Max Planck Research Group

Neurocognition of Decision Making

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The Institute has housed the **Max Planck Research Group "Neurocognition of Decision Making"** until September 2010 (Head: Hauke R. Heekeren). Using a combination of psychophysical methods, functional and structural neuroimaging, modeling, and pharmacological intervention, this group investigated mechanisms of decision making in the human brain.

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Research Agenda: Multimodal Approach to the Neurocognition of Decision Making

Decision making can be defined as the process of choosing a preferred option or course of action from among a set of alternatives. There is a long history of decision-making research in psychology and economics that has resulted in the development of formal models of behavior, which are inspired by behavioral data or the computational demands of a task. Examples for the former are sequential sampling models of decision making. Examples for the latter are reinforcement learning models for repeated choice tasks. Cognitive functions, such as decision making, can, however, not be completely understood on the basis of mathematical models and behavioral data alone; we have to investigate how mental (cognitive) and neuronal processes map onto each other. Therefore, a central goal of the Max Planck Research Group "Neurocognition of Decision Making" is to explicitly link brain function and behavior using formal models of decision-making behavior.

In pursuit of this goal, we investigate decision making in different domains. First, at the basis of a number of different decisions we are facing in everyday life stands *perceptual decision making:* the process of translating sensory input into some kind of motor output (cf. Figure 1). Second, many of our decisions are influenced by the potential outcomes associated with different options; hence, *reward-based decision making* is another important topic for our group. Finally, *decision making in social contexts* relies not only on perceptual and reward-related processes but also includes more complex cognitive processes and emotional aspects as well as the interaction between the two. We believe that the investigation of the neurocognition of decision making requires a multimodal meth-
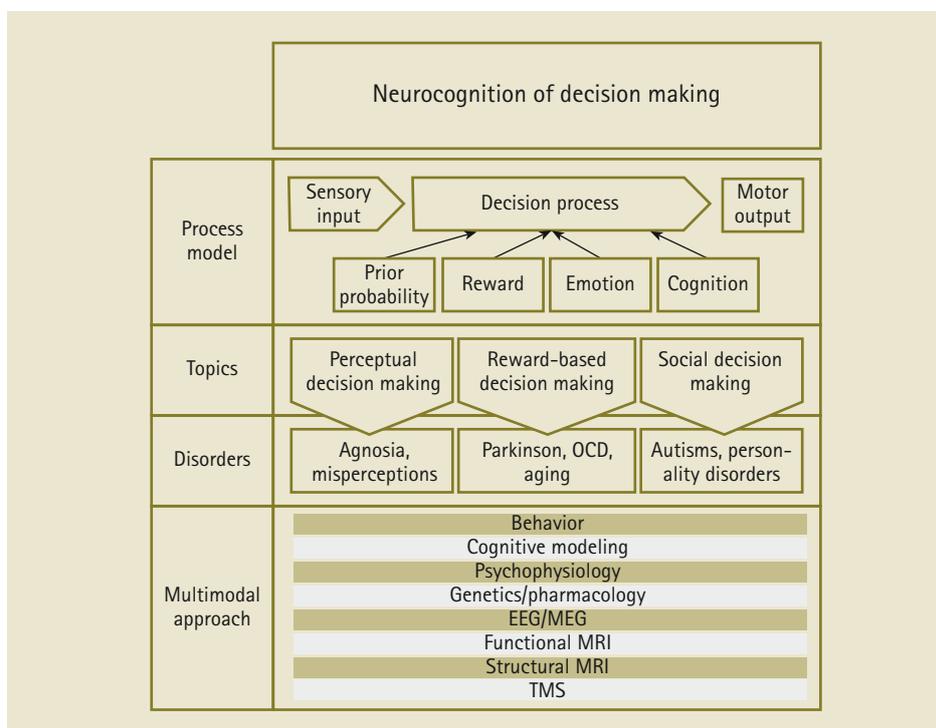
Figure 1. Multimodal approach to neurocognition of decision making.

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Key Reference

Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience, 9,* 467–479.

odological approach that integrates information from an array of methods, ranging from cognitive modeling based on behavioral data to fMRI and MEG experiments (cf. Figure 1). On the following pages, we briefly describe research in the three topics in more detail. Each section begins with a brief introduction, which is followed by short descriptions of individual projects.

Neurocognition of Perceptual Decision Making

Perceptual decision making is the act of choosing one option or course of action from a set of alternatives based on the available sensory evidence (Heekeren, Marrett, &

Ungerleider, 2008). Thus, when we make decisions, sensory information must be interpreted and translated into behavior. For example, in a motion-direction discrimination task, motion signals need to be interpreted and translated into a saccadic eye movement. In a face-house discrimination task, degraded images of faces and houses have to be interpreted and translated into a button press with the right or the left hand (see Figure 2). Decision-making research has resulted in mathematical models of the assumed underlying cognitive processes. Sequential sampling models are particularly successful in explaining response time data and accuracy in two-choice reaction time tasks, such as the ones described
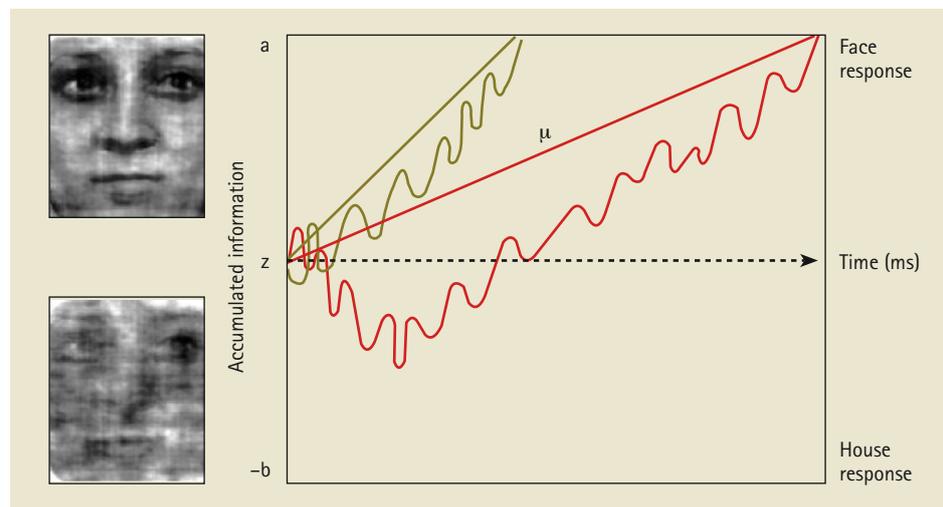
Figure 2. Decision-making research has led to the development of mathematical models of the assumed underlying cognitive processes. Diffusion models are particularly successful in explaining response time and accuracy data in two-choice reaction-time tasks. These models assume that decisions are formed by continuously accumulating sensory information until one of the two response criteria (a or −b) is reached (see figure). Once a boundary has been reached, the decision process is concluded and a response is elicited. Moment-by-moment fluctuations in the sample path reflect noise in the decision process. The drift rate (μ) is related to the efficacy of information processing and depends on the strength of the sensory signal and on the accumulation rate (i.e., the increase in the decision variable that quantifies how much evidence is accumulated per time interval). Clear images of faces contain more sensory evidence than degraded images, and, therefore, the drift rate is greater for clear images (green trace in the figure) than for degraded images (red trace). Recent studies have also modeled neurophysiological data as a diffusion process: a dual-diffusion model provides a quantitative account of both the behavior in simple perceptual decision making and the patterns of activity in competing neuron populations. In these studies, monkeys performed a brightness-discrimination task and made saccades to one of two peripheral targets. Task difficulty was manipulated by varying the ratio of black to white pixels. A diffusion model was fitted to the behavioral data. Based on the hypothesis that the neuronal firing rate is linearly related to the accumulated evidence, simulated paths from the model were compared with neural activity. Similar to the behavioral data, the firing rate data showed delayed availability of discriminative information for fast, intermediate, and slow decisions when activity was aligned on the stimulus. By contrast, the firing rate showed very small differences in discriminative information when activity was aligned on the saccade. The first study to link human brain signals with parameters of the diffusion model was that of Philiastides and Sajda (2007). These authors estimated diffusion rates for different noise levels on the basis of behavioral data from a face–car categorization task.

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above. A prominent version of sequential sampling models are diffusion models, which assume that decisions are formed by continuously accumulating sensory information until one of the two response criteria (a or –b) is reached (cf. Figure 2). Once a boundary is reached, the decision process is concluded and a response is elicited. Moment-by-moment fluctuations in the sample path reflect noise in the decision process. The drift rate (μ) is related to the efficacy of information processing and depends on the strength of the sensory signal as well as the accumulation rate (the increase in the decision variable that quantifies how much evidence is accumulated per time interval). Clear images of faces contain more sensory evidence than degraded images, therefore, the drift rate is greater for clear images (green) than for degraded images (red) (see Figure 2).

More recent studies in monkeys and humans have begun to model not only psychophysical but also neurophysiological data as a diffusion-to-barrier process providing a quantitative link between behavior (decision outcome) and neural activity (decision processing) (Heekeren et al., 2008). In ongoing projects, we build on our previous work and provide causal evidence for a role of the dorsolateral prefrontal cortex (DLPFC) in perceptual decision making, try to disentangle motor preparation and decision-related processing, and test how task instructions and reward information modulate perceptual decision making. Finally, we investigated, how human decision makers adapt thresholds to maximize reward in a perceptual decision-making task.

