Collaborative Research Center 991

The Structure of Representations in Language, Cognition, and Science

Heinrich-Heine-Universität Düsseldorf



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3.1 About project D03

3.1.1 Title: Conceptual representation in social cognition: Frame-theoretical representation of "social partner"

3.1.2 Research areas:

206-04 Systemische Neurowissenschaft, Computational Neuroscience, Verhalten, 110-01 Allgemeine, Biologische und Mathematische Psychologie

3.1.3 Principal investigator(s)

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Do the above mentioned persons hold fixed-term positions? no

3.1.4 Legal issues

This project includes

1.	research on human subjects or human material.	no
2.	Clinical trials	no
3.	experiments involving vertebrates.	yes
4.	experiments involving recombinant DNA.	no
5.	research involving human embryonic stem cells.	no
6.	research concerning the Convention on Biological Diversity.	no

3.2 Summary

As the scientific study of conceptual representations often focuses on tangible concepts, remarkably little is known about the cognitive representation of abstract concepts, even from the perspective of traditional cognitive theories. However, abstract concepts appear to play a central role throughout human cognition, especially in social cognition and social interaction (Barsalou 2008). We constantly classify people, based on our experience with them, their biographic information and other sources, into socially relevant categories, such as whether they are friendly, whether favors will be reciprocated etc. Once a perceived individual has been assigned to a social category, rich inferences (attributions) result about the causes of the person's behavior and their likely actions. In our project, we aim to apply Frame Theory to social cognition, especially prosocial behavior. The key notion is that an agent may perceive someone else either as a social partner, as a competitor, or as a non-social object. In this project, we plan to investigate the conditions and consequences of a 'partner' frame representation on the attitude towards the partner, in particular with respect to choice behavior during social interaction. Because animal models allow for better standardization and thus more rigorous testing than human studies, we will use rats (rattus norvegicus) as model organisms. With the help of a rat model of prosocial choice, we plan to characterize the nature of the conceptual representation 'partner' during social interaction. We will contrast the predictions of Barsalou's frame theory (Barsalou 1992) with the predictions from other accounts, mainly flat feature list representations (Rosch & Mervis 1975). To this end, we will systematically eliminate (experiments 1-3) or manipulate (experiment 4) the attributes vocalization, odor and appearance that are believed to play a central role in recognizing another object as an animate social partner.

3.3 Research rationale

3.3.1 Current state of understanding and preliminary work

Conceptual representation of "others"

Imagine you are walking home, and, turning around the corner of your street, you bump into George Clooney. He beams and looks straight into your eyes. Shaken, you grab his hands to greet him, but he does not respond. Only then do you realize that it is not a real person, but a waxwork figure of stunning similarity with George Clooney manufactured by your neighbour, who is an artist specializing on wax figures. Even the fake skin of this hand feels real. You step back and inspect the figure with curiosity. Interestingly, you now show a drastically different behavior towards the figure: as long as you still thought the figure was a real person, you were surprised, you wanted to engage in the convention of social approach (greeting, hand shaking), you had non-verbal communication (smiling) etc. Once you realized that this figure was only made of wax, your behavior changed completely: you stop adhering to social convention, but instead step back and show alternative behavior that would be considered socially inappropriate if George Clooney had been real (visual inspection, intense staring). What changed? Clearly, the figure's looks are strikingly similar to the real George Clooney, even the texture of the wax skin of its hands is comparable to real skin. So, it is not the physical features that determine your behavior, but the concept you have of a social being versus artificial/inanimate object. Thus, this cartoon illustrates that our behavior strongly depends on the conceptual representation of our social world.

This insight is certainly not new. It is intuitively evident that the ability to form conceptual representations of our social world is of prime importance for social cognition (Fiske & Taylor 1984; Kunda 1999). However, our understanding of social cognition and their evolution is still incomplete. One likely reason is that we lack a proper conceptual framework to comprehend the cognitive, emotional and motivational processes associated with social behavior. For instance, it is unclear how the recognition of the social identity of an interaction partner – one of the main drivers of prosocial behavior – is cognitively and neurally represented, and what features discriminate a social element as social from a non-social item with no social relevance. Simply speaking, as our introductory cartoon has sketched, individuals behave differently when interacting with a living, social interaction partner as opposed to a similar-looking, but inanimate object. However, it is unknown how individuals disambiguate between social and non-social contexts, and how they form a representation of the concept "social partner".

