Independent Junior Research Group

Neurocognition of Decision Making

Contents

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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. An example for the former are sequential sampling models of decision making. An example 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 2). 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 and the interaction between the two.

We believe that the investigation of the neurocognition of decision making requires a multimodal methodological approach that integrates information from an array of methods, ranging from cognitive modeling based on behavioral data to simultaneous functional magnetic resonance imaging (fMRI) and encephalographic (EEG) experiments (cf. Figure 1). On the following pages, we briefly describe research in the three topics in more

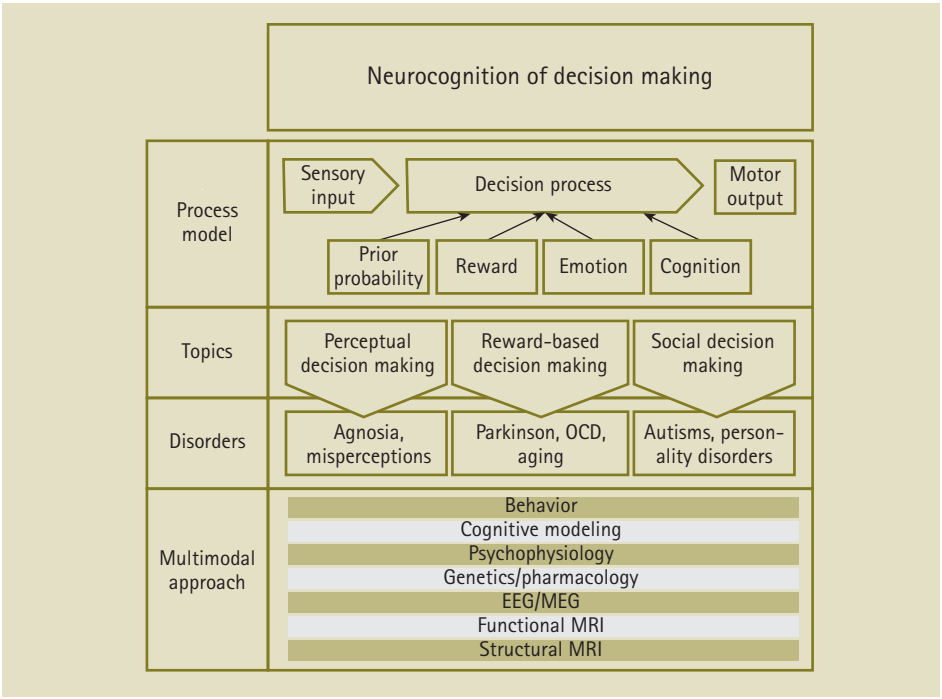

Figure 1. Multimodal approach to neurocognition of decision making.

Key Reference

Heekeren, H. R., Marrett, S., & Ungerleider, L. G. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience, 9*(6), 467–479.

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

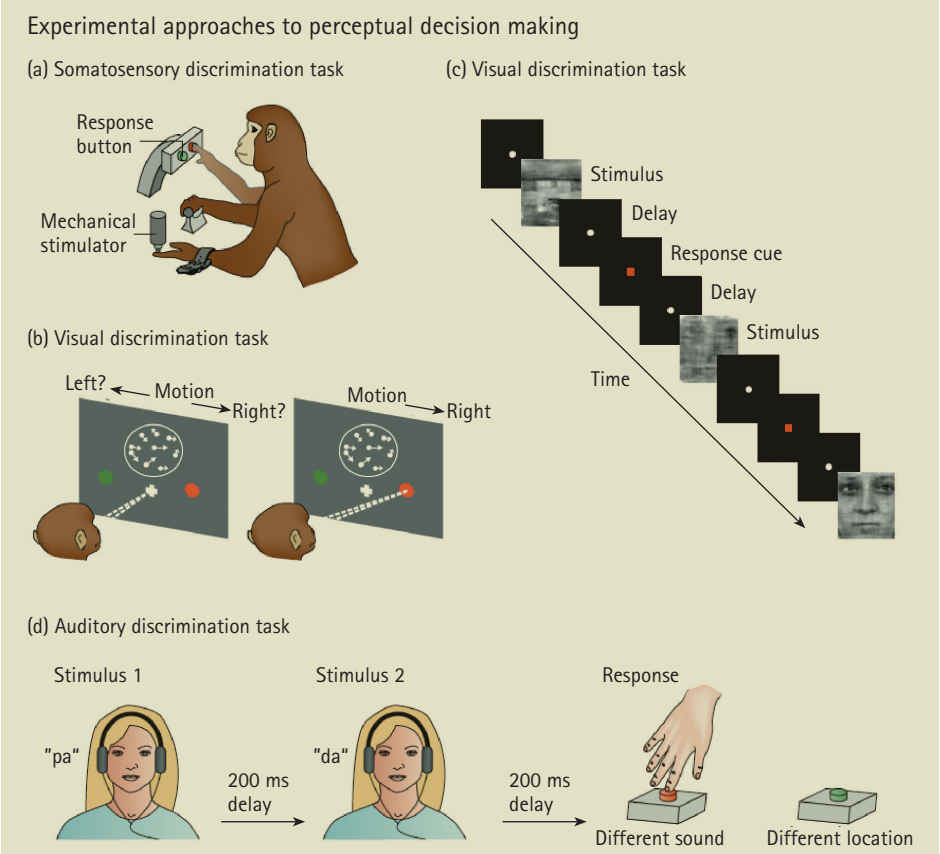

Figure 2. Experimental approaches to perceptual decision making: The general experimental approach to study perceptual decisions is to have subjects perform sensory discriminations, with more or less degraded input. To study perceptual decision making in the somatosensory domain, several studies used a vibrotactile frequency-discrimination task. In this task, subjects had to decide which of two sequentially presented flutter stimuli had a higher frequency (e. g., Preuschhof, 2006, p. 97) (a). To study perceptual decision making in the visual domain, many studies have used a direction-of-motion discrimination task (e. g., Heekeren, 2006, p. 87), in which subjects had to decide whether a noisy field of dots was moving in one direction or its opposite direction (e. g., leftward or rightward) and indicated their choice either with a quick eye movement to the target on the respective side (b) or with a button press (Heekeren, 2006, p. 87). Also in the visual domain, Heekeren et al. (2004) used a face-house categorization task (Heekeren, 2004, p. 127), in which subjects decided whether an image presented on a screen was a face or a house and responded with a button press (c). To investigate perceptual decision making in the auditory domain, Kaiser et al. (2006) used a two-alternative forced-choice task, in which individuals had to decide whether two syllables presented sequentially were: (1) the same or different with respect to identity or (2) the same or different with respect to their perceived location (Kaiser, 2006, p. 146) (d).

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 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 3). 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 (blue) than for degraded images (red) (see Figure 3). More recent studies in monkeys and humans have begun to model not only psychophysical but also neurophysiological data as a diffusion-to-barrier process (e. g., Philiastides & Sajda, 2007) providing a quantitative link between behavior (decision outcome) and neural activity (decision processing) (Heekeren et al., 2008). In ongoing projects,

Key Reference

Philiastides, M. G., & Sajda, P. (2007). EEG-informed fMRI reveals spatiotemporal characteristics of perceptual decision making. *Journal of Neuroscience, 27,* 13082–13091.

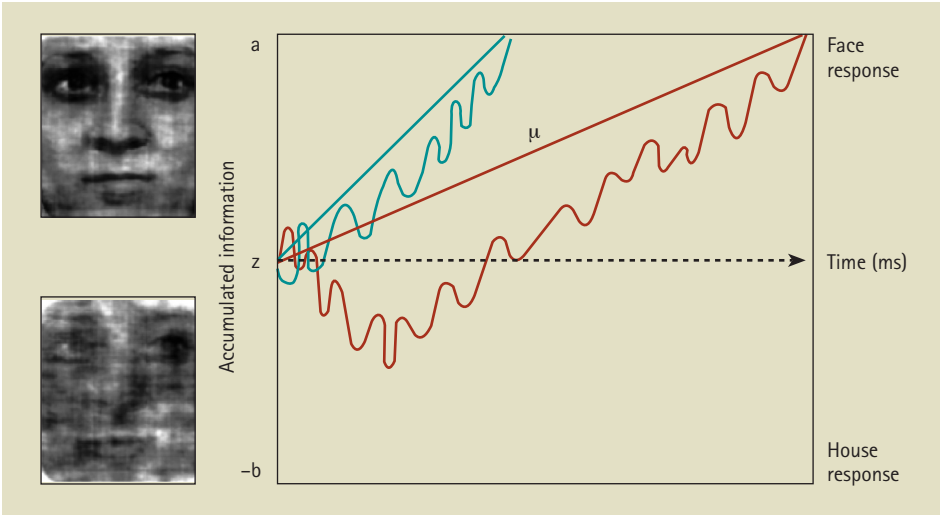

Figure 3. Decision-making research has led to the development of mathematical models of the assumed underlying cognitive processes. Diffusion models are particularly successful in explaining response time and accuracy data in two-choice reaction-time tasks. These models assume that decisions are formed 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 (blue 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.