A Causal Role for the DLPFC in Perceptual Decision Making

The way we interpret and interact with the world entails making decisions on the basis of available sensory evidence. As highlighted above, perceptual decisions are often thought to involve an integrative process in which sensory evidence accumulates over time until an internal decision bound is reached. Based on previous reports, one possible region that might be involved in this integrative process is the DLPFC (cf. Heekeren et al., 2008). Despite

the importance of this finding in advancing our understanding of the neural correlates of perceptual decision making, human studies have not yet provided causal evidence linking these candidate areas directly to the mechanism of evidence accumulation.

The major limiting factor in establishing this link has been the correlational nature of most neuroimaging methods, which provide no causal (i.e., interventional) evidence for the functional contribution of activated brain regions to a particular task or underlying neuronal process. In this project, we combined rTMS and computational modeling to help establish the missing causal link between prefrontal cortex and the process of evidence accumulation during human perceptual decision making.

Specifically, we used a speeded perceptual categorization task designed to induce a time-dependent accumulation of sensory evidence through rapidly updating dynamic stimuli after having disrupted the func-
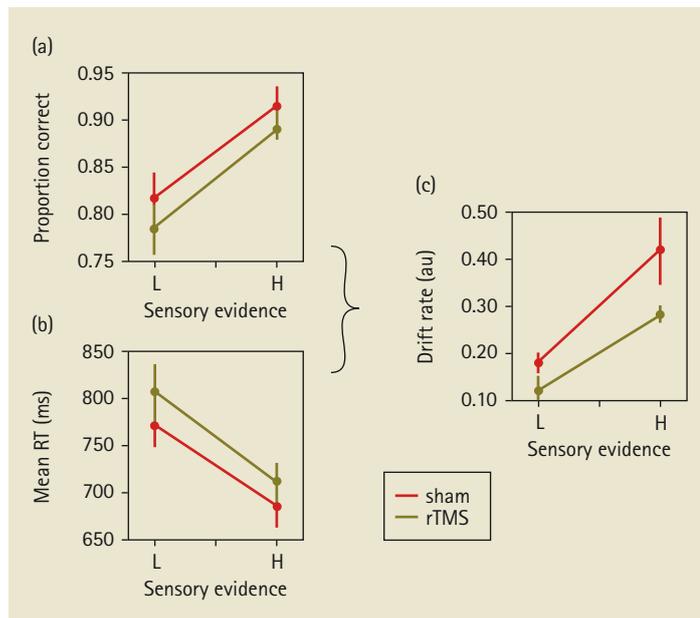

Figure 3. Behavioral performance during the rTMS (green) and sham (red) conditions. (a) Mean accuracy and (b) mean response time (RT) across participants for two levels of sensory evidence (L: low, H: high). Disruption of left DLPFC with rTMS reduced accuracy and increased RTs relative to the sham condition. (c) Modeling this behavioral performance with the diffusion model revealed that the effects were due to a reduction in the rate of sensory evidence integration during rTMS of left DLPFC. Error bars represent standard error of the mean.

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tion of left DLPFC with rTMS. We found that disruption of left DLPFC with rTMS reduced accuracy and increased response times relative to a sham condition (cf. Figure 3a, 3b). Importantly, using the drift diffusion model, we showed that these behavioral effects correspond to a decrease in drift rate, the parameter describing the rate, and thereby the efficiency of the sensory evidence integration in the decision process (cf. Figure 3c). These results provide causal evidence linking DLPFC to the mechanism of evidence accumulation during perceptual decision making.

Disentangling Perceptual Decision Making and Motor Preparation
It has been claimed that sensorimotor areas involved in planning a response, such as an eye movement or a button press, also participate in decision making. For instance, the LIP of the macaque, which is involved in planning eye movements, also shows a response profile compatible with integration of sensory evidence leading to a perceptual decision. Specifically, LIP neurons fire more strongly, and show a greater build-up of activity, during viewing of a stimulus that contains more sensory evidence (less noise) compared to a stimulus with less sensory evidence (more noise).

However, perceptual decisions (deciding if a visual image is a face or house, or if a field of dots is moving right or left) should, in principle, be possible without having to produce a motor response. In fact, more often than not, we make perceptual decisions without having to produce a button press or an eye movement to indicate that decision. Previous fMRI and single-unit recording studies have (with very few exceptions) always paired preassigned motor responses with perceptual decisions and thus may have confounded representation of sensory evidence with processes related to motor preparation. For instance, rightward dot motion was paired with a rightward saccade and leftward motion with a leftward saccade; the motor targets were thus already known at the time of the perceptual decision. This suggests that the perceptual decision might have automatically triggered preparatory motor activations

that do not, in fact, have anything to do with the act of reaching the decision per se.

To investigate the involvement of sensorimotor regions as opposed to an abstract decision-making area in perceptual decision making, we designed an experiment where participants are asked to decide if visual images represent a face or a house. There are two levels of sensory evidence, high and low, produced by mixing low or high levels of noise in the images, respectively. In other words, half the faces and houses are relatively easy to categorize, while the other half are harder to categorize. Importantly, subjects do not know how to indicate their decision (hand or eye movement and direction of movement) at the moment of the decision. Rather, subjects receive instructions to prepare either a button press or an eye movement to one of four possible targets only after the decision stage (and a variable delay). There are thus eight possible motor plans (hand or eye, four possible targets), which can only be formed after the decision has been reached. To ensure subjects reach a decision before the motor preparation stage, they are given sufficient time during the perceptual decision stage.

fMRI results indicated that, at the moment of the perceptual decision, sensorimotor regions, such as LIP, are in fact *not* involved in integrating sensory evidence leading to that decision. A psychophysiological interaction analysis showed that changes in BOLD signal in DLPFC positively correlate with face and house decisions, and with the absolute difference in activation between the brain regions representing faces and houses (cf. Figure 4a). This correlation between BOLD signal changes in prefrontal cortex and face- and house-responsive brain regions was modulated by the amount of sensory evidence, as predicted by diffusion models of decision making.

Interestingly, area LIP showed greater activation for greater sensory evidence, but only *after* the motor plan was known, and, specifically, only after subjects were able to start planning an eye movement to a specific target (cf. Figure 4b). In other words, only once subjects knew they would be indicating their decision with an eye movement did area
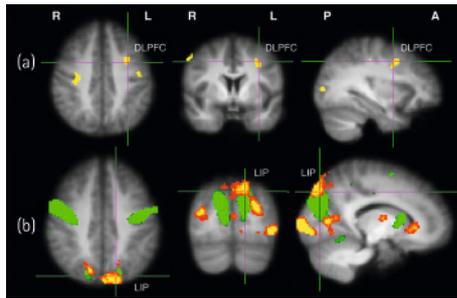
Figure 4. Averaged fMRI BOLD activations ($p < 0.01$) from 16 subjects. (a) Yellow: results of a psychophysiological interaction analysis revealing areas that correlate with the absolute difference between face and house BOLD signals (from areas FFA and PPA) during presentation of high- versus low-sensory evidence images. Area DLPFC, but not posterior parietal cortex, correlates with face versus house decisions and is modulated by the amount of sensory evidence. (b) Overlay of two BOLD activation contrasts. Green: BOLD activations greater for saccade preparation than button press preparation. Area LIP in posterior parietal cortex is indicated with crosshairs. Yellow-to-red: saccade preparation activations following a high- versus low-sensory face or house trial. Area LIP is modulated by the amount of sensory evidence, but only during the saccade preparation stage following presentation of the motor targets. R: right; L: left; P: posterior; A: anterior.

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LIP show greater activation for easy compared to difficult decisions. Thus, LIP could be characterized as representing *motor decisions,* but not *perceptual decisions* per se. This explains previous studies in which LIP was shown to correlate with the sensory evidence leading to a perceptual decision, but where the motor stage had not been disentangled from the decision stage. The confidence of the perceptual decision is passed onto the motor system, exemplifying how perception and action interact (see also Green & Heekeren, 2009).

Task Instructions and Reward Information as Modulators of Perceptual Decision Making
The diffusion model predicts that a decision (and response) will be made as soon as the boundary or threshold representing one of the possible options is reached. It is still unclear how different levels of certainty and time pressure influence the setting of this decision boundary in humans.
Furthermore, decisions often entail either positive or negative outcomes. The rewards

and punishments that are associated with different choice options are, therefore, an important factor in decision making. Recently, ideas about how the brain values different choices have been developed; however, to date, it is unclear how the systems that are involved in perceptual decision making interact with the systems that are involved in valuation. Rewards might affect sensory representations as well as motor planning or action selection; however, how this occurs in the human brain is an open question. At the most basic level, it is of interest how humans trade off speed and accuracy in decision making to optimize rewards.

