified by using regressors from a conventional GLM. A model is a “full model” in a sense that it incorporates all plausible reciprocal fixed connections between and within the nodes of interest (A-Matrix), and, if applicable, their modulation by modulatory input (B-Matrix). The driving input can enter one or n nodes (C-Matrix). The specified model can then be inverted, that is, estimated.

c. Post-hoc model selection

To explore all possible DCMs, a post-hoc model selection routine can be applied (Friston and Penny, 2011; Rosa et al., 2012). The post-hoc search takes a subset of parameters with the least evidence, and searches over all reduced models within that subset (by turning connections “off”). With more than 8 parameters, the post-hoc routine implements a “greedy search” over all models formed by removing all permutations of eight parameters whose individual removal produces the smallest reduction in model evidence, resulting in 2^8 reduced models. All possible combinations of disabling these parameters are evaluated, the model with the greatest evidence is selected, and the steps are repeated until no more connections can be pruned (Crone et al., 2015; Friston and Penny, 2011; Rosa et al., 2012). Post-hoc routines were shown to yield results comparable to conventional DCM model selection procedures (Rosa et al., 2012).

4.2.2 *Applications of DCM in value-based decision making*

Making causal inferences about the structure of a neuronal network is highly attractive for decision neuroscientists.

For instance, Hare and colleagues (2011a) used DCM to examine the mechanism through which the activity in regions related to self-control (that is, three sub-regions of the dlPFC) modulated value signals in the vmPFC. Next to classical, bilinear DCMs, the authors allowed brain regions to influence the coupling strengths between other brain regions (using so-called “non-linear” DCM). “These modulation parameters capture the degree to which changes in the activity of one region modulate the coupling between two other regions” (Hare, 2011a), independent of experimental stimuli. They found that two regions that were more active during blocks in which participants had to consider health attributes in their decision modulated the coupling between another region of the dlPFC (where activity was correlated with obtained health ratings) and the vmPFC (which correlated with the overall subjective value, Hare et al., 2011a). Hence, the authors provided a computational model of how an individual employs self-control in value-based decisions.

As alluded to in previous chapters, it is conjectured that whenever an individual faces a choice between stimuli, the brain assigns values to each stimuli, compares them, and then activates a motor response to implement the decision. Thus, stimulus values need to be transformed into motor commands. In a study specifically addressing the brain's underlying computational model, Hare and colleagues found that the vmPFC, as expected, encoded stimulus values in a binary choice task. The authors found evidence that the vmPFC value signals are passed to regions in the intraparietal sulcus and dorsomedial prefrontal cortex, presumably stimulus values are compared. The output of these “comparator regions” then modulated activity in the motor cortex at the time of decision. This modulation was choice-dependent, in that these regions increased connectivity with the left motor cortex, whenever the right option was chosen, and to the right motor cortex, whenever the left option was chosen (Hare et al., 2011b). Therefore, DCM provides a model of how the brain computes values, compares them, and executes the decision.

Another important issue in value-based decision making is of course how motivation translates goals into actions. Ballard and colleagues (2011) analyzed where reward information enters the brain (“entering” as implied by the DCM framework), and how reward information modulates the mesolimbic reward system. Using DCM, they identified that goal-directed information enters the network in the dlPFC. Reward information predicting high (but not low) rewards then increased the directed connection strength from the dlPFC to regions of the mesolimbic reward system (ventral tegmental area and nucleus accumbens), structures important for motivated behavior. Thus, this study elegantly suggests a model how the dlPFC integrates reward information in a context-dependent manner and then implements goal-directed behavior by influencing the mesolimbic dopamine system (Ballard et al., 2011).

5 Published studies during the qualification phase: context and summary

As discussed in the previous chapters, various contextual factors, such as saliency, affect the choice process and choice outcomes. A unifying model accounting for such effects is missing. Most likely, observed effects of contextual cues on preference formation and choice behavior could be explained by changes in the computation of a subjective value via attention on the attribute or item (Fehr and Rangel, 2011). In four studies, I analyzed how contextual product cues change the valuation process and preferences on a behavioral and neural level. The studies are briefly summarized in the sections below and can be found using the citations below the header.