Key References

Heekeren, H. R., Marrett, S., Ruff, D. A., Bandettini, P. A., & Ungerleider, L. G. (2006). Involvement of human left dorsolateral prefrontal cortex in perceptual decision making is independent of response modality. *Proceedings of the National Academy of Sciences of the USA, 103,* 10023–10028.

Philiastides, M. G., Ratcliff, R. & Sajda, P. (2006). Neural representation of task difficulty and decision making during perceptual categorization: A timing diagram. *Journal of Neuroscience, 26,* 8965–8975.

we build on our previous work and investigate how the interplay between lower level sensory regions and higher order decision and motor-planning structures leads to decisions regarding ambiguous sensory information. In a first project, using single-trial analysis techniques, we examine how the accumulated sensory evidence is ultimately transformed into a specific action. In a second project, in the somatosensory domain, we investigate how and where in the brain short- and long-term memory representations are maintained and combined with current sensory evidence to make a decision.

Transforming Accumulated Evidence Into Action

Perceptual decisions are thought to arise after the temporal accumulation of the available sensory evidence leads to a selection of a motor response, which, in turn, determines one's choice (Green & Heekeren, in press; Heekeren et al., 2008; Philiastides & Heekeren, in press). The boundaries between evidence accumulation and selection of the appropriate behavioral response, however, are currently ill defined. In the monkey literature, the problem arises because the areas implicated in evidence accumulation are also the ones that select, plan, and execute motor responses. Therefore, one could conclude from these neurophysiological studies "to see and decide is, in effect, to plan a motor-response" like Rorie and Newsome wrote in 2005. In contrast, recent human neuroimaging studies identified decision-related activity independent of the response modality used, suggesting that humans might have evolved an abstract decision-making network that allows a flexible link between decision and action (Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006). To investigate if such a flexible link exists, we designed a "face"/"car" categorization task using a novel dynamic stimulus to provide accumulating evidence while simultaneously recording EEG data from 13 subjects. We manipulated the amount of sensory evidence by changing the percentage of phase coherence of our stimuli (cf. Figure 3).

We hypothesize that, once the sensory evidence has been accumulated, it needs to be transformed into a binary choice before the selection of the appropriate motor response can occur. In this sense, evidence "categorization" would provide the link between evidence accumulation and motor output. Furthermore, we hypothesize that, for such a categorization stage to exist, several important requirements must be fulfilled. First, it should appear late in the trial and correlate more with the response than the stimulus (i. e., response-locked activity). Second, it should reflect the strength of the evidence favoring a decision—that is, activity should be higher for easy than hard trials. At the same time, evidence for one category should be interpreted as evidence against the other (i. e., symmetric relationship between the activity from the two categories). Third, activity should not only correlate with behavioral performance but also predict the category of one's choice. Fourth, activity preceding this stage should exhibit evidence accumulation. Finally, the source of the activity should be localized in a region with connections to areas that have been implicated in evidence accumulation as well as those that plan and execute motor responses.

Using a single-trial analysis technique (Philiastides, Ratcliff, & Sajda, 2006), which integrates information across all EEG sensors, we identified a late response-locked component, which correlated with psychophysical

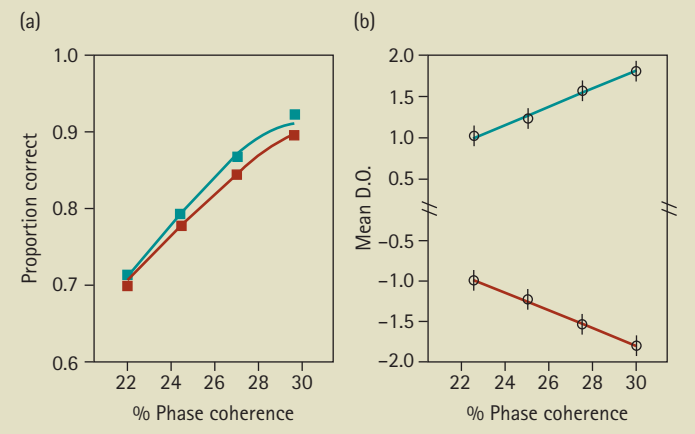

Figure 4. (a) Comparing behavioral with neuronal performance from a response-locked EEG component appearing on average 50 ms prior to the response. The average neurometric curve (red) was a good match to the corresponding psychometric function (blue). (b) Component strength as a function of stimulus evidence and image category. Positive values indicate a face trial and negative values a car trial.

performance (cf. Figure 4a) and responded more for easy than hard trials (cf. Figure 4b). Additionally, this component exhibited a symmetric relationship between face and car trials suggesting that evidence for one category can also be interpreted as evidence against the other (cf. Figure 4b). Time-course analysis of the period preceding this component revealed ramp-like activity consistent with evidence accumulation (cf. Figure 5a). Breaking trials into fast and slow, at each phase coherence level, had an additional effect on the slope of the accumulating activity (cf. Figure 5b). Furthermore, these slopes correlated significantly with mean drift rate in a diffusion model simulation. Most importantly, this component was also a good predictor of the content of a subject's choice. Source localization placed this component in left medial parietal cortex, a region that was shown to communicate with both areas exhibiting accumulator activity as well as premotor and motor cortices. Taken together, these results suggest that human perceptual decision making entails a separate categorization stage, which converts the accumulated evidence into a categorical decision and provides a flexible link between decision and action.

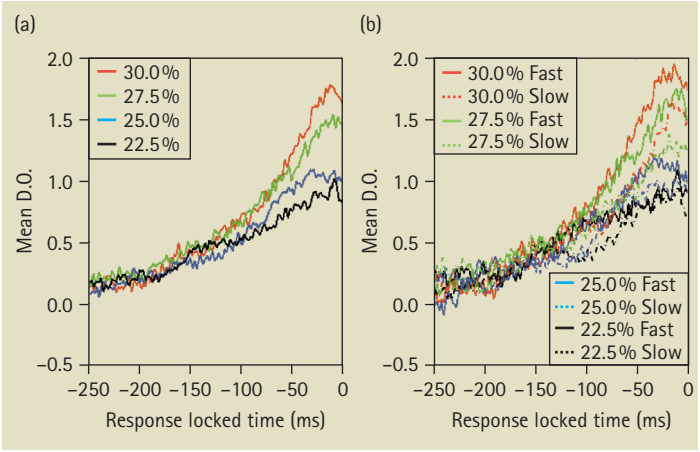

Figure 5. (a) Response-locked activity from the 250 ms preceding the motor response as a function of stimulus evidence. (b) The same activity as in (a) with trials further divided into fast (solid lines) and slow (dotted lines).

Perceptual Decision Making in the Somatosensory Domain

Another fundamental process in the formation of a perceptual decision is the contribution of memory. Our sensory experiences —stored in memory and brought online in working memory—are combined with the current sensory inputs to elaborate our perceptual decisions. In the monkey literature, this process has been extensively described by Romo and colleagues using the vibrotactile discrimination task, which allowed the authors to distinguish between working memory, the development of the comparison process (the combination of the memory trace and the current sensory stimulus), and the motor response. Two of our recent projects aimed at elucidating the role of somatosensory memory representations for human vibrotactile decision making.

The role of the primary somatosensory cortex (S1) for the short-term maintenance of sensory evidence is still under debate. In a previous fMRI study, we have shown that the blood oxygen level dependent (BOLD) signal in human S1 is enhanced during stimulus encoding but not during a 4 s long delay period (Preuschhof, Heekeren, Taskin, Schubert, & Villringer, 2006). It is possible, however, that S1 activity is still enhanced during the early delay period, an effect that cannot be disentangled from encoding activity due to the low temporal resolution of fMRI. Therefore, in a current study, we used the excellent temporal resolution of EEG to investigate the dynamics of the rolandic rhythms which are indicators of S1 activation during the encoding and delay period of a vibrotactile working memory task (cf. Figure 6a). In the pretrial period, the rolandic alpha and beta rhythms over somatosensory sites indicated an increased activity level of S1 in working memory, compared to a control condition. This likely reflects anticipatory attention, but no effect was observed during the delay period (cf. Figure 6b). In contrast to this, frontal and posterior alpha and beta power amplitudes were enhanced during the delay period, which might be related to the functioning of a fronto-parietal attentional network involved in top-down control. Together, our pattern of results suggests that S1 does not maintain the vibrotactile memory trace. The activation level of S1, however, seems to be dynamically adjusted to optimize task performance.

Key Reference

Preuschhof, C., Heekeren, H. R., Taskin, B., Schubert, T. & Villringer, A. (2006). Neural correlates of vibrotactile working memory in the human brain. *The Journal of Neuroscience, 26,*13231–13239.