Frame theory (Barsalou 1992) may provide the conceptual tools necessary to formalize the representation of the abstract social concept "social partner". According to Barsalou (Barsalou 1992), frames constitute the universal representation system of cognition. The frame approach holds that concepts can be represented in attribute value structures. Each attribute can be connected to a cluster of more specific attributes, and certain attributes can also constrain the range of other attributes putting the concepts into dynamical connection and relation. One implication is that the activation of a perceptual property of a concept in frame format may automatically lead to the representation of a whole conceptual system, which allows a structured description of knowledge (Barsalou 2005; see also project A04). As all attributes can be subject to constraints, they may not be considered equally important. Edwards and colleagues, for example, propose that attributes are differently weighted and that the importance of each attribute is relative to all others (Edwards et al. 1982). Barsalou's theory is supposed to be an alternative to flat feature list representations, but also to other theories prominent in the research literature such as prototype theory and exemplar theory (but see project D01). The classic feature list model for cognitive science was developed by Alba & Hasher (1983), Glas & Holyoak (1975) and Hampton (1979). They proposed that each category representation is a list of features, that is, a list of independent representational components forming a single level of analysis, whose sum represents the category. Feature lists treat attributes and values as the same kind and do not specify relations between features.

The feature- or attribute-list framework has been hypothesized to be species-general and could be applied to human and non-human cognition alike. Importantly, Barsalou also proposed his account of frame structures as a theory of concepts in humans as well as in non-human animals (Barsalou 2005).

In this proposal, we aim to formalize the conceptual representation in an animal model using frame theory as a tool of formalization. Because attribute (feature) list models as well as frame theory have been proposed to be valid cross-species, and because animal models of social behavior have a number of crucial advantages over human models (see below), we ask how rats represent their social world. Clearly, a rat's social environment is complex. But we know from studies in our lab (see below) that certain features of a rat's partner are particularly important for social behavior. These features include *vocalization, appearance* and *odor.* If we conceive of these features as attributes of a general category, e.g. social partner, which is influenced by and influences social behavior, we are able to systematically link these attributes to each

other and may find certain interactions between them, which would remain obscure if we consider each dimension as being represented independently from each other.

Figure 1 visualizes how frame theory and the feature list approach formalize the putative cognitive representation of the identitification of something as a social animal partner. Figure 1A) pictures the frame hypothesis for the representation of another rat as social partner. Here, *vocalization, appearance* and *odor* are attributes of the category "partner", each with different values like high/low vocalization rate, similar/different appearance and natural/artificial odor. The specific behavior of the rat towards its partner is mediated by the rat's representation of the other rat as either as a social partner, or as an inanimate object. This means that one of the attributes does not change the social behavior directly, but only indirectly by changing the representation of the other rat as either partner or inanimate object. Furthermore, taking possible constraints between values of different attributes into account, specific interactions between the three attributes may result, e.g. it is possible that appearance plays only a modifying role if the odor has a certain value. By contrast, feature lists (figure 1B) are not able to explain such interactions between factors that go beyond an additive effect. The feature list approach describes a rat's representation of another rat in the form of a flat feature list, where each dimension has a direct and mutually independent impact on social behavior.

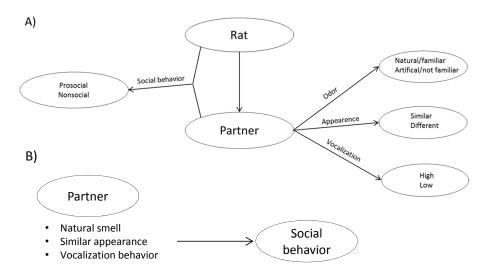


Figure 1: Social partner according to frame theory (A) or the flat feature list approach (B)

Communication and its effect on prosocial behavior

One crucial factor during social interaction is communication. Communication means the exchange of information through behaviors like gesture, appearance, gaze and "vocalization" (in rats, vocalization is expressed as high-frequent ultrasonic vocalization calls). Communication has a strong influence on human choices as it gives us the possibility to identify intentions and provides us with information about others' identity. In non-human primates it was shown that social vocalization elicits activity in neural networks representing associated social situations instead of concrete features of the calls (Gil-da Costa et al. 2004). Processing social and emotional content, just like any mental content, involves mental representations (Niedenthal et al. 2005): it is assumed that others are perceptually represented (Wyer & Carlston 1994) through four primary mental systems: i) visual, ii) verbal, semantic, iii) affective and iv) action. Each of these systems captures the relevant attributes, interacts with other modality-specific systems, i.e., distributes them across systems, and thus forms the basis of representing conceptual knowledge of social situations.