5.1 Nutrition labels influence value computations in the ventromedial prefrontal cortex

Published in: Enax, L., Hu, Y., Trautner, P., & Weber, B. (2015). Nutrition labels influence value computation of food products in the ventromedial prefrontal cortex. *Obesity*, 23(4), 786–792. <https://doi.org/10.1002/oby.21027>

As introduced in chapter 2.3 and 3.4, the basic model of subjective value computations assumes that the value computed at each point of time is the weighted sum of stimulus attributes, and the weight of attributes depends on attention allocation (Fehr and Rangel, 2011; Hare et al., 2011b; Rangel and Clithero, 2014), see Equation 1, Equation 7, and Equation 8. “Errors” in the computation process are thought to arise due to the inability of decision makers to take into account certain attributes, such as long-term health consequences (Fehr and Rangel, 2011, Hare et al., 2011). Policy-makers often want to positively influence choices and bias them towards choosing options with higher long-term benefits (Kable, 2014). These interventions may change the degree that certain attributes are employed in the computation of a decision value, thereby promoting healthier eating habits (Hawkes et al., 2015).

Nutrition labels have an important role in informing individuals about the health attributes food products (Sonnenberg et al., 2013). In this study, I used nutri-

tion labels as value modulators. In detail, I compared how a more salient, color-coded label, compared to an information-based numeric label influences product valuation on a behavioral and neural level. The study was based on two studies by Hare and colleagues (2009, 2011). As stated above, in the first study (2009), hungry participants were asked to make dietary choices between food items, which varied in taste and health attributes. They found that activity in the vmPFC correlated with stimulus value signals. In self-controlling individuals, the value signal incorporated both health and taste attributes, while it only reflected taste attributes in non-self-controlling individuals. They found that exercising self-control increased activity in the dlPFC, which in turn modulated the value signal in the vmPFC (Hare et al., 2009). In their follow-up study (2011), participants were asked to evaluate food items but the researchers exogenously manipulated the attention on certain attributes. Participants were asked to focus on health, taste, or no particular attribute. They found that the exogenous manipulation of attention towards health attributes increased activity in the dlPFC and changed the value signal in the vmPFC accordingly. As instructing subjects to focus on health attributes is not feasible in daily life, a more subtle way of increasing the integration of health attributes in the valuation process may be achieved with salient nutrition labels.

In this experiment, 35 healthy participants were instructed to evaluate different food items, which were presented in combination with a salient, color-coded, or a numeric, information-based label. They engaged in a BDM auction (see chapter 2.4, incentivized WTP). I conjectured that red labeling on unhealthy items, compared to numeric labeling on unhealthy items, should decrease WTP and increase activation in regions implicated in self-control and response inhibition, that is, the dlPFC (Hare et al., 2009, 2011a; Horn et al., 2003; Simmonds et al., 2008). On the other hand, green labeling on healthy items, compared to numeric labeling on health items, should increase WTP and activation in regions implicated in delayed reward anticipation, such as the posterior cingulate cortex (Kable and Glimcher, 2007; McCoy et al., 2003). The change in valuation should be reflected in the vmPFC. It is of course of interest to analyze the network that changes the valuation. For this reason, I investigated whether regions implicated in self-control and delayed reward expectation showed increased connectivity to the vmPFC at the time of valuation.

I found that salient labels indeed influenced the valuation process in the expected direction, in that the subjective value for green-labeled products increased, while it decreased for red-labeled products, compared to numeric labels. The vmPFC correlated with the subjective value of the items across label types. The functional MRI data suggested similarities between endogenous self-control in dietary choice and red labeling, as it activated a region of the dlPFC and exhibited increased functional coupling (PPI) with the vmPFC. The posterior cingulate cortex, implicated in top-down attention and internal goal representation (Gusnard and Raichle, 2001; Hopfinger et al., 2000) was more activated in response to green labeling and showed increased connectivity to the vmPFC valuation system, suggesting that green labeling may increase long-term reward expectations.