Key Reference

Preuschhof, C., Schubert, T. Villringer, A., **Heekeren, H. R.** (in press). Prior information biases stimulus representations during vibrotactile decision making. *Journal of Cognitve Neuroscience.*

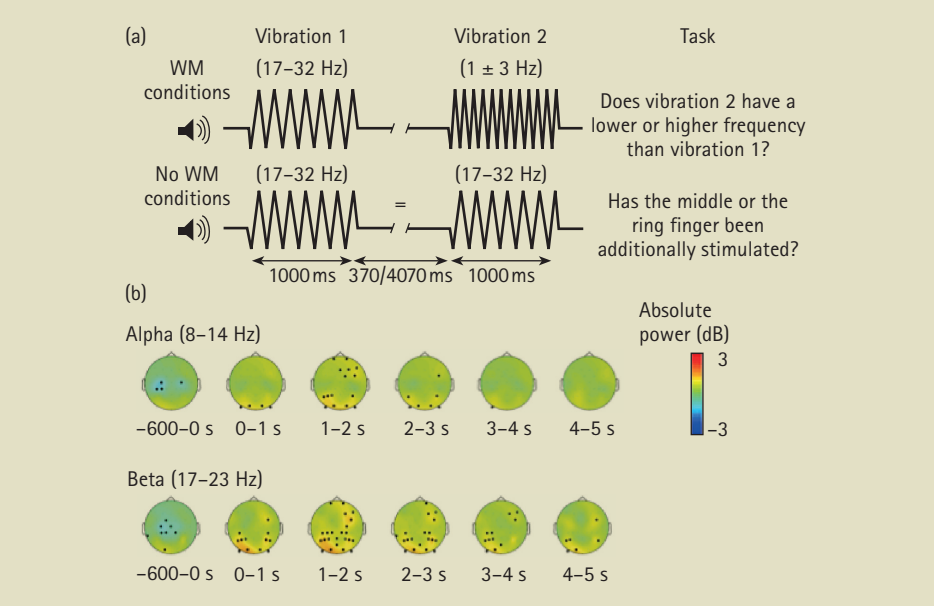

Figure 6. (a) Vibrotactile working memory task. (b) Average topographies representing differences in absolute power for the encoding period (0–1 s) and the delay period (1–5 s) for the alpha (8–14 Hz) and the beta frequency band (17–23 Hz). Bold dots indicate electrodes for which absolute power amplitude are significantly larger in the working memory, compared to the control condition ($p < 0.05$ corrected).

Another source of information which influences perceptual decision making are long-term representations of stimulus statistics in form of prior information. In a current study, we aimed to identify the brain structures involved in the integration of the current vibrotactile stimulus and prior information about the average frequency of the stimulus set (Preuschhof, Schubert, Villringer, & Heekeren, in press). Specifically, we investigated whether prior average information already biases vibrotactile decision making during stimulus perception and maintenance, before the actual judgment process. For this purpose, we used a vibrotactile delayed discrimination task and fMRI. To find neural evidence for the integration of prior average information, we used the time-order effect, a psychophysical phenomenon, which has been proposed to result from such a weighting of current sensory evidence provided by the currently presented stimulus and the average of all stimuli presented previously. The BOLD signal in the secondary somatosensory cortex during encoding and the intraparietal sulcus during maintenance mirrored individual differences in the degree to which subjects integrated prior average information. These findings provide strong evidence for a pivotal role of these regions in the integration process (cf. Figure 7) and demonstrate that prior information can influence perceptual decision making already at early processing stages.

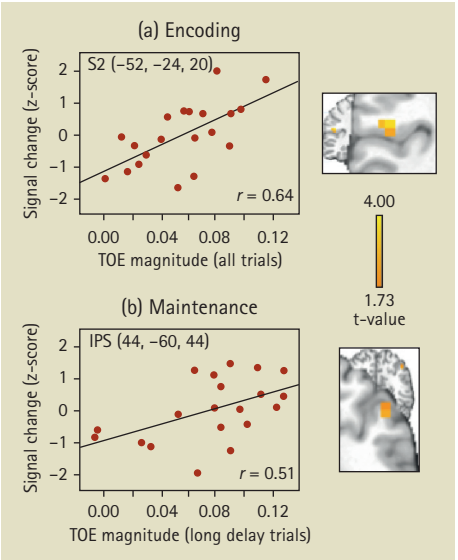

Figure 7. (a) Encoding activity in S2 is associated with individual differences in the weighing of the prior vibration frequency, (b) while activity in the IPS is associated with the weighting of prior information during maintenance. $p < 0.05$. S2: secondary somatosensory cortex; IPS: intraparietal sulcus.

Neurocognition of Reward-Based Decision Making

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-Based Decision Making examines how people use reward-related information to achieve desired outcomes.

To examine reward-based decision making, 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 prediction error (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 has been investigated by different disciplines, which focus on different aspects of decision making. Economics and Machine Learning describe procedures, which aim to maximize the decision maker's outcome. Psychological theories describe how people learn from feedback. 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, 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.

Integration of Possible Gains and Losses During Value-Based Decision Making

Decisions are often associated with potential positive and negative outcomes. From a standard normative point of view, decision makers would need to weight the possible outcomes by their probability and sum the weighted outcomes to synthesize the final evaluation of a choice option. However, this kind of model often does not describe the outcome of decision processes and is probably not an accurate reflection of the underlying psychological and brain processes. By contrast, sequential sampling models, of which the diffusion model described above is one possible instance, offer a mechanistic account of decision making. These models are traditionally applied to perceptual and memory tasks (e. g., Heekeren et al., 2008), but they can also be applied to describe economic decisions. This project uses fMRI to investigate the neurobiological basis of a diffusion-model type decision process in value-based decision making. In the experiment, participants were asked to accept or reject colored shapes, which were associated with different expected outcomes. Prior to the fMRI experiment, participants learned the associations of different gain and loss magnitudes with different colors and shapes, respectively. In the decision-making experiment, they had to combine these learned values to decide if they wanted to collect the payoff associated with a colored shape or not. This experiment tested the hypothesis that a diffusion process underlies the combination of information about potential gains and losses. From this, we derived the behavioral prediction that difficult decisions (i. e., similar gain and loss magnitudes) should lead to more incorrect decisions and to longer reac-

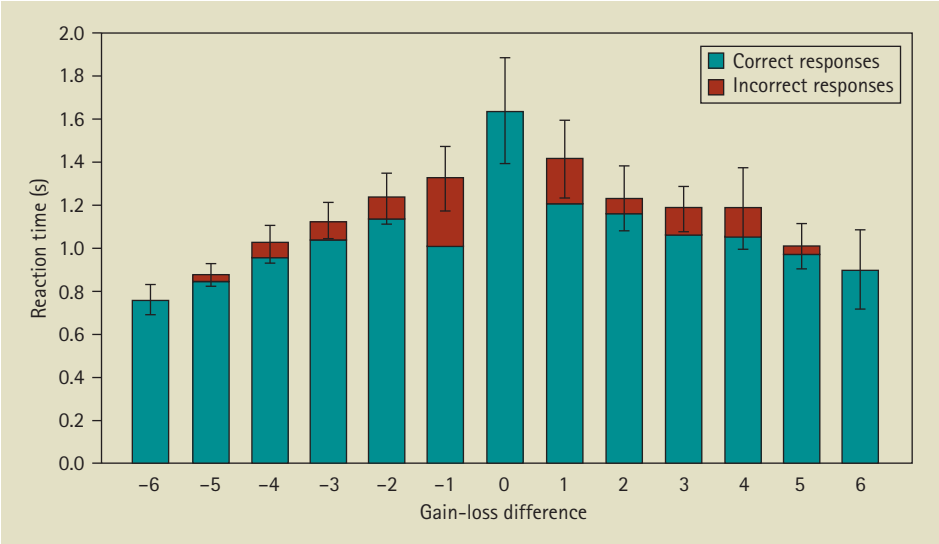

Figure 8. Response time and percentage correct as a function of choice difficulty. The height of the bars represents reaction time. The colors indicate the proportion of correct and incorrect choices. The figure shows that participants responded faster and made fewer errors when the difference between the gain and the loss associated with a colored form was larger.

tion times. On the neurobiological level, we expected a representation of gain and loss information that informs the diffusion process and of decision variables that characterize the diffusion process.

As predicted, Figure 8 shows longer reaction times and more errors when the difference between loss and gain associated with a colored shape was smaller.

For the neurobiological implementation of the diffusion process, we first identified three cortical regions that were modulated by the strength of evidence, the absolute difference between gains and losses (see Figure 9). Note that the strength of evidence is a proxy for the drift rate with which information is integrated in the diffusion model. The direction of the decision, accept or reject, was coded in the anterior-most portion of the rostral supracallosal ACC (rACC), which showed stronger activation for positive, compared to negative net outcomes. For a more direct connection of brain and behavioral data, we additionally modeled participants' choices with the diffusion model and examined if individual differences in latent decision variables are associated with different brain activity. Results of this analysis showed a covariation of participants' decision threshold, which determines how much information they require before settling on a decision, with activation in the ventromedial and anteromedial prefrontal cortex.