Speed-Accuracy Trade-Off in Perceptual Decision Making
Decisions often necessitate a trade-off between speed and accuracy, that is, fast decisions are more error-prone while careful decisions take longer. Sequential sampling models assume that evidence for either of two response alternatives is accumulated over time. In addition, they suggest that SAT modulates the decision system by setting a lower boundary on required accumulated evidence to commit a response under time pressure.
We used MEG and a face-house categorization task, in which we manipulated sensory evidence (low, medium, high) and instructions (speed vs. accuracy) to investigate how such a speed accuracy trade-off is implemented neurally under different levels of stimulus certainty. Diffusion modeling of the behavioral data revealed that the drift rate increased with increasing sensory evidence, but did not differ significantly between instructions (speed vs. accuracy) (cf. Figure 5a). In contrast, the response threshold (boundary) differed significantly between instructions. The response threshold was lower in the speed condition compared to the accuracy condition, but did not differ with regard to sensory evidence (cf. Figure 5b).
The MEG data show that SAT modulates the later decision- and motor-related systems rather than the early sensory systems. Source analysis revealed that the bilateral SMA and the medial precuneus were more activated

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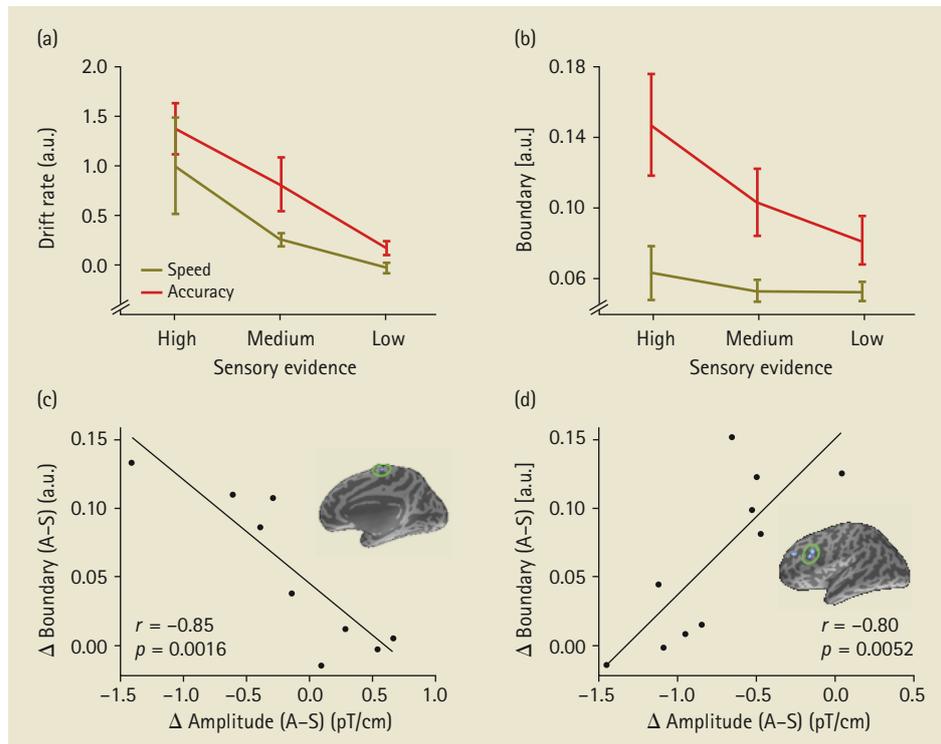
Figure 5. Modeling and neural data from a perceptual decision-making task on speed-accuracy tradeoff. Diffusion modeling of the behavioral data revealed that the drift rate increased with increasing sensory evidence, but did not differ significantly between speed and accuracy instructions (a), whereas the decision boundary differed significantly between instructions (lower in the speed than the accuracy condition and no difference over sensory evidence) (b). While pre-SMA was more active during the speed instruction and was correlated negatively with changes in decision boundary (c), DLPFC was more active during the accuracy condition and correlated positively with adjustments in the decision boundary (d).

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under speed instruction and correlated negatively (right SMA) with the boundary parameter (cf. Figure 5c), whereas the left DLPFC was more activated under accuracy instruction and showed a positive correlation with the boundary (cf. Figure 5d). The interpretation of these findings is that SMA activity dynamically facilitates fast responses during stimulus processing, potentially by disinhibiting thalamo-striatal loops, whereas DLPFC reflects accumulated evidence before response execution (Wenzlaff, Bauer, Maess, & Heekeren, 2011).

The Influence of Punishment on Perceptual Decision Making

In addition to the amount of sensory evidence and task instructions, perceptual decision making can also be influenced by other fac-

tors, such as reward and punishment. In this project, we studied how monetary punishment influences perceptual decision making. Specifically, we used a speeded perceptual categorization task in which the amount of sensory evidence and the degree of punishment were manipulated experimentally while simultaneously collecting EEG data. We subsequently combined the drift diffusion model with the EEG data to identify which of the model's internal variables (e. g., rate of integration, decision boundary) are influenced by punishment and to subsequently identify how and when these changes are represented in the brain.

As in previous studies, we found that manipulating the amount of sensory evidence had an influence on drift rate, with higher amounts of sensory evidence leading to

higher drift rates. Critical to the current project, we also found that increased punishment resulted, on average, in increased drift rates and increased decision boundaries. These findings are consistent with a decision optimization strategy in which the process of evidence integration becomes more efficient and lasts longer as punishment levels are increased.

Furthermore, we identified the EEG signals that were predictive of the changes in drift rate and boundary as a function of punishment using multiple regression analysis. We found that punishment-induced changes in EEG predicted drift rate and boundary in the diffusion model at a later stage of the decision process, starting around 400 ms after the onset of the stimulus and lasting until
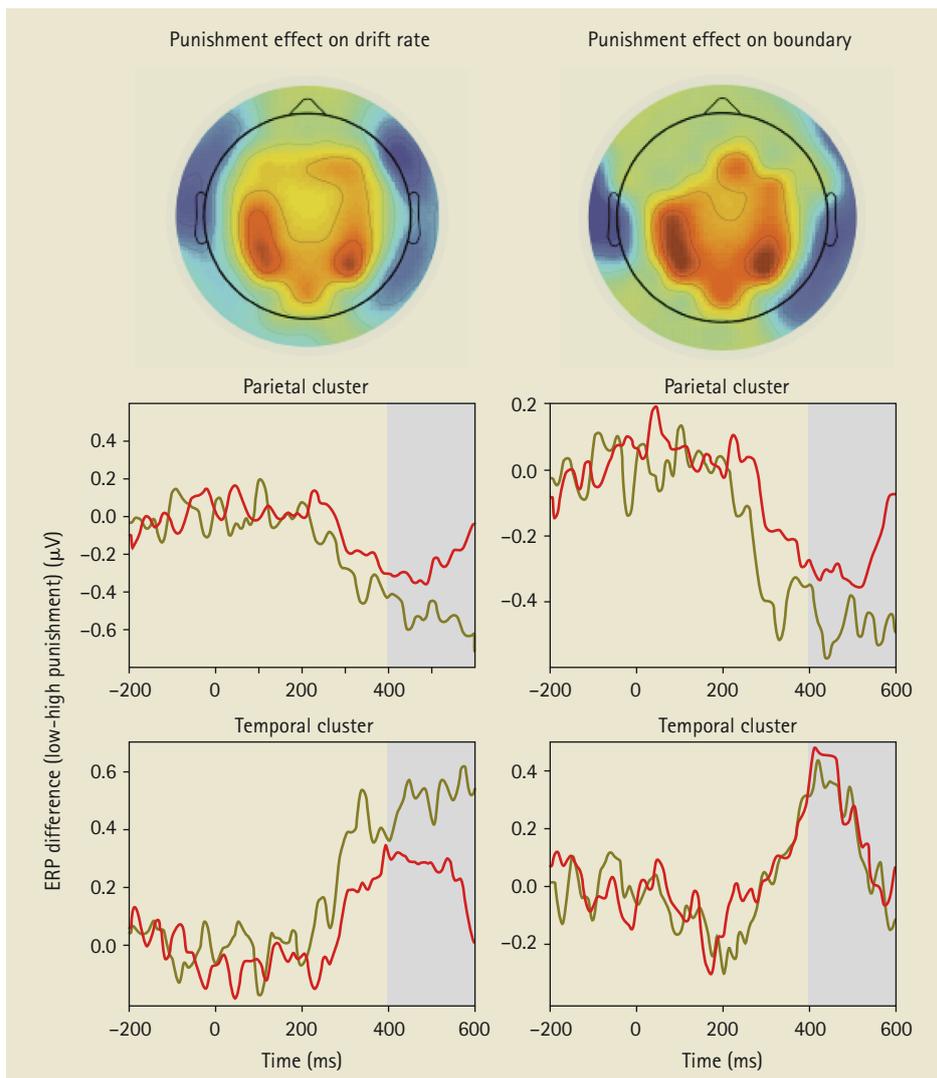

Figure 6. Spatial and temporal characteristics of the effect of punishment on drift rate (left) and boundary (right) during perceptual decision making. Note the late-onset and the ramp-like nature of differential activity between the low- and high-punishment conditions, which confirm that the effects are indeed decision related. Data are locked to the onset of the stimulus (at 0 ms). Black traces portray subjects with strong punishment effects on drift rate and boundary, whereas red traces portray subjects with smaller effects. Note that the neural data also reflect this dissociation. Finally, the similarity of the scalp distributions suggests that drift rate and boundary changes as functions of punishment are implemented in a common network.