The attentional DDM introduced in chapter 3.2 predicts that exogenous changes of attention, for example via nutrition labels, changes valuation processes. In particular, the model suggests that it biases valuations in favor of the more salient option when its value is positive, and it should have opposite effects when its value is negative (Fehr and Rangel, 2011). Indeed, this is what I found: the green label, compared to the numeric counterpart, more saliently highlights a product's (in this case positive) health attributes and increased the subjective value of the products. In contrast, red labels, compared to the numeric label, highlights a product's negative health attributes and decreased the subjective value. The neuroimaging data provide information on the mechanistic details. Due to the rather poor time resolution of functional MRI, what remains unclear is how exactly health and taste information are dynamically integrated in the decision process between items, and how the value comparison process is influenced by the more salient label, which can be investigated using dynamic models of the choice process, such as the DDM, see study 5.2.

5.2 Salient nutrition labels increase the integration of health attributes in dietary choice

Published in: Enax, L., Krajbich, I., & Weber, B. (2016). Salient nutrition labels increase the integration of health attributes in food decision-making. *Judgment and Decision Making*, 11(5), 460-471.

While ample evidence (Borgmeier and Westenhoefer, 2009; Gorton et al., 2009; Hawley et al., 2013; Jones and Richardson, 2007; Kelly et al., 2009; Roberto et al., 2012) suggests that salient health labels increase health consideration in choices, the underlying mechanism remains unclear. In order to more closely analyze the underlying processes I used the DDM to analyze decisions between two food items along with nutrition labels value modulators to investigate how numerical or color-coded nutrition information and subjective taste preferences are integrated.

In three experiments, 130 participants first rated the taste of various products, and then made binary choices between two products. Both products were either labeled with a salient or numeric label. In the three experiments, the complexity of the label was manipulated. Based on a study by Philiastides & Ratcliff (2013) who analyzed the effects of brand labels on clothing choices, I assumed that the nutrition information would influence the evidence accumulation process. The DDM can be used to test alternative hypotheses: If there is a direct influence of nutrition information on preferences, this should only affect the drift parameter (Philiastides and Ratcliff, 2013). Alternatively, the more salient TL labels might simply result in a stimulus-response association, which would affect the starting point parameter. Based on the previous study (5.1), I now explicitly also investigated whether salient nutrition labels decrease the weight on taste attributes (w_2) and increase the sensitivity to health features (w_1):

$$SV(\text{Food } A) = \sum w_1 * a_{health}(\text{Food } A) + w_2 * a_{taste}(\text{Food } A) + w_i * a_i(\text{Food } A)$$

$$w_{1(TL)} > w_{1(GDA)}$$

$$w_{2(TL)} < w_{2(GDA)}$$

Equation 10

The results show that participants more frequently chose the healthy option when a product was shown along with a color-coded, in contrast to a purely numeric label. The DDM provided information on the underlying cognitive processes: I found that only the parameter estimates for the drift rate significantly varied between the two labels, suggesting that health information and taste preferences are dynamically

integrated. Further, I found that the weight on taste attributes (w_2) decreased, while the sensitivity to health features (w_1) increased.

5.3 Effects of social sustainability signaling on neural valuation signals and taste-experience of food products

Published in: Enax, L., Krapp, V., Piehl, A., & Weber, B. (2015). Effects of social sustainability signaling on neural valuation signals and taste-experience of food products. *Frontiers in Behavioral Neuroscience*, 247.
<https://doi.org/10.3389/fnbeh.2015.00247>

Social sustainable production is a rather abstract product attribute, which can be conveyed using a Fair Trade emblem in a consumer context. As consumer decisions are not only influenced by physical product characteristics but also by contextual marketing cues (see chapter 3.3), a Fair Trade emblem should lead to attribute awareness (that is, most decision makers will take into account this attribute and assign a value to it) and subsequently increased weight on the attribute, leading to a change in valuation. Due to the positive connotation of ethical production (Greibitus et al., 2009) the valuation should be shifted towards increases in WTP. However, what remains unclear is which brain regions are responsible for mediating the increased valuation for Fair Trade products.

In this study, 40 participants valued products presented with a Fair Trade emblem or no emblem in a functional MRI setting using a BDM auction.