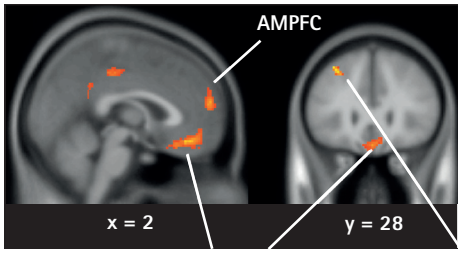

Figure 9. Covariation of BOLD response and strength of evidence. Strength of evidence was operationalized as the absolute difference between the gain and the loss associated with a colored form. The strength of evidence can be thought of as the drift rate in a diffusion model, which is usually defined as the difference of the evidence for one alternative minus the evidence for the other alternative. Increased activity for strength of evidence was observed in the ventromedial prefrontal cortex (VMPFC), anteromedial prefrontal cortex (AMPFC), and right dorsolateral prefrontal cortex (DLPFC).

Taken together, the behavioral and fMRI results support the hypothesis that the mechanism that underlies the integration of potential gains and losses in reward-based decision making has characteristics of a diffusion process, in which information is sampled and integrated until the collected evidence in favor of one alternative versus the other reaches a decision threshold. This project was realized in collaboration with U. Basten and C. Fiebach (fim lab, University of Heidelberg).

Neurophysiological Signatures of Valence, Feedback Magnitude, and Prediction Error

The prediction error (PE) is a central variable when organisms learn from experience. It codes the difference between expectations and actual outcome, which is needed to adjust expectations for more accurate prediction. Consequently, the last years showed a strong interest in the neurobiological implementation of the PE. While earlier work focused an important role of mesencephalic dopaminergic neurons for PE signaling, recent research has highlighted the role of a target of these neurons, the anterior cingulate cortex (ACC). While the role of the ACC is undisputed, the details of cortical PE processing are still unclear. In particular, it remains unclear whether the error-related negativity (ERN, a negative reflection that occurs typically 200–250 ms after feedback) codes the valence, the magnitude, or both aspects of the PE. Furthermore, the role of subsequent processes reflected in the positive deflection (P300) that follows the ERN are even less explored.

To address these questions, we designed a simple reinforcement learning task which ensured a wide range of both positive and negative PEs and was conducted while we measured EEG signals. In each trial, participants were presented with two out of three choice options, which differed in their reward probability. The reward probability changed as soon as participants consistently chose the best option. To investigate the mechanisms of cortical PE processing, we related PEs estimated with a reinforcement learning model to EEG data. Specifically, we used a single-trial linear classification technique to discriminate positive and negative PEs (to test for valence) as well as low- versus high-magnitude PEs (to test for size). This procedure resulted in single-trial discriminator amplitudes, which we then correlated with the single-trial PEs estimated by the model.

The results indicate that a centro-frontal component around 220 ms following feedback, consistent with the well-known ERN, is most sensitive to the valence of an action outcome (red line in Figure 10). Contrary to common belief, our results argue against a role of the ERN in coding the magnitude of the PE (absence of a significant peak around 220 ms for the blue line in Figure 10). An effect of PE valence is also found around 300 ms after feedback, as indicated by the sustained discriminability for the red line in Figure 10. The relevant sensor contributions come from more posterior scalp sites, suggesting a different process than the earlier time window. The effect of PE magnitude is maximal at centro-frontal locations around 300 ms after feedback (blue line in Figure 10). This is also the time window where the size of the PEs correlate positively with the single-trial discriminator amplitudes ($r > 0.4$, $p < 0.01$), suggesting that larger PEs elicit larger physiological responses.

In summary, we show that, within the first 250 ms, the system evaluates mainly along a negative—positive axis. This is followed by two processes (around 300 ms), which happen nearly simultaneously, but appear to have distinct neural generators. While a centro-frontal component codes the valence of an event, a more posterior component evaluates

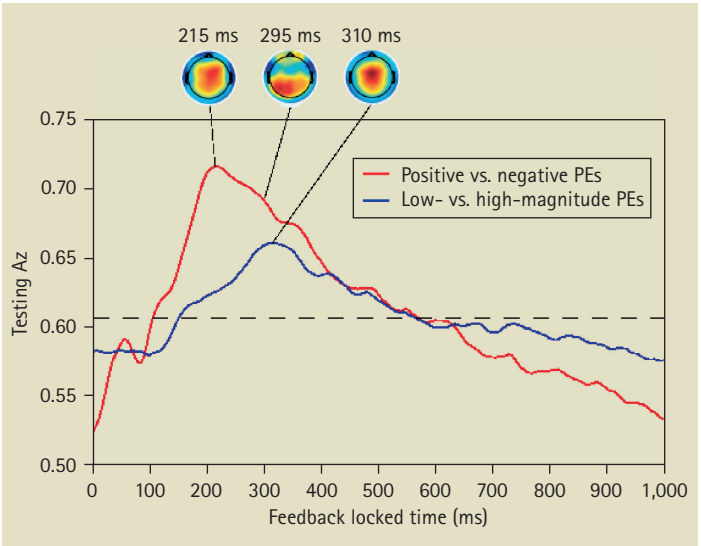

Figure 10. Single-trial EEG discriminator performance. The performance of the classifier is quantified by computing the area under receiver operating characteristics (ROC) curve (Az value) when discriminating between conditions of interest (e.g., positive vs. negative PEs [red] and low vs. high-magnitude PEs [blue]). Scalp maps demonstrate the spatial extent of the discriminating components at the times indicated by the arrows. Data are aligned to the onset of feedback. The dotted line indicates an Az value leading to a significance level of $p < 0.01$ estimated using a bootstrap procedure.

how expected the event was. Both components together provide the PE information required to adjust expectations. Note that, without our single-trial approach, it would have been difficult to differentiate between these two later components, which explains the confusion about the role of the P300 reported in traditional EEG studies.

Embrace the Change—Ability to Quickly and Flexibly Adapt Decisions to Available Rewards is Influenced by Genetic Variation in Dopaminergic Neuromodulation

Most theories of associative and instrumental learning assume that learning is driven by the deviation of predicted and experienced outcomes, the PE. Pioneering electrophysiological experiments showed that the PE signal, which is also central to psychological and optimal models of reinforcement learning, originates, amongst others, from dopaminergic cells in the midbrain, which project to the striatum and the prefrontal cortex where learning is implemented. We hypothesized that genetically based variations in dopamine metabolism should also influence performance in instrumental learning tasks. Specifically, we predicted that the uniquely human Val[158]Met polymorphism in the enzyme catechol-O-methyltransferase (COMT), which influences prefrontal and importantly also striatal dopamine availability, should be related to performance differences in instrumental learning. Most studies on performance effects of the COMT genotype emphasize better performance of Met homozygotes due to higher prefrontal dopamine levels. By contrast, we reasoned that the reciprocal relationship of prefrontal and striatal dopamine levels should lead to a better representation of PEs and, therefore, better performance of Val homozygotes in an instrumental learning task. To test this hypothesis, we conducted an fMRI experiment where Val homozygotes and Met homozygotes performed a reversal learning task. In the task, participants repeatedly chose from four different choice options with different reward probabilities, which changed as soon as participants had learned which option had the highest reward probability (e.g., task reversal). The task had a minimal demand on explicit declarative capacities, yet it afforded constant adaptation to a changing environment. Figure 11 shows, as predicted, that Val homozygotes performed better in the reversal task. To better understand this result, we implemented a reinforcement learning model with an adaptive learning rate that accounts for the requirements of reversal learning in a dynamic environment. According to this model, an increasing difference between expected and actual rewards signal that the adaptation to new reward contingencies is necessary. This is implemented by adapting the learning rate, so that it increases when absolute PEs become larger and decreases when absolute PEs become smaller. The modeling results showed that Val homozygotes had overall higher learning rates and showed a greater increase in the learning rates in the first trials after a reversal (see Figure 11).

The fMRI results confirmed that the better learning performance of the Val type is related to a better representation of PEs. First, as Figure 12 shows, the sign of the PE correlated more strongly with the BOLD response of

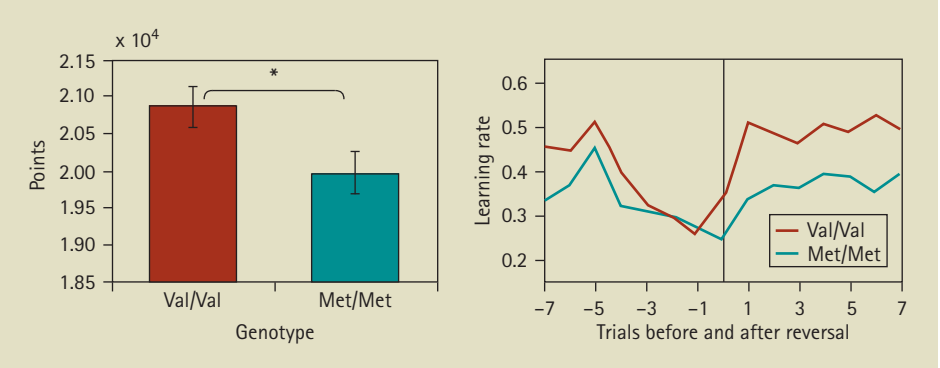

Figure 11. Left panel: Val homozygotes collected more points than Met homozygotes ($P = 0.038$). Right panel: Adaptive learning rate of Val and Met homozygotes before and after reversal (indicated by vertical line). Val homozygotes show a faster increase of the learning rate in response to a changing environment.