Studying social cognition concepts in animals

Referring to the work of Sutherland and Mackintosh (Mackintosh 1965; Sutherland & Mackintosh 1971), Barsalou already proposed in 1992 (Barsalou 1992) that animals use attribute-value sets in discrimination learning, supporting the idea that frame theory could be applied to understand conceptual representation in animals, too. For example, in a rat version of the set shifting task (Birrell & Brown 2000), the animals had to choose between two different bowls where one contained a food reward. The bowls differed in three attribute values: odors, mediums that filled the bowl, and surface textures. One of these attributes cued which of the two bowls contained the reward. Once rats learned to identify the reward-predicting cues, the cue-reward contingencies were shifted. Results showed that learning a novel discrimination was faster when it was based on the previously relevant perceptual dimension (e.g. odor-odor cue reversals: oregano to cinnamon; intra-dimensional shift) than when attention had to be shifted to the previously irrelevant dimension (e.g., odor-filling reversals: oregano to sand; extra dimensional shift). The shift-costs, i.e., the post-reversal reacquisition rate, should be identical after intra- and extra-dimensional shifts if the cue was represented as a feature list. However, this was not the case: the animals were slower to reach pre-shift performance after an extra- compared to an intradimensional shift. This observation cannot be explained by the hypothesis of isolated feature list representations. A better way to understand these phenomena is that the stimulus is represented by each of its attributes and attribute-values, e.g. "odor" with the values oregano or cinnamon. A shift between the values of the same attribute should be easier than a shift between different attributes.

We propose that frame theory can be extended to understand animal social behavior. Over the last decades, evidence accrued that not only humans, but also many non-human animal species show prosocial behavior towards conspecifics, i.e., they revealed preference for actions that increased the well-being of other animals (Rutte & Taborsky 2007; Lakshminarayanan & Santos 2008; Bartal et al. 2011). Our main claim that frame theory can be extended to animal social behavior is supported by recent evidence from Gil-da Costa et al. (2004) who suggested that a similar (anatomical) architecture for representing category knowledge exists across species and can be extended to the social domain (Barsalou 2005; Gil-da Costa et al. 2004). In their study, specific calls of nonhuman primates conveyed information about the signaler and its socioecological context (Gil-da Costa et al. 2004). This study focused on two different call types. The first was named *coos* and was associated with positive social context, such as friendly approach behavior and call to conspecifics out of sight. The second type was termed *screams*, which are usually emitted after threat or attack by a conspecific. By using Positron-Emission Tomography, it was found that these conspecific vocalizations elicited activity in neural networks which strongly correspond to the network shown to support the representation of conspecifics and affective information in humans.

Thus, we propose that animals use similar attribute-value structures to conceptually organize their social and non-social world. Frame theory could provide the key solution to describe and understand how organisms represent, and distinguish between animate and inanimate partners during prosocial choice. Social interaction is multi-faceted and notoriously sensitive to cultural, experiential, cognitive, expectational and gender-specific influences. It is therefore imperative to control for all possible confounding factors when studying social interaction. Although there is a rich literature on social cognition in the human domain (Fehr & Gächter 2002; Fehr & Fischbacher 2003), the best way to control confounding variations in cultural backgrounds, prior expectations and the tendency to show socially desirable behavior is to study social behavior in non-human animals. Moreover, we have recently argued in favor of complementing traditional human research with careful comparisons across species because such comparative approaches offer possible answers to the question why humans make social and economic decisions as they do (Kalenscher & van Wingerden 2011). Here, we plan to use rats as model organisms. Rats are highly social animals (Blanchard et al. 1988; Blanchard & Blanchard 1990) and have been shown to exhibit prosocial behavior in various contexts and ways (Rutte & Taborsky 2007, 2008; Bartal et al. 2011). We have recently developed a prosocial choice task (see next section for details) in which rats made decisions either yielding a benefit for themselves and another rat, or only for themselves alone. (Hernandez-Lallement et al. submitted).