I expected increased activation in regions implicated in reward and saliency processing, such as the ventral striatum, a region important for reward processing and decision making (Haber, 2011), which was shown to be more activated in response to organic labeling (Linder et al., 2010). I hypothesized that the change in valuation due to a Fair Trade emblem should be reflected in the vmPFC. Additionally, regions implicated in reward and saliency processing should show increased (and directed) connectivity to the vmPFC.

As expected, I found that Fair Trade products were valued higher, in that WTP was significantly increased for labeled products. This is in line with previous studies demonstrating that consumer's natural and ethical concern are important drivers of

dietary choices, and consumers are willing to pay more for such products (de Ferran and Grunert, 2007; Honkanen et al., 2006). I further found increased activation in regions implicated in reward and saliency processing when comparing the onsets of Fair Trade versus conventional product presentation. The vmPFC correlated with the subjective value, and parts of the ventral striatum and vmPFC correlated with the increment value of Fair Trade products over conventional products. I additionally analyzed the brain network that may promote the increased valuation of Fair Trade products and analyzed functional (Psycho-Physiological Interaction) and effective (DCM) connectivity. Regions involved in reward and saliency processing exhibited increased task-related functional connectivity with the vmPFC. However, only DCM analyses provide information on the causal structure of the network. I found a highly probable directed modulation of the vmPFC by these regions. The results reveal a potential neural mechanism underlying valuation process of certified food items.

Coming back to the model of subjective value computations based on the considered attributes

$$SV(\text{Food } A) = \sum w_1 * a_{Fair}(\text{Food } A) + w_i * a_i(\text{Food } A)$$

Equation 11

I have demonstrated that the subjective value of food items changes due to the addition of a rather abstract product attribute a_{Fair} . As this attribute has a positive connotation (Greibitus et al., 2009), the subjective value of a food item increases. I provide evidence for a neural mechanism for the change in the valuation process by applying advanced DCM analyses. As introduced in chapter 4.2.

What remains unknown is their long-term effect, as individuals may fail to notice the labels after being sufficiently acquainted to them. Likewise, social ethics claims may induce so-called health-halo effects, as they may promote misperceptions about a food's healthiness, as consumers seem to extrapolate attributes with a positive connotation, such as social sustainable production, to health evaluations (Schuldt et al., 2012)

5.4 Food packaging cues influence taste perception and increase effort provision for a recommended snack product in children

Published in: Enax, L., Weber, B., Ahlers, M., Kaiser, U., Diethelm, K., Holtkamp, D., Faupel, U., Holzmüller, H.H., & Kersting, M. (2015). Food packaging cues influence taste perception and increase effort provision for a recommended snack product in children. *Frontiers in Psychology*, 6, 882. <https://doi.org/10.3389/fpsyg.2015.00882>

Based on the findings from the Fair Trade study in adults, I examined whether attributes signaling “fun” and “health” can likewise influence preferences in children. As most industrial marketing strategies targeted at children promote unhealthy food items (No et al., 2014), I specifically addressed the effect of marketing labels on a healthy, recommended food item. I therefore analyzed the causal relationship between marketing actions and children’s preferences, *i.e.*, subjective liking ratings and the motivation to provide effort for receiving an item. I specifically investigated whether

$$SV(\text{Food } A) = \sum w_1 * a_{Fun}(\text{Food } A) + w_2 * a_{Health}(\text{Food } A) + w_i * a_i(\text{Food } A)$$

Equation 12

the subjective value of a recommended snack food changes due to the addition of a cartoon character, that is, a “fun” attribute, similar to how the subjective value changes in adults when confronted with items containing an abstract, social sustainability attribute. In contrast, a “health” attribute conveyed via a health label should have a smaller effect on subjective value computations, *i.e.*, I expected $w_1 > w_2$.

As introduced in chapter 2.5.2, various studies suggest that explicit liking measures of food items do not fully explain dietary choices (Epstein et al., 2003; Me-la, 2006; Temple, 2014). I therefore also measured the motivation to work for an item, which has been previously confined to research in adults. I used a novel method to measure the amount of effort a child is willing to expend in order to receive the food item, *i.e.*, handgrip strength.