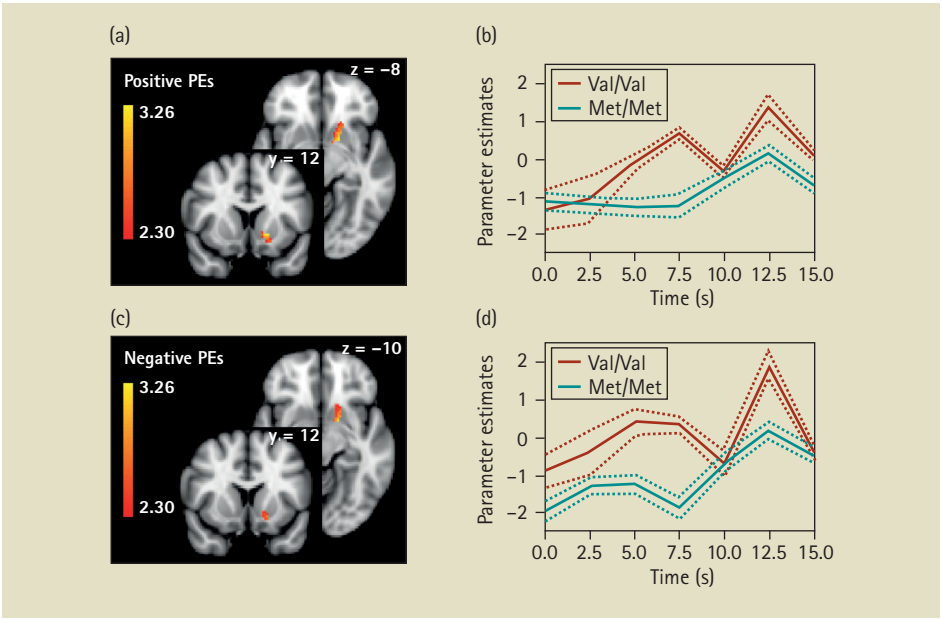

Figure 12. Genotype-related differences in fMRI responses to positive and negative PEs. (a) Greater ventral striatal fMRI responses to positive PEs in Val than in Met homozygotes in the ventral striatum. (b) Averaged time courses (+/–SE) of parameter estimates for voxels within the cluster shown in (a) for Val and Met homozygotes. (c) Greater BOLD responses to negative PEs in Val than in Met homozygotes in the ventral striatum. (d) Averaged time courses of parameter estimates for voxels within the cluster shown in (c) for Val and Met homozygotes.

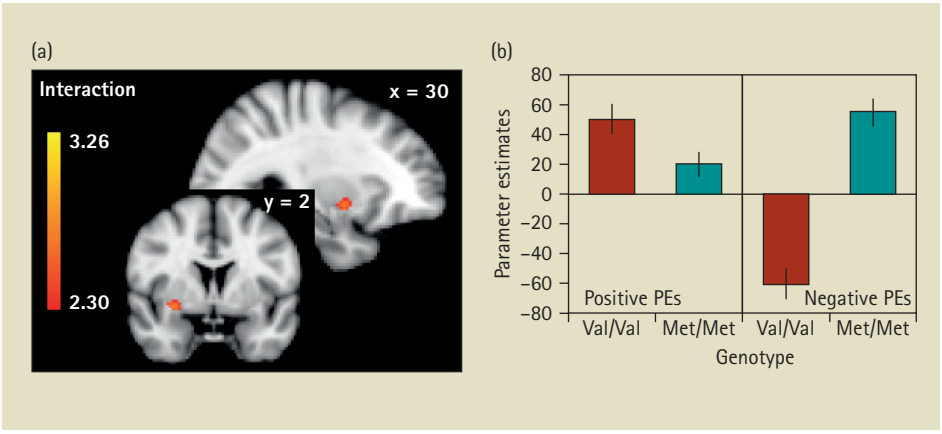

Figure 13. Genotype-related differences in the covariation of fMRI responses with parametric positive and parametric negative PEs. (a) Only Val homozygotes show a positive fMRI signal covariation with positive PEs and negative covariation with negative PEs. (b) Averaged changes in BOLD signal in (+/–SE) in voxels within the cluster shown in (a) for covariation with positive and negative PEs, and for Val and Met homozygotes, separately.

the Val homozygotes in the ventral striatum, which is known to represent PEs.

Second, as depicted in Figure 13, the expected correlation between PE (sign and magnitude) and ventral striatal activity could only be observed for the Val type, which showed increasing BOLD response to increasingly positive PEs and decreasing BOLD response to increasingly negative PEs.

In sum, the results of this study show an effect of the COMT genotype on instrumental learning and suggest a mechanistic explanation for this. The better performance of Val homozygotes seems to be mediated on the computational level by a more successful adaptation of the learning rate and on the neurobiological level by a more effective representation of PEs. Finally, our finding of a functional advantage of Val homozygotes contrasts with prevalent results of an advantage of the Met homozygotes in tasks with higher demands on explicit declarative capacities that more strongly recruit prefrontal brain regions.

Parallel Learning Mechanisms for Model-Based and Model-Free Learning

Most reinforcement learning research has focused on model-free learning, where one learns to predict outcomes based on averaged

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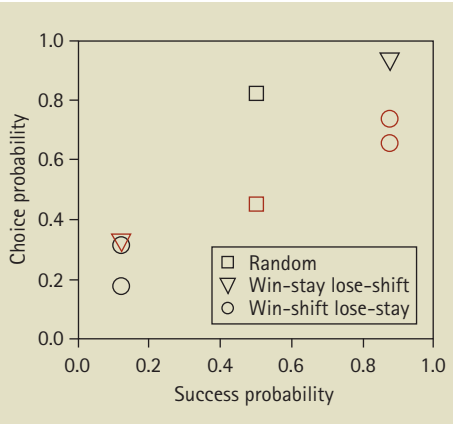

Figure 14. Choice probabilities are adapted to success probabilities. Different symbols forms refer to environments with different reward probabilities. Red symbols depict the probability of being rewarded when repeating a rewarded choice (stay after win). Black symbols depict the probability of being rewarded when not repeating a rewarded choice. In the win-shift lose-stay environment (circles) the probability of success (i. e., a high reward) for repeating an unrewarded choice (red circles) was high and participants frequently repeated y choice after it was not rewarded. The figure also shows that participants learned to stay after a win more easily than to stay after a loss.

past action outcomes only. In contrast, model-based learning uses an internal representation of the task to predict action outcomes, so that—depending on different states of the world—the same actions can lead to different outcome predictions. For instance, a child might like it when the father offers pizza for lunch for the first time in a week, but dislike it if he or she had pizza for the last 10 days. Our previous research showed that learning in simple dynamic environments where outcomes follow sequential patterns is better explained by a model that assumes that decision makers learn and update an internal model of the payoff governing rules (Biele, Erev, & Ert, in press). This project tests the hypothesis that model-based and model-free learning work in parallel, so that PEs and expected rewards for the two learning mechanisms are represented separately in the brain.

In the experiment, participants were exposed to two dynamic environments where they had to learn to play either win-stay lose-switch, or win-switch lose-stay, and one static environment without patterns. The behavioral results confirmed sensitivity to reward patterns. Figure 14 shows that participants played win-stay lose-shift in the task where this strategy lead to frequent rewards and learned to play the less intuitive win-shift

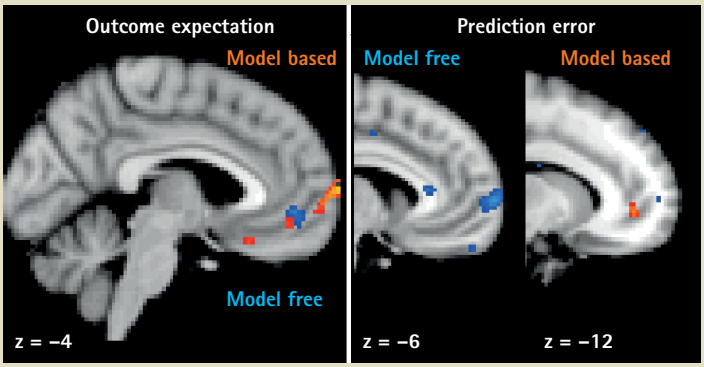

Figure 15. Representation of learning variables for model-free and model-based learning. The left panel shows separate regions in the medial frontal and orbitofrontal cortex that covary with reward expectations from model-free (in blue) and model-based (in yellow/red) learning mechanisms. The right panel shows separate medial frontal and cingulate regions that covary with PEs from model-free (in blue) and model-based (in yellow) learning mechanisms. The learning variables were derived from a learning model that assumes separate parallel learning mechanisms for model-free and model-based learning. While the model-based mechanisms can increasingly determine choices, it is assumed that reward predictions are continuously updated in both mechanisms.

lose-stay strategy when it led to more frequent rewards.
To investigate the neurobiological basis of pattern learning, we tested if the brain represents information about the two parallel learning processes. Participants' behavior was modeled with a new learning model that assumes that the brain updates outcome expectations from model-free and model-based learning in parallel. The fMRI analysis shows that expected payoffs for chosen options as well as PEs predicted by the model were correlated with the BOLD response (see Figure 15). The results showed a separate representation of both expected payoffs and PEs for model-free learning of average payoffs and model-based learning of conditional payoffs in the (medial) prefrontal cortex. These results suggest that instrumental learning does not rely on a single learning mechanism, but that multiple learning mechanism with different sensitivity for patterns in payoff distributions work in parallel to support adaptive choices from experience.