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a response was given (cf. Figure 6, bottom). These findings suggest that, even though the components of interest are originally seen as stimulus-locked, they gradually evolve and ultimately persist until subjects make a choice, consistent with a model of temporal evidence accumulation to a decision bound. Note also the similarity in the spatial distribution of the two components (cf. Figure 6, top), which suggests that the influence of punishment on drift rate and boundary is expressed on the same neuronal populations.

Threshold Adaptation for Reward Maximization

When we make decisions under changing circumstances, the outcome depends on different trade-offs between deliberation and evidence. Decision makers determine (rewarded) perceptual decisions by collecting evidence until reaching a point of choice, the decision threshold. They can either make decisions quickly, thereby risking more errors, or make decisions carefully, thereby risking to have fewer opportunities for being maximally rewarded.

Single unit recording studies in monkeys and fMRI studies in humans have shown that frontal (e. g., DLPFC), cerebellar and striatal brain regions are involved in this form of decision making. However, it still remains unclear how their interaction gives rise to threshold adaptation. Neurocomputational models propose a modulation of the interaction (synaptic efficacy) between striatal and cortical neurons as the neurobiological mechanism by which decision makers adapt their decision criterion and thus their behavior to maximize reward.

To investigate this connectivity hypothesis, participants performed a two-alternative forced-choice direction-of-motion discrimination task (as used in many of the monkey studies by Newsome, Shadlen, and coworkers as well as some of our previous work) while we recorded changes in the BOLD signal using fMRI. Twentytwo participants performed the task repeatedly in blocks, in which reward schedules emphasized either accuracy, speed,

or were neutral (cf. Figure 7a). Hence, participants had to trade off speed and accuracy depending on the reward schedule to maximize their net reward. Assuming that participants' behavior is well described by a sequential sampling model of decision making, they could maximize their overall task reward by adjusting the amount of evidence required and the amount of elapsed time spent before making a decision.

Behavioral results and computational modeling show an effect of reward schedule on threshold modulation (cf. Figure 7b). An effective connectivity analysis (PPI) of the neuroimaging data revealed a significant modulation of the interaction of the bilateral DLPFC and striatum (stronger for the accuracy condition) and cerebellum to striatum (stronger for the speed condition) when comparing the different threshold conditions (cf. Figure 7c). If the decision process is modelled by the cognitive processing model and the fMRI data describe the same decision mechanism, threshold modulation as reflected in the strength of effective connectivity and the extent to which the decision boundary is separated between high- and low-threshold conditions should be correlated. Thus, we correlated the estimate of interaction between DLPFC and the striatum with the estimate of the boundary separation from the diffusion model. We found a significant positive correlation between those measures (shown: left DLPFC to striatum, $r = .8$ (16), $p < .0001$ and left dentate region of cerebellum, $r = -.64$ (16), p (2-tailed) = .004). The significant change in effective connectivity together with the strong positive correlation with the boundary separation provide evidence that the adjustment of decision thresholds is instantiated by a modulation of interaction between cortico-cerebellar-striatal brain systems.

This study shows that adapting decision thresholds to maximize reward is instantiated by a change in interaction between brain systems that mediate decision making. Notably, the diffusion model describes both behavioral and fMRI data well (Figure 7b, 7c).
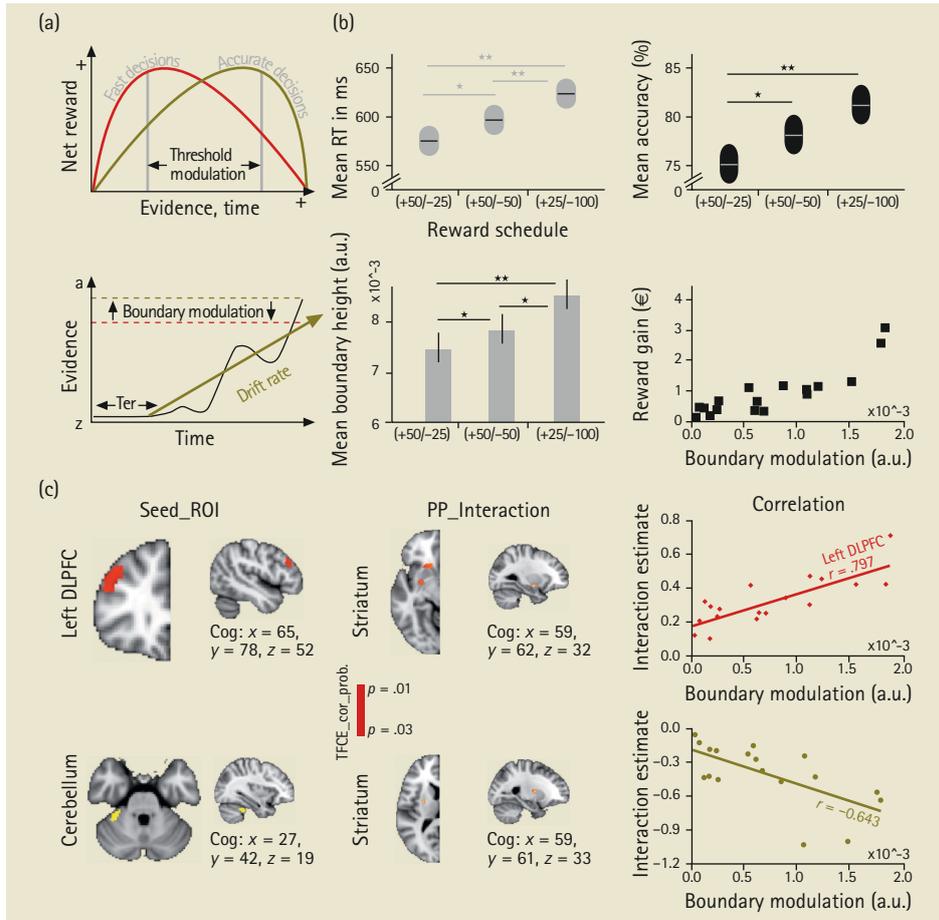
Figure 7. (a) *Top:* Threshold modulation. Distinct threshold settings are net reward maximizing for different reward schedules (red and green lines). *Bottom:* Sequential sampling framework of perceptual decision making. Modulating the boundary adjusts the tradeoffs between evidence and time. (b) Behavioral Results. *Top left:* black lines indicate mean and grey forms standard errors of mean reaction time (RT): low threshold state = 576.41 ms, ± 17.48; intermediate state = 597.04 ms, ± 17.30; high threshold state = 624.07 ms, ±19.35 % correct mean, ± SEM. *Top right:* grey lines indicate means and black forms standard errors of response accuracy (RA): low threshold state = 75.45 %, ± 2.13; intermediate state = 78.45 %, ± 2.16; high threshold state = 81.62 %, ±1.89. RT and RA differed significantly between threshold states (* = $p < .05$, ** = $p < .001$; Bonferroni corrected). *Bottom left:* Normalized group boundary parameter estimates for all threshold states from the best-fitting diffusion model: low threshold state: .0739 a.u., ± .0035 SEM; intermediate state = .0778, ± .0028; high threshold state = .0848 a.u., ± .0027. Boundary heights are significantly different between threshold states (* = $p < .01$, ** = $p < .001$). *Bottom right:* Magnitude of boundary modulation relates to reward gain. (c) *Top, from left to right:* left DLPFC seed ROIs, interacting region of the striatum (zmax = 3), correlation of neural connectivity parameter with boundary modulation estimate (high–low threshold states) from diffusion model; Cog = Center of gravity. Red diamonds indicate individual participants' estimates of neural interaction parameters and magnitudes of boundary modulation comparing high to low threshold states. *Bottom, from left to right:* Cerebellar seed ROI. Interacting left striatal region (zmax = 3.1). Cerebellar-striatal neural interaction estimates correlate negatively with boundary parameter modulation between high and low threshold conditions (from diffusion model). Green circles indicate individual participants' values.

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Neurocognition of Reward–Based Decision Making and Decision Making Under Risk

Many of our decisions are influenced by the potential outcomes associated with different choice options. For instance, consumers consider positive and negative product attributes prior to purchase or people use past experience to decide which means of transportation is the best to commute to work. The project *Reward & Risk* examines how people use reward- and risk-related information to achieve desired outcomes. To examine these kinds of decisions, we abstract basic features from real-life decisions, such as the type of information and feedback available, and implement them in simpler tasks, which are amenable to manipulation in an fMRI environment and to precise modeling. Conducting fMRI experiments allows us to test models and theories by examining decision variables that cannot be measured directly in behavioral experiments. Such variables are the PE in reinforcement learning models, which represents the deviation between expected and actual outcomes, or the decision threshold in sequential sampling models, which determines how much information needs to be collected before a decision is made. Further, neuroimaging techniques allow us to develop theories that describe how the brain implements decision-making mechanisms. Reward-based decision making and decision making under risk have been investigated by different disciplines that focus on different aspects of decision making. Economics and Machine Learning describe procedures that aim to maximize the decision maker's outcome or utility. Psychological theories describe how people learn from feedback and process information in general. Neuroscientific research describes which kind of information is represented in the brain and how it is manipulated to reach a decision. While it is a challenging task to examine behavior across these different levels, we believe that a solid understanding of reward-based decision making has to consider how a decision should be made, the psychological mechanisms that explain coherence with, and deviation from, maximization, and the neurobiological substrates of those mechanisms. Therefore,

to further our understanding of reward-based decision making and decision making under risk, we develop and test simple mathematical models that are derived from adaptive models of decision making and learning. These models are a central tool of our research because they allow to derive predictions for behavioral and neuroimaging data, thereby supporting the development of integrative theories that explain reward-based decision making on different phenomenological levels.