In a sample of 179 children between 8 and 10 years of age, explicit liking of food items and effort provision for obtaining a food item were measured. Three rec-

commended yoghurts with a plain, a “health” and a “fun + health” label were presented. Notably, all three items were of identical composition. The main hypothesis was that the use of a “fun” attribute, but not of a “health” attribute alone, would increase explicit liking. Further, effort provision was measured using a handgrip dynamometer as a novel tool in the domain of children’s food choices and hypothesized increased effort provision for the product that contained a “fun” label. Importantly, I conjectured that both measures separately explained a significant amount of variance in subsequent choice behavior.

I found a causal relationship between marketing cues and two measures of preferences of an identically composed snack item in children. Child-directed cues significantly increased subjective liking ratings and increased effort provision. In contrast, a health label alone did not have a similar effect. Moreover, I could demonstrate that both stated subjective preference ratings as well as the effort provision measure explained variance in food choices.

Most research in the domain of value-based decision making is confined to adults. As dietary preferences develop very early in life and influence future behavior (Beauchamp and Mennella, 2009; Benton, 2004; Birch and Fisher, 1998; Harris, 2008), it is of interest to more deeply analyze how preferences evolve. Future studies in this direction are hence certainly necessary. Also, most studies in the decision making literature have been using liking ratings or binary choice behavior as measures of preferences. As various lines of research suggest that reward processing can be distinguished into *liking* and *wanting* components (Berridge, 1996; Berridge and Krangelbach, 2008; Berridge and Robinson, 2003), it is of interest to further elicit also the motivation to work for an item and include them in formal models of decision making.

6 Published review articles during the qualification phase: context and summary

In addition to the above mentioned studies, I published two review articles during my doctoral work. These are briefly summarized here due to their relevance to the overall topic of investigation.

Contextual variables strongly affect preferences. Whether such cues can be employed to induce positive behavior change is reviewed in the first review article. In addition, although food items are frequently used as stimuli in the laboratory, food decisions are a special case of decision making due to the tight regulation by homeostatic and reward systems (see chapter 2.5). A multidisciplinary view on dietary choice is reviewed in the second review article.

6.1 Marketing Placebo Effects – from behavioral effects to behavior change?

Published in: Enax, L., & Weber, B. (2015). Marketing Placebo Effects – From Behavioral Effects to Behavior Change? *Journal of Agricultural & Food Industrial Organization*, 13(1), 15–31. <https://doi.org/10.1515/jafio-2015-0015>

As the previous chapters have highlighted, contextual variables, such as marketing cues, can change the hedonic value derived from consumption, inducing a so-called “Marketing Placebo Effect”. For example, a wine with a higher price tag is perceived to be tastier, compared to the same wine with a lower price tag on a behavioral and neural level (Plassmann et al., 2008). The review summarizes current findings from various research disciplines, such as marketing, health psychology and neuroscience. I further suggest that insights can be used to actually positively influence consumer decision making and provide examples for this supposition.

6.2 Neurobiology of food choices – between energy homeostasis, reward system, and neuroeconomics

Published in: Enax, L., & Weber, B. (2016). Neurobiology of food choices—between energy homeostasis, reward system, and neuroeconomics. *E-Neuroforum*, 1–9. <https://doi.org/10.1007/s13295-015-0020-0>

Food decisions are influenced by a myriad of internal and external factors and lie at the core of many increasing health issues. Because of the biological necessity to consume sufficient amounts of energy, different systems, such as homeostatic and reward systems, regulate feeding behavior and energy expenditure. The systems are interdependent, as for example homeostatic signals can change the rewarding properties of food items, while cognitive control mechanisms may override hedonic valuation processes (Morton et al., 2014; Rangel, 2013). In this review, I present findings from neurobiology, nutrition science, hormonal research, genetics and neuroeconomics to provide a joint perspective on dietary choice.

7 Unpublished study during the qualification phase: context and summary

I additionally worked on an additional experiment on dietary choice and taste preferences during my doctoral work. The manuscript stemming from this work is not published yet but briefly summarized due to its relevance to the overall topic of investigation.