The Influence of Advice on Reinforcement Learning

The final project in this section makes the link between reward-based decision making and decisions in social contexts. The starting point for this project was a previous finding that people behave as if advice changes the evaluation of decision outcomes (Biele, Rieskamp, Gonzalez, in press; see also Social Rationality section of the ABC group). More specifically, the comparison of various augmented reinforcement learning models showed that people add an advice bonus to outcomes from recommended choices, so that, after following advice, positive outcomes are evaluated more positively and negative outcomes less negatively. Even though this explanation can predict the long-lasting influence of advice and a rebound of following advice after initial exploration, it seems to contradict everyday experience. To further test the assertion that following advice influences the evaluation of rewards, we used the fact that reward processing is a well-examined phenomenon in neuroscience. Based on the modeling results, we predicted that reward-representing brain regions should show a greater BOLD response for positive outcomes after following advice than after not following advice. Moreover, these brain regions should signal reward even after a loss, if this loss originates from following advice. To test these hypotheses, participants performed an instrumental learning task in an MRI scanner, after they had received advice from another experienced participant who was motivated to give good advice. Advice indicated which option the advice taker should preferably choose. Consistent with the outcome bonus hypothesis, behavioral results showed again a long-lasting influence of advice on choices, so that recommended options were preferred over nonrecommended options with the same expected rewards (cf. Figure 16).
To investigate the fMRI hypothesis, we focused on the striatum and the medial prefrontal cortex, regions that are known to show increased BOLD response to increased rewards. We first identified reward-sensitive foci within the striatum and the medial prefrontal cortex (see Figure 17). The analysis of the average BOLD time course in the striatum showed an increased BOLD response to gains

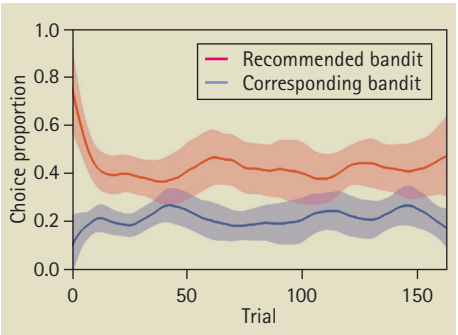

Figure 16. Preference for recommended choice options. Participants' average choice proportions (running average of 11 trials +/–2SEM) for the recommended and the nonrecommended corresponding deck. Advice influenced not only the initial choices. In particular, participants also preferred the recommended deck throughout the experiment. The long-lasting influence of advice is easily explained by the outcome bonus model.

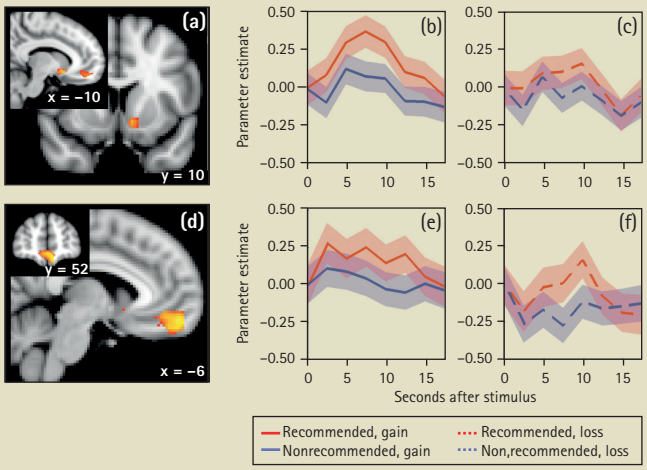

Figure 17. Influence of advice on reward representation in the ventral striatum (VST) and the ventromedial prefrontal cortex (VMPFC). (a) Greater BOLD response for positive versus negative feedback in the VST. (b) Peak BOLD response (+/−1SD) in the VST for positive feedback was greater after following advice (red) than after not following advice (blue). (c) BOLD response time course in the VST for negative feedback. (d) BOLD response for positive versus negative feedback in the VMPFC. (e) BOLD response time course in the VMPFC for positive feedback. (d) BOLD response time course in the VMPFC for negative feedback was greater after following advice than after not following advice.

after following advice, compared to after deviation from advice. Moreover, Figure 17 shows that the reward-sensitive medial prefrontal focus signaled rewards even after losses, if losses originated from following advice.

In sum, the behavioral study and the fMRI study suggest that advice influences instrumental learning by changing the evaluation of outcomes. While a simple manipulation of reward perception might superficially appear as a crude implementation of social learning, it can be considered as adaptive because it maintains exploratory behavior and is particularly influential when choice options seem similar.

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 referred to as 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 prosodic 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 emotional processes. In fact, in a collaborative project with the Center for Adaptive Behavior (ABC), 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 parameters, 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 processes have on social decision making. Using structural and fMRI 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 so-

cial decisions are made. Moreover, to complement our understanding of the "social brain," we are studying individuals with neuropsychiatric conditions that involve socioemotional impairments, such as autism, borderline personality disorder, and narcissistic personality disorder. Insights from our studies in individuals with and without impairments in social decision making have helped our recent development of the Social Cognition Training Tool (SCOTT), an ecologically valid software targeting socioemotional competence, such as face and prosodic processing as well as more complex mindreading abilities.

The Bedrock of Social Decision Making: Face Processing

The study of face processing abilities, such as facial emotion or identity recognition, is of particular importance for social decision making because faces represent a crucial source of social information and their decoding is a precursor for more complex social inferences. Deficits in face processing are among the core features of autism spectrum conditions (ASC) and together with the well-described problems in mindreading they are thought to underlie the defining social impairments of these conditions. Although abnormalities have been reported for a variety of static face processing tasks including visual scanning and emotion recognition, it is not clear to date if those findings apply to online face processing, that is, face processing during social interaction. Moreover, while, in typically developed individuals, face perception involves a distributed set of brain regions comprising a core system (extrastriate visual cortex, fusiform gyrus) and an extended system (e.g., amygdala, superior temporal suclus), it is not clear which of these structures are affected in face processing impairments in autism. We are currently addressing these open questions using a multidimensional approach.

Using eye tracking, we are investigating, for the first time in an online naturalistic fashion, fixation patterns of individuals with and without autism using the Virtual Video Interaction (VII) that involves participants in a standardized dialogue situation (cf. Figure 18). The results of the study showed that individuals with autism fixate less on the face and eyes of a dialogue partner than neurotypical control participants. These findings were especially pronounced when individuals were actively engaged in the dialogue, that is, when they were speaking rather than listening to the interacting partner. Those results indicate that, especially under conditions in which attentional resources need to be allocated to different processes, such as during naturalistic social interactions, face processing is

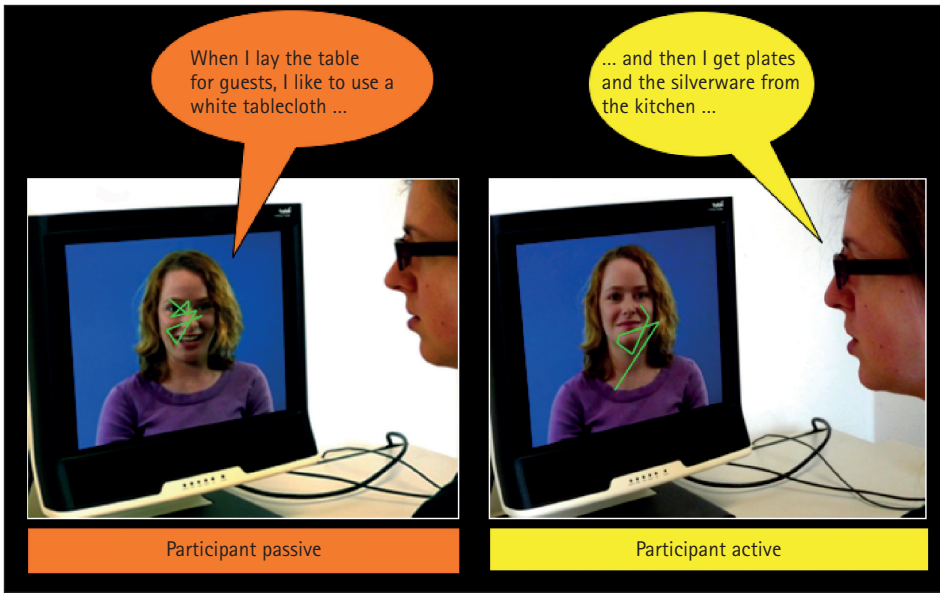

Figure 18. Investigation of gaze patterns using the naturalistic Virtual Video Interaction (VII). Participants are required to watch a 4-minute video on the eye-tracking monitor, facing a virtual dialogue partner, who involves the participant in a conversation about food (passive: participant is listening to dialogue partner; active: participant is speaking).