Beyond Perception: Do the Mechanisms Identified for Perceptual Decision Making Generalize to Value-Based Decisions?

Do the principles discussed above for perceptual decisions also hold for more complex decisions that are based on reward outcome, such as economic decisions?

A Mechanistic Account of Value Computation in the Human Brain

Despite much progress in understanding the neural systems that mediate reward- and value-based decision making in humans and recent results showing value-based modulations of activity in sensory cortex, it remains unclear how the brain represents different sources of probabilistic information and how they are used to compute the value signal necessary to make a decision. As discussed above, research on perceptual decision making has already established that category-selective regions in sensory cortex encode the amount of perceptual information (i.e., *sensory* evidence) used in the decision process. It was unclear, however, whether sensory regions also represent the amount of probabilistic reward information (i.e., *probabilistic* evidence) associated with different decision alternatives during value-based decisions. The lack of empirical affirmation that such regions represent probabilistic information has made it difficult to provide a mechanistic account of how different sources of probabilistic evidence are combined to compute value. Despite the fact that several studies on value-based decision making have consistently implicated the medial prefrontal cortex in encoding expected value signals, it remains unknown whether it is directly involved in

computing the value signal needed to make the decision (by combining different sources of probabilistic evidence) or whether it merely reflects the consequence of the decision process. Notably, work on perceptual decision making may provide mechanistic insights into the computation of choice values. Specifically, as discussed above, this line of research has shown that, for binary perceptual choices, decision variables are computed by integrating the difference of the outputs of neural populations, tuned to sensory evidence for each decision alternative. It has been unknown whether this mechanism also applies to the neural implementation of value-based decision making. To investigate whether a similar mechanism might be at work during value-based decision making based on perceptual information, we formed two hypotheses. First, we hypothesized that distinct brain regions represent probabilistic evidence for the different decision alternatives during value-based decision making. Second, we hypothesized that, similar to perceptual decision making, signals from these regions are combined, using a difference-based comparator operation, to compute decision value signals.

fMRI data revealed that, during binary value-based decision making, distinct regions in human ventral temporal cortex (i. e., PFG and PHG) encode abstract probabilistic evidence conferred by each of the stimulus categories. Crucially, this is the case even when the absolute amount of sensory evidence, per se, is equalized between the two categories. Furthermore, our results show that VMPFC integrates information from these regions into a value signal using a difference-based comparator operation.

These findings strongly support the hypothesis that the VMPFC is directly involved in computing the value signal by combining the different sources of probabilistic evidence using a simple subtraction operation. In this study, we thus provide a mechanistic account that directly implicates the medial prefrontal cortex in value computation. Specifically, we showed that a region in VMPFC is involved in computing decision value signals by integrating the different sources of probabilistic evidence encoded in ventral temporal cortex

(i. e., PFG and PHG) using a difference-based comparator operation. Importantly, this mechanism appears to be consistent with neurobiological and computational accounts already proposed for perceptual decision making. Single-unit recordings in primates and our own previous neuroimaging experiments in humans have shown that the DLPFC might be involved in forming a decision by comparing the output of lower level regions that encode the sensory evidence for each of the perceptual choices using a similar difference-based operation. Even though the brain regions appear to be distinct (e. g., DLPFC and VMPFC, resp.), these results suggest that perceptual and value-based decision making might share a common neural computational mechanism.

How Does the Brain Integrate Costs and Benefits During Decision Making?
When we make decisions, the benefits of a decision option often need to be weighed against accompanying costs. Thus, cost-benefit integration is an important aspect of decision making. However, value-based decision making is typically investigated in the context of decision uncertainty (e. g., Philiastides, Biele, & Heekeren, 2010), so that little is known about the neural mechanisms underlying the integration of costs and benefits as such. Cost-benefit-based decision making involves the binary decision to either accept or reject a choice option based on two competing attributes—the option's expected rewards and losses. Such binary accept versus reject decisions bear a strong resemblance to two-alternative choices in perceptual decision making discussed above. Thus, we hypothesized that cost-benefit decisions involve an analogous decision mechanism, that is, the computation of a decision variable that is based on the difference of neural reward and loss-anticipation signals. Using fMRI and choice modeling, we showed that decision making based on cost-benefit comparisons can be explained as a stochastic accumulation of the cost-benefit difference (see Figures 8 to 10). Model-driven fMRI showed that VMPFC and left DLPFC compare costs and benefits by computing the difference between

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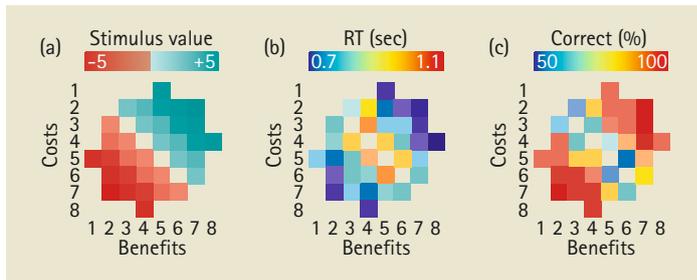
Figure 8. The cost-benefit decision task and behavioral results. Panel (a) shows combinations of costs (X axis) and benefits (Y axis), which participants could either reject or accept. The color code (not visible to participants) displays the net value of a stimulus. Panels (b) and (c) show reaction times and accuracy for the different stimuli. Consistent with basic properties of diffusion models of decision making, participants were faster and made fewer errors when the absolute cost-benefit difference was larger. Accordingly, we could successfully model participants behavior with a diffusion model and used the resulting drift-rate parameters in the fMRI analysis.
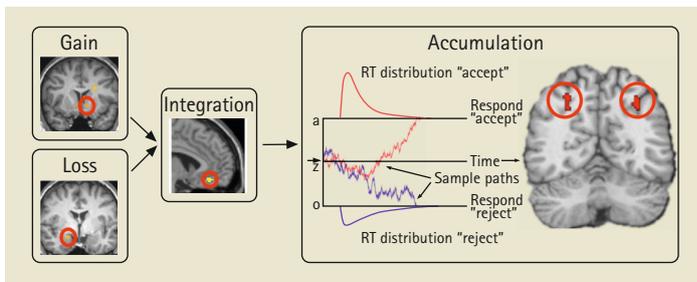
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Figure 10. Summary of the fMRI results. The expected gain and loss of stimuli were represented in the ventral striatum and the amygdala, respectively. The difference between these neural value signals is computed in the ventromedial prefrontal cortex. A decision is formed by accumulating this difference signal in the middle intraparietal sulcus until a decision threshold is reached.
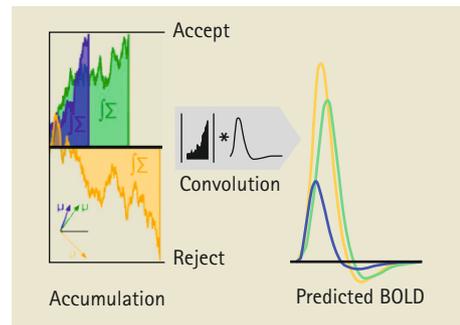
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Figure 9. Relation between drift rate and brain activation. The left side of the figure shows hypothetical decision processes with high (blue), medium (green) and low (yellow) drift rates. Convolving this accumulation activation with a hemodynamic response function results in the greatest BOLD activation for easy decisions characterized by a high drift rate and weakest BOLD activation for hard decisions characterized by a low drift rate.

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neural benefit and cost signals in ventral striatum and amygdala, respectively. Importantly, a PPI analysis showed that participants with higher drift rates as estimated in a diffusion model showed a better integration of neural cost and benefit signals in the VMPFC. Moreover, changes in BOLD signal in the bilateral middle intraparietal sulcus reflect the accumulation of the difference signal from VMPFC. Activation in these regions was weaker when the cost-benefit difference was high and it correlated negatively with the cost-benefit differences signal in the VMPFC (see Figure 10). In sum, these results show that a neurophysiological mechanism previously established for perceptual decision making,

that is, the difference-based accumulation of evidence, is fundamental also in value-based decisions. The brain thus weighs costs against benefits by combining neural benefit and cost signals into a single difference-based neural representation of net value, which is accumulated over time until the individual decides to accept or reject an option.

This project was carried out in collaboration with Ulrike Basten and Christian Fiebach (Emmy Noether Group, University of Frankfurt a. M.).

How Does the Brain Integrate Different Attributes of One Choice Option?
In a related study, we investigated more closely how different values of an object are integrated into an overall subjective value. Behavioral economics has investigated value-integration mechanisms to predict choice behavior across a distribution of positive and negative values. Multiattribute-utility theory suggests that the subjective value of multiattribute options equals the attributes' weighted sum. Although these models can predict choice behavior well, they are only applicable when preferential independence of the attributes is given. However, human choice often violates the independence principle; that is, when selecting a dinner menu, together with cheese, red wine has a higher

value over white wine. But, with fish, white wine has a higher value. Here, an independent model fails to predict choice, whereas an interactive integration model would successfully predict choice by permitting an extra term for the dependence of attributes. Here, we investigated how the brain integrates values across discrete stimuli into one subjective value to guide decision making. For this, we have developed a decision-making task with multiattribute choice options. We measured the BOLD signal with fMRI while subjects accepted or rejected choice options that were combinations of monetary reward and physical pain. Hence, the attributes of a choice option not only have different valence (positive and negative values) but also are qualitatively different.