7.1 Oxytocin influences expectancy effects on taste pleasantness

As mentioned chapters 3.3 and 3.4, the experienced utility (at the time of consumption) does not only vary as a function of subjective product liking and physical product properties, but also critically depends on consumer's expectations. The hypothalamic peptide oxytocin (OXT) has been demonstrated to be important for social decision making (Averbeck, 2010; Churchland and Winkielman, 2012; Kosfeld et al., 2005; Shamay-Tsoory and Abu-Akel, 2016), and was shown to increase placebo analgesia (Kessner et al., 2013). What remains unclear is whether OXT also contributes to every-day consumer decisions by modulating the experienced utility of identical food items.

In a double-blind, placebo-controlled, randomized, parallel-group design with 113 male participants, I investigated the influence of intranasal OXT on MPEs.

I hypothesized that OXT does not increase taste ratings of products *per se*, but that it increases taste pleasantness ratings for products presented with a frequently used marketing cue, increasing the MPE (see chapter 3.3 and review 6.1 for a detailed definition and previous studies in the field).

As expected, I found increased taste pleasantness ratings for products presented with a frequently used marketing cue, which was significantly enhanced in the OXT group. I found that MPEs vary as a function of trust. Further studies are needed to substantiate or refute the putative mechanism of trust on MPE via the OXT system. This study provides the groundwork for future research elucidating the role of signaling molecules in the generation of MPEs. Particularly, computational modeling would

be promising, as for example the DDM allows to directly test which underlying cognitive processing components are influenced by OXT levels.

8 Overall discussion and outlook

Value-based decisions are made almost continuously. Stimulus values are thought to be dependent on the degree an individual computes and weights individual stimulus attributes. Since value computations are dynamic (Rangel, 2013), providing information about a certain attribute, or making this attribute more salient, may change behavior (Fehr and Rangel, 2011).

For instance, an individual may not be able to take into account certain long-term attributes when computing a subjective value and making a choice. Thereby, exogenous cues, such as reminding individuals of health attributes in food decisions (Hare et al., 2011a), may aid in positively influencing behavior. In several studies, I could show that exogenous cues as modulators of value influence value computations and the experienced utility of products. Specifically, the published manuscripts provide evidence that 1) salient vs. numeric nutrition labels alter the valuation of products and that the neural mechanism resembles endogenous self-control. 2) Salient vs. numeric nutrition labels influence attribute weighting. 3) Social sustainability signaling alters valuation processes, with directed (causal) influence of regions implicated in reward and saliency processing on the vmPFC. 4) Child-directed, but not health-directed marketing cues increase subjective liking ratings and effort provision in children. Critically, both measures explain a significant amount of variance in subsequent food choices.

A critical question for future research is to understand the long-term effects of such marketing techniques, and how they interact with prices, familiarity, and other attributes (Fehr and Rangel, 2011). Although preferences influence decisions, the deeper analysis of different reward components, such as “liking” versus “wanting” (Berridge, 1996) would provide valuable insights in decision making research. Albeit a special focus was placed on the fact that dietary choices are special cases of value-based decisions in this dissertation, the studies during the qualification phase (just like virtually every study in this domain) ignored that aspect. Future research should hence more closely analyze the tight interaction between the reward, homeostatic, and decision making circuitry. An important aspect in decision making research in general, and in our studies in particular, is the external validity of the obtained results.

Eliciting real-world decision making, in combination with laboratory experiments, will certainly be an indispensable future research endeavor. Also, it is important to acknowledge that the subjective value (and experienced utility signals) depend on the entire history of previous choices, and not on a single choice or consumption episode (Fehr and Rangel, 2011) as measured in a laboratory experiment.

Additionally, although the DDM and the attentional DDM are valuable tools for inferring cognitive mechanisms, it is important to note that these models are actually rather simple models of the choice process. Although the simplicity is intriguing when considering how well they fit choice data, it is highly likely that the brain uses a much more sophisticated algorithm. While the effect of attention on preference formation has been demonstrated in various studies (Armel et al., 2008; Krajbich et al., 2010; Milosavljevic et al., 2012; Shimojo et al., 2003), the causal effect of fixations on preferences remains to be studied in much more detail. Also, it would be of high interest to unravel so-called “boundary conditions”, that is, conditions in which these models fail to account for choice data. To the best of my knowledge, no published studies have tried to falsify the models mentioned above in decision making research. Moreover, much more work remains to be done in defining computational models in complex settings, for instance when decisions have important long-term consequences, such as financial investments.