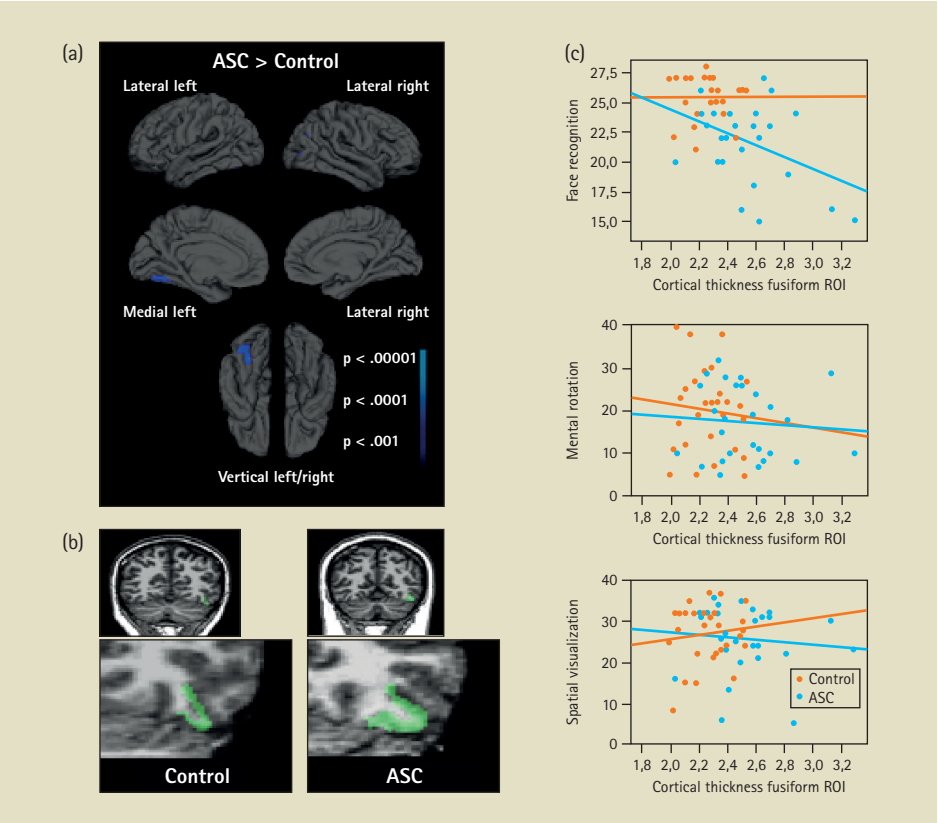

Figure 19. (a) Cortical regions are thicker in the ASC group than in controls. Statistical map depicting between-group differences in thickness at each vertex on the cortical surface overlaid on the group's average brain. All points meeting a $p < 0.001$ threshold (uncorrected) are displayed. (b) Coronal section displaying area of significant regional thickening for one control and one ASC participant. (c) Scatter plots of mean cortical thickness of each participant in the left fusiform gyrus ROI plotted versus face recognition, mental rotation, and spatial visualization, respectively, split by diagnostic group.

impaired in individuals with autism. Moreover, in the autism group, fixations on face and eyes were strong negative predictors for social symptomatology as measured with autism diagnostic interviews and tests of social cognition performance: Those individuals that fixated more on the face and eyes of a dialogue partner showed less severe social impairments and better performance in recognizing emotions from faces.

Applying structural and fMRI, we are currently seeking to elucidate the neuronal correlates of face processing in individuals with and without ASC. In a first morphometric study, carried out in collaboration with the Center for Brain Health, New York University (Antonio Convit), we applied an automated measurement to estimate fusiform gyrus cortical thickness and a manual tracing method to obtain amygdala volumes in 27 adults with ASC and 29 well-matched typically developed controls. Anatomical connectivity was estimated by analyzing volumetric covariance among those brain regions. We found specific local increases in cortical thickness of the fusiform gyrus and associated impairments in face processing in individuals with autism (cf. Figure 19). Amygdala volumes further predicted face reading (dys)functionality in all study participants. Anatomical covariance between amygdala and fusiform gyrus local thickness increase was significantly smaller in the ASC group. As such, our data provide the first anatomical evidence for an abnormal amygdala-fusiform axis and its behavioral relevance for face processing deficits in ASC. While autism has been theorized as a condition of reduced connectivity in higher order association cortices, our findings extend this conception to lower level perceptual systems involving subcortical regions, suggesting disconnectivity to be a more universal correlate of ASC brain dysfunction.

In an fMRI study, we are currently following up on our findings from eye tracking and structural MRI studies in ASC (Dziobek, Rogers, Fleck, Wolf, & Convit, 2006b), seeking to identify whether differential involvement

of amygdalar subregions may account for the specific gaze behavior and face processing impairments observed in autism. Specifically, a two-component model for autism gaze behavior with specific amygdalar activation patterns recently proposed that a failure to actively orient to the eyes, as observed in patients with amygdala lesions, coexists with an aversion to directly fixate the eyes. To validate and potentially expand on this model, we developed, in collaboration with the University of Hamburg (Christian Büchel), a new facial emotion discrimination task, which targets (a) the effect of aversion when focusing on the eye region and (b) the effect of attentional capture by the eyes when directed to focus on the mouth region.

Differentiating Empathy in Psychopathology

Empathy builds on more basic social perceptive functions and enables us to infer the mental states of others and to share emotional experiences, both of which are essential for the formation of close bonds. Thus, as a socioemotional construct, empathy entails cognitive (understanding others' mental states, social cognition) and affective (emotional reaction to the observed experiences of others) components. Our Multifaceted Empathy Test (MET; Dziobek et al., 2008) gives us an objective test for this multidimensional conception for the first time by simultaneously assessing cognitive and affective components while study participants process social picture stimuli. An important goal of our work is to make it applicable for *clinical* cognitive neuroscience questions. In pursuit of this goal, we are investigating empathic abilities in clinical populations, such as autism and borderline and narcissistic personality disorder, in collaboration with the Department of Psychiatry and Psychotherapy of the Charité—University Medicine, Campus Benjamin Franklin in Berlin (Isabella Heuser, Stefan Röpke).

Despite the lack of research, deficient empathy is considered a central characteristic of autism. Using the MET, we have recently shown that, while individuals with autism have impairments in inferring others' mental states (cognitive empathy), they are as empathically concerned for others (emotional empathy) as control individuals (Dziobek et al., 2008). In a next step, we sought to elucidate the brain underpinnings of cognitive and emotional empathy and its differential representation in individuals with and without autism. To this end, we developed an fMRI compatible adaptation of the MET and contrasted brain activations of 20 individuals with autism and 18 controls. The results showed that both groups activated similar networks for cognitive as well as emotional empathy (Figure 20). When contrasting cognitive empathy between groups, individuals with ASC showed more activation in an emotional network encompassing the right amygdala, anterior insula, and orbitofrontal cortex (Figure 21), possibly reflecting a mechanism by which deficient cognitive empathy is compensated for in individuals with ASC. During the emotional empathy condition, however, the autistic individuals showed reduced activity in a region of the inferior frontal gyrus, which has been equated with the human mirror neuron system.

In a recent study, we also found that, in contrast to individuals with autism, patients with borderline personality disorder (BPD) show deficits in both cognitive and emotional empathy. BPD is a psychiatric disorder characterized by unstable relationships, impulsivity, and affective dysregulation. Results of our first behavioral study showed that the level of comorbid posttraumatic stress disorder and a history of childhood sexual

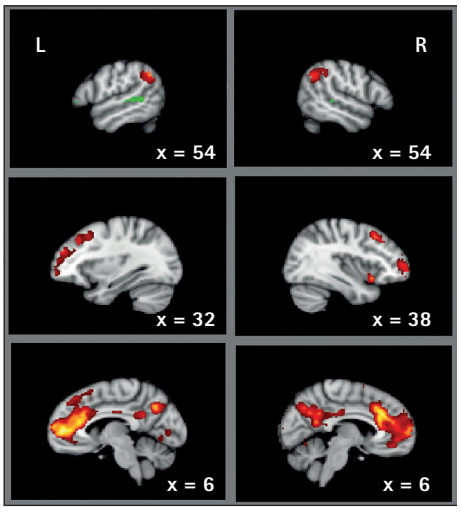

Figure 20. Conjunction analysis (ASC group and neurotypical controls) for the contrasts emotional > cognitive (red-yellow) and cognitive > emotional empathy (green; $p = 0.001$, uncorrected).