A well-established approach to investigate cognitive processes underlying decision making is to compare cognitive models on behavioral data. However, if competing models predict the same pattern of choices, behavioral data are limited. In these cases, forcing the models to predict neural activity can provide decisive evidence.

Here, we compare computational models directly on both behavioral and neural data. These models either integrate values independently (each value contributes to the overall subjective value) or interactively (the value of one attribute impacts the valuation process of the other attribute). Interestingly, these models all made similar predictions of individual choice behavior, suggesting that behavioral data alone are not sufficient to uncover the underlying integration mechanism. A direct model comparison on brain data decisively demonstrated that interactive value integration predicts neural activity in value sensitive brain regions, such as VMPFC and DLPFC, significantly better than the independent mechanism (see Figure 11). Furthermore, our effective connectivity analyses revealed that value dependent changes in valuation are associated with modulations in SGACC-amygdala coupling. These structures have been shown to play a key role in regulating hedonic experiences, such as fear and pain regulation, via placebo, suggesting a more generalized role of these regions.
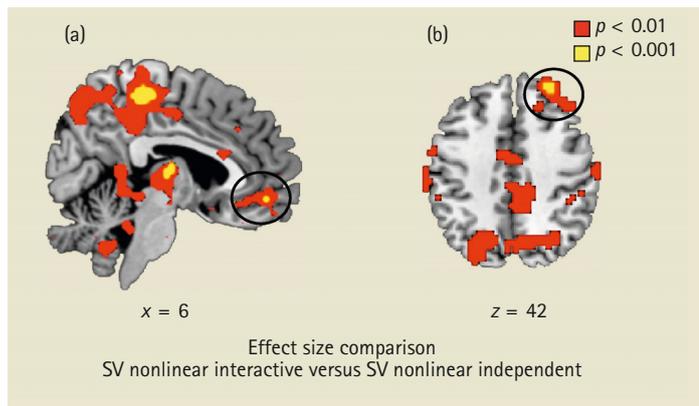

Figure 11. *Direct comparison between nonlinear interactive versus nonlinear independent models on neural data. Brain regions showing significantly larger effect sizes for the nonlinear interactive model compared to the nonlinear independent model. Slices represent sagittal (left) and transversal (right) views of structural brain images with superimposed statistical maps. The circled areas indicate (a) anterior VMPFC (BA 11, [6, 48, −9], $t_{92} = 3.18$, p < .001) and (b) DLPFC (BA 9, [30, 45, 42], $t_{92} = 3.78$, p < .001).*

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With this study, we show that value impacts valuation when advantages and disadvantages are integrated into an overall subjective value. This study provides a concrete example of how neuroimaging allows to test between computational models of decision making and facilitates the evaluation of models of cognitive computations. This study was carried out in collaboration with Jörg Rieskamp (Economic Psychology, University of Basel). A manuscript reporting these findings is currently under review.

Neural Processing of Risk
In our everyday life, we often have to make decisions with risky consequences, like choosing a restaurant for dinner or choosing a form of retirement saving. To date, however, little is known about how the brain processes risk. Recent conceptualizations of risky decision making highlight that it is generally associated with emotions, but do not specify how emotions are implicated in risk processing. Moreover, little is known about risk processing in nonchoice situations and how potential losses influence risk processing. Here, we investigated (a) how risk processing is influenced by emotions, (b) how it differs between choice and nonchoice situations, and
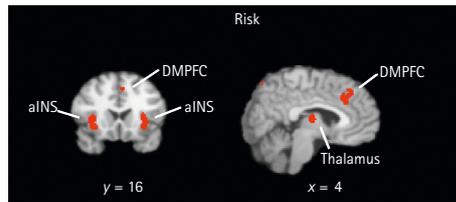
Figure 12. Neural representations of risk. Results from an ALE meta-analysis on risk independent of the context (choice or nonchoice situation) and the domain (gains+losses or only gains in which risk was investigated). Activated clusters included bilateral aINS, DMPFC, and thalamus (FDR < .05; cluster size > 200 mm^3).

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(c) how it changes when losses are possible. By using the ALE meta-analysis, we can base our argumentation not only on a single study or a qualitative view on several studies but also on a quantitative integration of many studies investigating risk. Importantly, the ALE meta-analysis can also be used to contrast two independent sets of foci.

We identified a network including bilateral aINS, dorsomedial thalamus, posterior thalamus, DMPFC, right DLPFC, and right parietal cortex for processing risk (see Figure 12). The aINS was active in both choice and nonchoice situations, but predominantly when
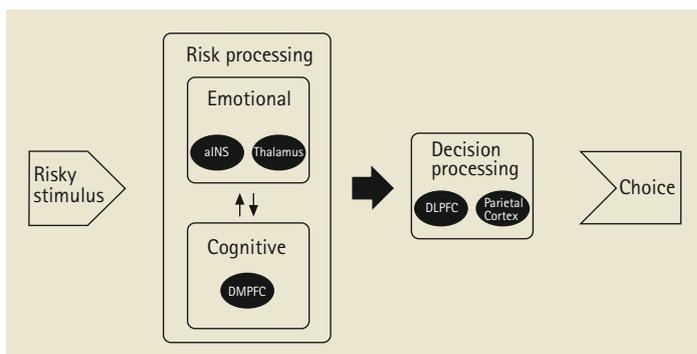

Figure 13. A potential mechanism of risky decision making. A risky stimulus, such as a gamble, with uncertain outcomes or a choice menu with different financial investments is initially evaluated on an emotional level. Activity in the aINS thereby serves as an estimate for the potential of the risky stimulus to result in an unwanted outcome, whereas the thalamus reflects important aspects of potential outcomes (e.g., their variability). At the cognitive level, the risky stimulus is processed in the DMPFC. Both parts of risk processing (emotional and cognitive) inform the actual decision process performed in DLPFC and parietal cortex. In situations in which no decision has to be made, such as in the bingo game, the process concludes after risk processing.

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individuals were faced with potential losses. The aINS is regarded as a key brain region in emotion processing and arousal and also in the mapping of internal bodily states. Several studies related activity in the aINS especially to aversive emotions, such as fear, sadness, disgust, or anxiety. Thus, our results support the hypothesis that aversive emotions are implicated in risk processing independent of the context, but predominantly (not solely) when individuals are faced with potential losses.

In sum, our finding of insula activity supports the hypothesis that emotions are implicated in risk processing. We also find differential activation patterns for choice and nonchoice situations and for the gain versus gain+loss domain that suggest that risk processing on the neural level is context dependent and specifically influenced by potential losses. Based on the results of our meta-analyses, we propose the account of a risk-processing mechanism illustrated in Figure 13.

Neural Foundations of Risk-Return Trade-Off in Investment Decisions

Many decisions people make—such as whether to try to catch a yellow light, choosing a journal for submission of an article, or choosing a financial investment—can be described as decisions under risk. Understanding the mechanisms that drive these decisions is an important goal in decision neuroscience. But while recent research has generated some progress in the understanding of value-based decision making, the underlying mechanisms of risky decision making are still debated.

Two classes of risky decision-making models have been proposed that can be applied to investment decisions in general, one based on a transformation of outcomes and/or probabilities (EUT and PT) and the other based on a risk-return trade-off (risk-return models). To be superior to other models, a better model should, in the best case, explain behavioral and neural data better than the other models. As value and choice predictions of both classes of models are usually highly consistent with each other, we focused on the question of which class of models better

describes the valuation process in the brain. In this case, fMRI data can serve as a tiebreaker because they provide additional insight into the neurobiological processes that subserve the cognitive processes ultimately leading to decisions.

Using the RPID task, which mimics real-life investment decisions by providing subjects with past returns of investments, we found that brain activity in bilateral DLPFC, PCC, VLPFC, and MPFC covaried with value and return. Activation in these regions has usually been observed in the context of value and reward. Changes in the BOLD signal in these regions correlate with the magnitude of experienced and anticipated rewards as well as with the subjective value of (delayed) rewards and the willingness to pay for consumer goods.

We found that *perceived risk* correlated significantly with the BOLD signal in the aINS. Risk-related brain activity in the aINS was observed in a variety of studies (e. g., Mohr, Biele, & Heekeren, 2010). None of these studies, however, used lotteries with continuous distributions. Thus, our finding supports the results of previous studies and extends them by showing that risk is represented in the aINS in situations where subjects have to make a choice between two independent alternatives where one alternative is described by a continuous distribution of possible outcomes. Most importantly, the existence of a neural representation of risk during choices offers neural support for risk-return models because, in the case of EUT and PT, one would not expect a neural representation of risk, whereas risk is explicitly specified in risk-return models.

We further found that interindividual differences in decision-related brain activity in LOFC and PCC covaried with interindividual differences in risk attitudes derived from the psychological risk-return model, which provides additional support for this model. The more risk averse a participant was, the greater was her decision-related change in brain activity in LOFC and PCC (independent of current risk and value). In sum, we found support for the hypothesis of a risk-return trade-off in investment decisions.