What the DDM and the attentional DDM discussed in this dissertation do not explicitly model are processes related to a dual-systems theory: The dual system theory suggests that two “competing” systems interact, that is, System 1 (evolutionary older, limbic system, “visceral” or “hot” system) versus System 2 (evolutionary recent, neocortex, also called self-control system, the “cool” system, or “non-visceral motivation”, Evans, 2008; Loewenstein, 1996; Metcalfe and Mischel, 1999; Monterosso and Luo, 2010). Indeed, a very recent modeling approach explicitly models the competition between these two systems (Alós-Ferrer, 2016). Notwithstanding, various lines of research propound that a “multiple-self” account of human behavior is, from a neuroscientific viewpoint, rather unlikely. Many researchers suggest a convergence rather than a competition between limbic and prefrontal regions, and a “final common currency” (Brosch and Sander, 2013; Clithero and Rangel, 2014; Hare et al., 2011a, 2011b; Hutcherson et al., 2015; Kable, 2014; Monterosso and Luo, 2010; Plassmann et al., 2008; Platt and Plassmann, 2014). This would suggest that for ex-

ample dlPFC activity modulates vmPFC activity, rather than competes with “visceral motivations”, a view that was supported for instance in the study on self-control in dietary choice by Hare and colleagues (2009). Nevertheless, the debate between “dual-self” versus “modulated self” is not fully resolved. Based on recent literature, it would be important to explicitly model self-control as a modulator in the subjective value computation and comparison process.

In sum, understanding the neurobiological and computational foundations of the choice process is an important research endeavor, because

“Life is the sum of all your choices.”

Albert Camus (1913-1960)

The study of neuroeconomics is a relatively novel field, and much of the groundwork remains to be done (Fehr and Rangel, 2011). While I have shown that it is possible to bias the value computation processes, preferences, and the motivation to work for an item, various specific and general questions, some of them specified above, remain unanswered. But: *“Parvis imbutus tentabis grandia tutus”* – Once small things are accomplished, you can try to attempt greater things (Motto of Barnard Castle School). Future research projects aiming at understanding the “big picture” of value-based decision making are hence certainly on their way.

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10 Acknowledgements

The time as a Ph.D. candidate always constitutes a challenging journey. One transforms from a student who learns what she is told to someone who is actually doing science, with all of its joys, difficulties and pitfalls. Of course, this journey would not have been possible without support, assistance and guidance. Therefore, I would like to take the opportunity to express my gratitude.

First and foremost, I want to thank my advisor Prof. Bernd Weber for giving me the opportunity to conduct functional imaging studies in the Life & Brain. I appreciate his contributions, his time, ideas, and funding. I want to thank Prof. Ulrich Ettinger, my doctorate supervisor. Although he was not directly involved in my dissertation projects, I enjoyed his uncomplicated and friendly support and advice.

I gratefully acknowledge the funding source that made my Ph.D. work possible, which is the competence cluster Diet-Body-Brain. The cluster has provided many interesting and insightful seminar lectures. I believe that the cluster will yield many excellent research results, which I am excited to read in future papers.

I would like to thank the members of the group in the Life & Brain who have contributed to various aspects of my studies. From the CENs team, foremost I want to thank Xenia Grote and Sophia Konrad for their constant support. The discussions with all other members and affiliates of the CENs are greatly appreciated. I would also like to thank my main external collaborator during my thesis, Ian Krajbich, for his support.

For this dissertation, I would like to sincerely thank my PhD committee members: Prof. Dr. Martin Reuter, PD. Dr. Sarah Egert, and of course Bernd and Uli for their time, interest and expertise.

Lastly, I would like to thank my family for their unconditional encouragement and love, for their support and all the opportunities I could enjoy throughout my life. Danke, Ulla, dem größten Fan meines Dr. s. c. l., für all deine so liebevolle Unterstützung und deine Ratschläge. Last but definitely not least, thank you, Christoph, for constant understanding, patience and encouragement.