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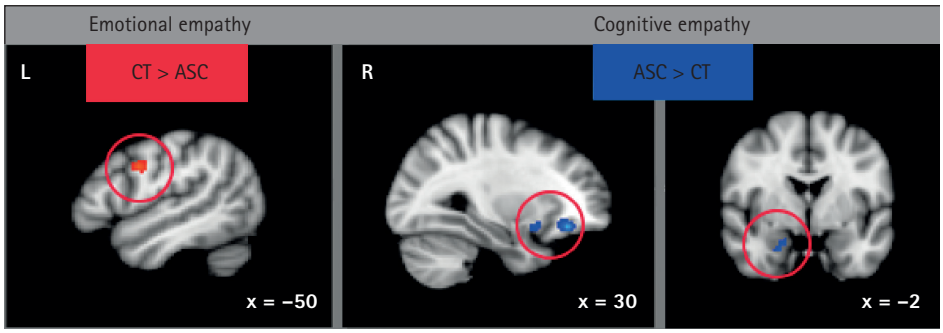

Figure 21. Contrasts between ASC group and neurotypical controls for emotional and cognitive empathy ($p = 0.001$, uncorrected).

and physical abuse were strong predictors for the deficits in cognitive empathy, pointing to the importance of psychosocial factors in the etiology of BPD. In a subsequent fMRI study contrasting cognitive and emotional empathy using an adaptation of the MET in 30 patients with BPD and 30 controls, we confirmed the traumatic experiences as crucial predictors for the ability to infer mental states of others: Patients with BPD showed reduced activation in the superior temporal sulcus (STS) during cognitive empathy, where this reduced activation was highly correlated with levels of intrusive symptomatology in the BPD group. Thus, in BPD, the involvement of the STS region as a key mediator for cognitive empathy might be adversely affected early in development by childhood trauma that leads to the intrusive symptoms seen in adult patients. Individuals with narcissistic personality disorder (NPD) are characterized in the DSM-IV by an inflated sense of self-importance, need for admiration, extreme self-involvement, and lack of empathy for others. In an effort to validate the DSM-IV criterion of lack of empathy for the first time empirically in affected individuals, we recently conducted a study using the MET and the Movie for the Assessment of Social Cognition (MASC; Dziobek et al., 2006a). The results showed that, while NPD

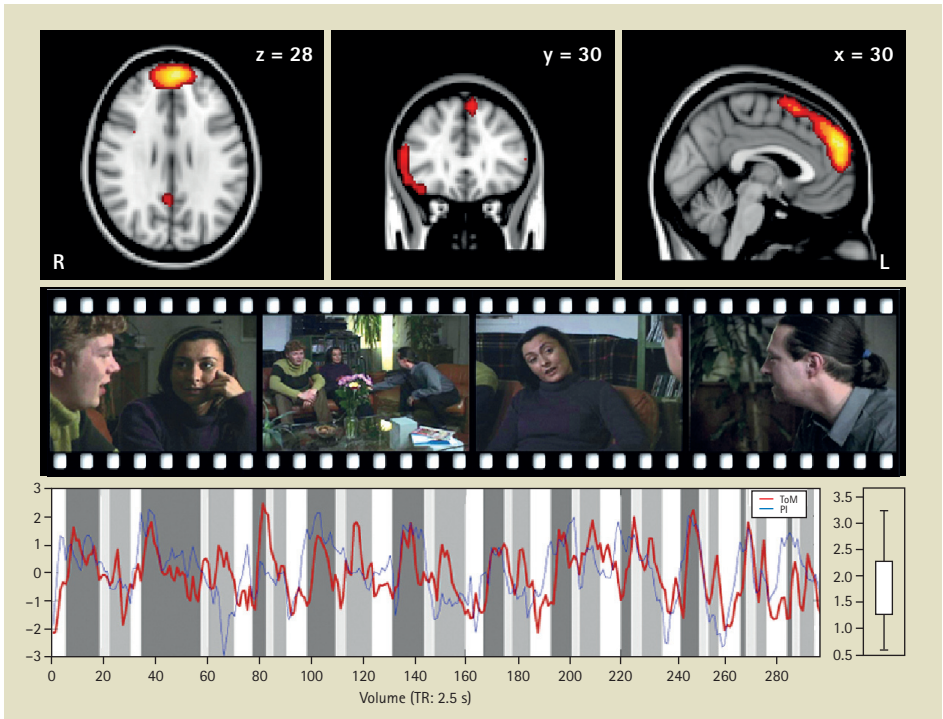

Figure 22. Upper panel: T-PICA results showing a functional network including dorsomedial prefrontal cortex, inferior frontal gyrus and precuneus activation during social decoding of naturalistic scenes (middle panel). The associated time course (lower panel) indicates the component's sensitivity during social processing.

involves impairments in emotional empathy, cognitive empathy is generally well preserved, which represents a mirror image pattern of the empathic abilities found in autism. We are currently using fMRI and the MET to identify brain correlates of this double dissociation between cognitive and emotional empathy by contrasting brain activation of individuals with autism and NPD.

According to recent conceptions, social cognition entails both decoding of visual-perceptive socioemotional cues and reasoning about mental states. Using social cognition tests, such as the video-based MASC (Dziobek et al., 2006a), we are currently investigating those processes and their neural underpinnings in close to naturalistic settings. We used an fMRI adaptation of the MASC that allows separate analysis of decoding fast-changing perceptual cues as demanded in naturalistic settings versus social reasoning. Imaging data were analyzed by means of both a standard General Linear Model (GLM) approach and a tensorial probabilistic independent component analysis (T-PICA), a novel model-free approach that allows for the fine-grained analysis of specific neuronal activations and functional connectivity between brain regions. Interestingly, while results of the GLM approach identified a set of brain regions known to be part of the social brain, such as the superior temporal sulcus, temporo-parietal junction, medial prefrontal cortex, and precuneus as important for social reasoning, the T-PICA showed that those regions are not represented in a functionally connected network. Instead, T-PICA results seem to indicate that more circumscribed and smaller networks, such as the medial prefrontal cortex and parts of the frontal operculum (cf. Figure 22), might mediate differential aspects of social cognition, such as self-referential mental activity.

Our previous research has shown that individuals with autism have relatively more accentuated impairments in the decoding of social cues than in the reasoning about mental states (Dziobek et al., 2006a). Moreover, in eye-tracking studies using adaptations of MASC and MET, we recently found evidence that, already at the level of social attention, autism seems to involve an attenuated orienting response to socially salient features of a scene. Based on those observations, we have developed the Social Cognition Training Tool (SCOTT), a computer-based intervention for the improvement of socioemotional competencies. SCOTT uses lifelike video-based stimuli to increase the understanding of 40 simple and complex emotions and is composed of four training modules of varying complexity, each targeting specific aspects of socioemotional attention, perception, and cognition (for an example cf. to Figure 23). As a core element, SCOTT's Emotion Library includes 40 emotions, which users will encounter in the different training modules (cf. Figure 24). Communicative

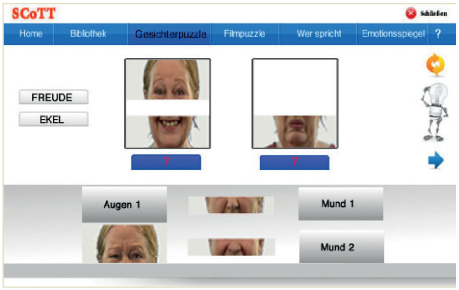

Figure 23. The SCOTT's module Face Puzzle. The stimuli of this module are made up of video sequences of different emotional facial expressions of the same person, which were cut into several parts. The parts are shuffled and presented simultaneously to the user whose task it is to match the emotion congruent pieces to holistic faces.

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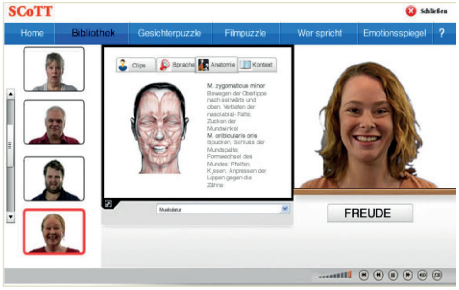

Figure 24. The SCOTT's Emotion Library. Each of a set of 40 emotions is explained at semantic, audio-visual, and physiological levels by using verbal definitions, video and audio excerpts of the emotional expression, and educational maps of emotion-specific psychophysiological correlates, respectively.

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relevance was the most important criterion when deciding on the emotions to be included in the software. However, given the lack of emotion taxonomies allowing for communicative relevance, we conducted a survey with 100 participants who were specifically asked to rate the frequency with which 60 different emotions are encountered in everyday life. Of those 60 emotions, the 40 most communicatively relevant ones were chosen for SCOTT. We expect this specific emotion selection to increase the relevance and generalization of effects of SCOTT. In a 3-month intervention study, we seek to evaluate the effectiveness of SCOTT in improving social attention and cognition at the behavioral and neuronal level.

The Independent Junior Research Group in February 2009

From left to right: Marios G. Philiastides, Holger Gerhardt, Nikos Green, Soyoung Park, Helen Blank, Isabel Dziobek, Peter N. C. Mohr, Anja Marwitz, Flavia Filimon, Niki Vavatzanidid, Claudia Preuschhof, Dorit Kliemann, Sandra Preißler, Niels Kloostermann, Rosa Steimke, Agniezska Zofia Burzynska, Hauke R. Heekeren.

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