Neuroeconomics and Aging: Neuromodulation of Economic Decision Making in Old Age

Neuroeconomics has made important progress in grounding different aspects of decision making in neural systems and the neurotransmitters therein. Evidence from a range of fMRI studies indicates that the VST and the VMPFC are implicated in the representations of reward and value (see above). In the context of risk processing, many studies have shown two key regions to be involved—the ACC and the aINS (e. g., Mohr, Biele, & Heekeren, 2010). Some recent studies have also investigated the effect of delayed rewards and showed that the subjective value of delayed rewards covaries with brain activity in VST, VMPFC, and PCC. The dopaminergic and serotoninergic brain systems have been identified as key neurotransmitter systems involved in economic behavior influencing all three aspects of economic decision making discussed above (reward, risk, and delay). Whereas dopamine and serotonin separately influence both reward and risk processing they are also assumed to interact in implementing prediction signals that reflect the temporal information about the outcome.

Both neurotransmitters are known to be prone to significant changes during the adult lifespan (see the Center for Lifespan Psychology's project Neuromodulation of Lifespan Cognition, pp. 183–189). Similarly, economic behavior undergoes significant age-related changes over the course of the adult lifespan. Several studies indicate that older adults are more risk averse than younger adults and that discount rates increase with age. These changes were reflected in changes in activation patterns observed while individuals make economic decisions. Although older adults show intact striatal activation during gain anticipation, one can observe a relative reduction in activation during loss anticipation. They also show higher activations in the aINS when choosing risky choice alternatives, indicating that they perceived the alternative as more risky compared to younger adults. Together with our colleagues from the Center for Lifespan Psychology, we have recently

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begun investigating the triadic relationship between (a) economic decision making, (b) dopaminergic and serotoninergic neuromodu-lation, and (c) aging.

Decision Making in Social Contexts

Most of our decisions in everyday life have to be taken in social contexts, and much of our success in life depends on how well we do in interacting with others. Making inferences about the mental states of others, which is an important aspect of social cognition, is at the core of what enables us to predict the behavior of others. Basic perceptual and cognitive processes, such as the reading of facial expressions and the decoding of pro-sodic cues, represent a prerequisite for social cognitive functions. Social decision making, however, is not only the result of perceptual and cognitive operations but also of emo-tional processes. In fact, in a collaborative project with the Center for Adaptive Behavior, we recently found that emotional personality characteristics as measured via self-report questionnaires, such as levels of empathic concern, are much stronger predictors for prosocial behavior in economic games, such as the dictator game, than cognitive parame-ters, such as the ability to take other people's perspective. Thus, the common goal of our subprojects within the topic of decisions in social contexts is to elucidate the unique as well as combined contributions that these perceptive, cognitive, and emotional process-es have on social decision making.

Using structural and functional MRI as well as psychophysiological measures, such as eye tracking and skin conductance, our group is trying to elucidate how and where in the brain of healthy individuals social decisions are made. Moreover, to complement our understanding of the "social brain," we are studying individuals with neuropsychiatric conditions that involve socioemotional im-pairments, such as autism.

Emotional Face Processing

The study of face-processing abilities, such as facial emotion or identity recognition, is of particular importance for social decision mak-ing because faces represent a crucial source of social information, and their decoding is a precursor for more complex social inferences. In ASC, abnormalities in processing informa-tion from faces, in particular from the eyes, are characterized by specific scan paths on emotional faces. The first two subprojects in this section follow up on our findings from eye tracking and structural MRI studies in ASC (Dziobek, Bahnemann, Convit, & Heekeren, 2010; Kirchner, Hatri, Heekeren, & Dziobek, 2011) seeking to further specify atypical gaze behavior and emotional face-processing impairments observed in autism.

Atypical gaze in ASC is prominently charac-terized by a reduced focus toward the eyes, yet the reason for this abnormality remains a puzzle. A long-standing view suggests that a general lack of social attention—and specifi-cally less attention toward the eyes—leads to a reduced orientation toward the eyes. Another view, however, underlines the poten-tial aversiveness of direct eye contact in ASC, resulting in an active avoidance of direct eye contact. Importantly, these two processes do not have to be mutually exclusive, instead, the interplay of the two components may, in fact, account for the observed scan paths.

In the first project (Kliemann, Dziobek, Hatri, Steimke, & Heekeren, 2010), we sought to investigate the influence of reduced orien-tation and active avoidance of the eyes on atypical gaze in ASC by analyzing partici-pants' eye movements during emotional face processing. To this end, we applied a new behavioral facial emotion classification task, which was developed in collaboration with Matthias Gamer and Christian Büchel (University of Hamburg). The task varies the initial fixation position of faces (displaying happy, fearful, or neutral expressions), so that participants started processing a face either at the eyes or at the mouth (cf. Figure 14a). Thereby, the task allows investigating both avoidance- and orientation-guided reflexive gaze behaviors, triggered by focusing the eyes or the mouth, respectively. Participants in the control group (NT, $n = 12$) showed an increased preference for the eye region, with more eye movements toward the eyes (when starting on the mouth) than away from the eyes (toward the mouth) (cf. Figure 14b, 14c),
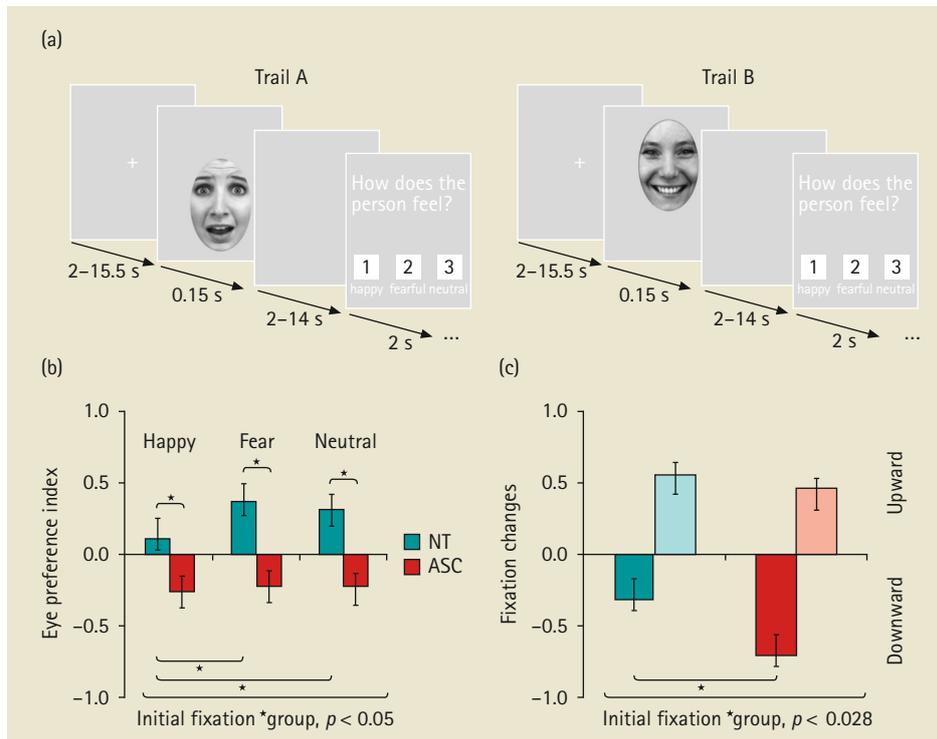
Figure 14. (a) Emotion classification task. Each trial started with the presentation of a fixation cross (2 s), followed by an emotional face (150 ms). After a blank screen for 2 s participants indicate the emotion displayed. Faces were shifted vertically on the screen so that subjects started gaze either on the eyes (Trial A) or on the mouth (Trial B) of the presented emotional face. (b) Eye preference index. Generally, the NT group showed an increased preference for the eyes, compared to ASC. For the NT group, the preference was stronger for fearful and neutral faces, compared to happy faces. There was no effect of emotion in the ASC group. (c) Eye movements as a function of initial fixation. The ASC group showed more fixation changes downward away from the eyes than the NT group.

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replicating findings from our collaboration partners. In contrast, participants in the autism group (*n* = 11) showed a clear reduction of eye preference, prominently characterized by more and faster eye movements away from the eyes than toward the eyes. In addition, eye preference in ASC predicted emotion recognition performance independent of general illness severity. These findings emphasize an increased avoidance of eye contact on the occulomotor level.

Impairments in emotional face processing in autism, however, are not only prominent on a behavioral and occulomotor level but also on the level of brain function and structure. As previous studies from our group showed, problems in face processing in autism are associated with pathological structural characteristics of brain regions relevant for face processing, such as increased cortical thickness of the fusiform gyrus and distinct connectivity patterns of the amygdala in autism (Dziobek et al., 2010).

On a functional level, emotion processing and atypical scan paths have been repeatedly reported along with aberrant amygdala activity during face processing in ASC as compared to control participants. Whereas, in controls, amygdala function seems to be linked to the above reported strong and immediate focus toward the eyes, the functional role of the amygdala within emotional face processing in autism has been rather controversial. Previous studies reported both hyper- and hypoactivation of the amygdala as compared to controls in response to facial stimuli. Find–

ings of decreased amygdala activation in ASC rather emphasize the hypothesis of a missing orientation as an explanation for the observed reduced eye focus. On the contrary, findings of increased amygdala activation together with a positive correlation of eye fixation duration rather favor the avoidance hypothesis in ASC. To further specify the functional role of the amygdala in atypical gaze during emotional face processing, we conducted a second subproject where participants performed the same task as in the behavioral subproject while in an MRI scanner. A significant cluster of activation in the right amygdala for the interaction of initial fixation position (eyes vs. mouth) and group (ASC vs. NT) revealed an increase of amygdala activity when control participants started looking at faces from the mouth (and orient toward the eyes) as com-

pared to starting at the eyes (cf. Figure 15). This is consistent with previous studies and the idea of an involvement of the amygdala in successful orientation toward the eyes. Contrarily, the ASC group showed increased amygdala activity in the same cluster when starting fixation at the eyes, along with reduced amygdala activity when starting at the mouth as compared to controls.

These data provide new and important insights into the aberrant functioning of the amygdala within social information processing in autism: The increase in amygdala activity triggered by direct eye contact along with previously reported increased gaze away from the eyes, supports the hypothesis of active eye avoidance, modulated via avoidance processing in the amygdala. The decrease of BOLD response in the amygdala in ASC when starting gaze at the mouth further underlines dysfunction of the amygdala within social saliency detection and face processing. The results of this subproject describe a specific dysfunctional mechanism of social relevance mediation in the amygdala in autism, further supporting the emerging opinion that the amygdala is not the cause of the entire autistic pathophysiology, but rather represents a dysfunctional node within the neuronal network underlying effective social functioning resulting in the social phenotype of autism.

Complex Social Decision Making

Successful functioning within the social environment does not only involve decisions about emotional states from visual features of other agents' faces but also demands to predict and explain behavior of others based on mental state inference within complex social situations. Another core symptom of ASC compromises difficulties in recursively inferring intentions and beliefs of others within complex social interactions. To further specify the cognitive dysfunctions that determine the heterogeneity in ASC, we employed a game-theoretic approach to characterize unobservable computational processes implicitly involved in social interactions and their dysfunctions in ASC. The subproject was realized in collaboration with Wako Yoshida, Karl Friston, and Ray Dolan (University College of
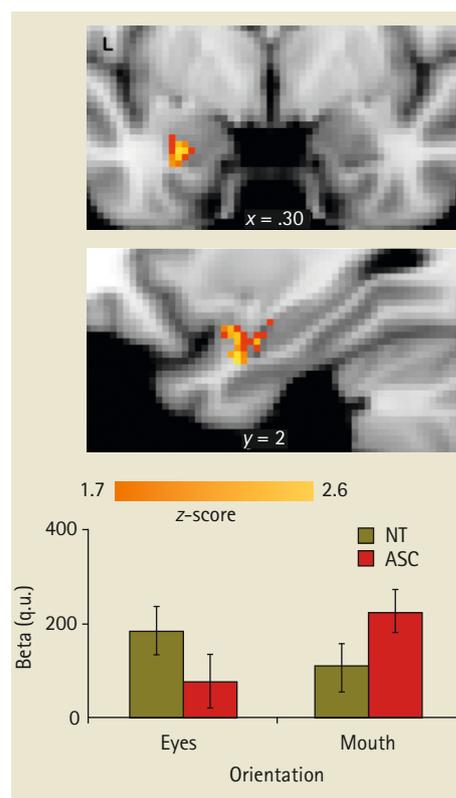

Figure 15. Amygdala region showing a significant interaction of initial fixation position and group. The upper two panels show statistical maps of coronal and left (L) sagittal planes. The lower bar shows the extracted beta values of the cluster ($p = .05$ [FWE corrected]). Error bars represent SE.
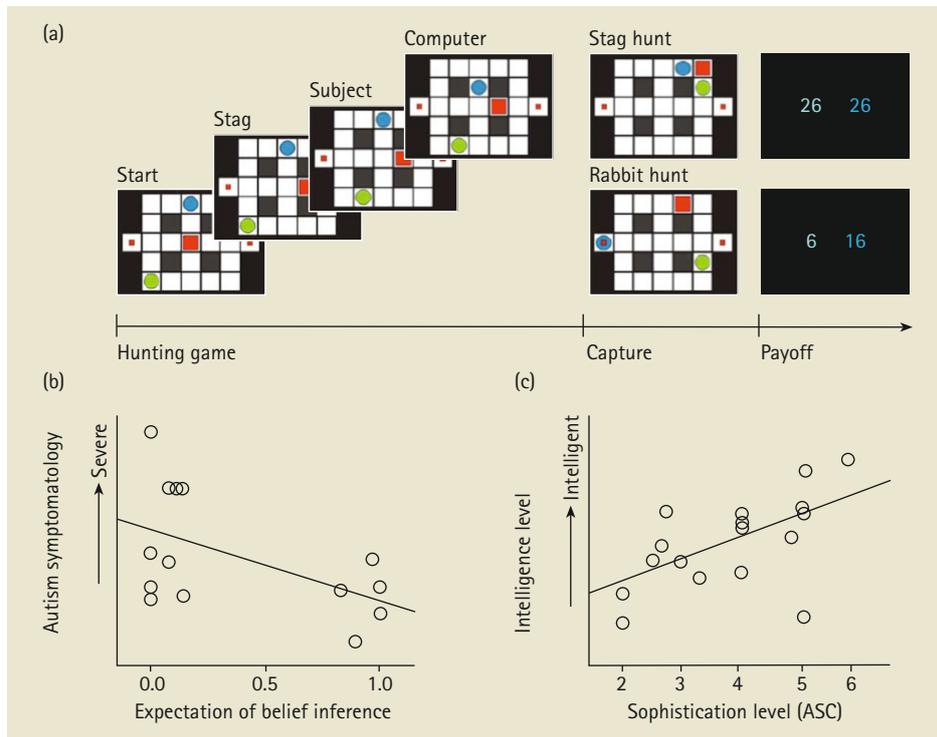
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Figure 16. (a) Stag-hunt game. Two players, the participant (green circle) and a computer agent (blue circle), try to catch prey: a mobile stag (big square, big payoff) by cooperation or two stationary rabbits (small squares, small payoff), by moving in a sequential manner. When a game if finished, both players receive points according to the sum of prey and points regarding to the remaining time. (b) The greater the expectation of recursive belief inference, the more sever was the autistic symptomatology ($n = 14$, $r = -.52$, $p = .055$). Autistic symptomatology was measured by the sum of scores of the autism diagnostic interview revised (ADI-R) and the autism syndrome diagnostic interview (ASDI). (c) Estimated sophistication for the ASC group was significantly correlated with individual IQ –scores ($n = 17$, $r = .54$, $p = .026$).

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London). The approach employed a stag-hunt game, in which participants interacted with a computerized agent to hunt stags together (high value) or defect to hunt rabbits alone (low value) (cf. Figure 16a). Within the game, cooperation depends on recursive representations of others' intentions, since, if I decide to hunt the stag, I must believe that you believe that I will cooperate with you. Cooperation emerges, when highly sophisticated players interact. Over the course of the game, a computerized agent shifted its sophistication (by three degrees of recursion) without notice. For optimal behavior, participants were required to (1) estimate the agent's sophistication level (recursive belief inference), (2) update their own strategies continuously (cognitive flexibility), and (3) behave optimally on the basis of their inference (interactive planning). To tease apart cognitive processes implicit in social interaction, we applied a previously developed theoretical model, in which participants behave optimally with respect to the goal of maximizing the payoff based on these three processes. ASC showed a general understanding of the stag-hunt game, but the observed behavior was guided to a lesser degree by belief inference than that of the control group. Instead, ASC participants' behavior was better explained by a fixed strategy model, that is, disregarding the other player's beliefs during the decisions in the game. Strikingly, the extent to which they behaved according to the fixed strategy was predicted by symptom severity (cf. Figure 16b). In addition, intellectual levels predicted the ability in iterative

planning: highly intelligent players behave cooperatively as if they make predictions with a longer time horizon (cf. Figure 16c). This study not only provided the first quantitative approach revealing the underlying computational dysfunctions that represent the autistic "spectrum" but also highlights the power of simple assessments for psychopathology for describing and understanding core psychiatric deficits in terms of computational dysfunctions.

Abbreviations

ACC – anterior cingulate cortex
aINS – anterior insula
ALE – activation likelihood estimation
ASC – autism spectrum conditions
DLPFC – dorsolateral prefrontal cortex
DMPFC – dorsomedial prefrontal cortex
EEG – electroencephalography
EUT – expected utility theory
fMRI – functional magnetic resonance imaging
LIP – lateral intraparietal area
LOFC – lateral orbitofrontal cortex
MEG – magnetencephalographic
MPFC – medial prefrontal cortex
NT – neurotypical subjects
PCC – posterior cingulate cortex
PE – prediction error
PFG – posterior fusiform gyrus
PHG – parahippocampal gyrus
PPI – psychophysiological interaction
PT – prospect theory
RPID – risk perception and investment decision
rTMS – repetitive transcranial magnetic stimulation
SAT – speed-accuracy trade-off
SGACC – subgenual anterior cingulate cortex
SMA – supplementary motor areas
VLPFC – ventrolateral prefrontal cortex
VMPFC – ventromedial prefrontal cortex
VST – ventral striatum

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