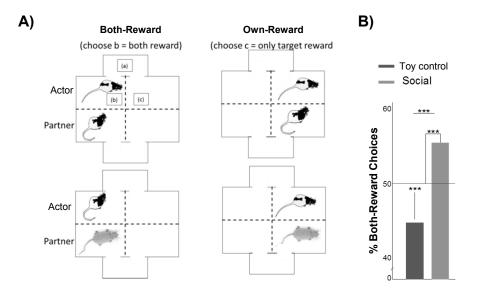
Preliminary work

Prosocial choice behavior can be descriptively defined as the preference for outcomes that produce a benefit for another conspecific. We demonstrated in a controlled environment that rats show behavior that meets this definition of prosociality. Importantly, the rats had a higher tendency to produce benefits for a living social partner than for an inanimate puppet partner, although the reward contingencies and other task-related aspects were kept constant (see figure 2 and below for more details on the task). Thus, actor rats distinguished between live and inanimate interaction partners – one of the principle prerequisites of social cognition.

3.3.2 Project-related publications

Crockett, M. J., B. R. Braams, L. Clark, P. N. Tobler, T. W. Robbins & T. Kalenscher. 2013. Restricting temptations: neural mechanisms of precommitment. *Neuron* 79(2). 391–401. doi: 10.1016/j.neuron. 2013.05.028

Kalenscher, T. & M. van Wingerden. 2011. Why we should use animals to study economic decision making - A perspective. *Frontiers in Neuroscience* 5. 1–11. doi: 10.3389/fnins.2011.00082



- Figure 2: **Prosocial choice task procedure and results.** A) **Procedure**. The apparatus consisted of two T-maze facing each other. Each T-maze consisted of a starting box connected to two decision chambers. The T-mazes were separated by a transparent and perforated wall allowing olfactory, auditory and visual exchange. Two rats (actor and partner rats) interacted. In both reward trials, the actor entered one compartment (here: compartment b), which resulted in food delivery to the partner rat directed to the compartment facing the actor (social condition, left upper panel) or an inanimate toy rat (toy condition, lower left panel). Own-reward trials resulted in reward delivery only for the actor, but not the partner (upper right panel), or toy rat (lower right panel). B) **Results**. Rats in a social condition (with a rat as partner) chose the both reward alternative (self & other reward) significantly more often than in a toy condition (with a puppet as partner). p<0.001
- Kalenscher, T. & C. M. A. Pennartz. 2008. Is a bird in the hand worth two in the future? The neuroeconomics of intertemporal decision-making. *Progress in Neurobiology* 84(3). 284–315. doi: 10.1016/j.pneurobio. 2007.11.004
- Kalenscher, T., S. Windmann, B. Diekamp, J. Rose, O. Güntürkün & M. Colombo. 2005. Single units in the pigeon brain integrate reward amount and time-to-reward in an impulsive choice task. *Current biology : CB* 15(7). 594–602. doi: 10.1016/j.cub.2005.02.052

Kalenscher, T. 2007. Decision making: don't risk a delay. Curr. Biol. (17). 58-61

Kalenscher, T., C. Lansink, L. J.V. & P. C.M. 2010. Reward-associated gamma oscillations in ventral striatum are regionally differentiated and modulate local firing activity. *J. Neurophysiol.* (103). 1658– 1672

3.4 Research Plan

3.4.1 Research questions, aims and hypothesis

General approach

Our goal is to characterize the nature of the conceptual representation *social partner* during social interaction. To this end, we will contrast the predictions of Barsalou's frame theory (Barsalou 1992) with the predictions from other accounts, mainly feature list representations (Rosch & Mervis 1975). To test our predictions, we will systematically eliminate (experiments 1-3) or manipulate (experiment 4) the attributes *vocalization*, *odor*, and *appearance* that are believed to play a central role in recognizing another object as an animate, social partner.

Aims and hypothesis

We propose the fundamental hypothesis that a similar architecture for representing category knowledge of social situations exists across species, and that the cognitive and neural mechanisms underlying prosocial behavior are shared among them. Specifically, we hypothesize that the abstract concept "social partner"

can be formalized in the frame-theoretical format depicted in figure 1. We propose that *vocalization*, *appear ance* and *odor* are attributes of the category "social partner", each of which can take up different values, such as high/ low vocalization rate, similar/different appearance and natural/artificial odor. We do not claim that these are the only attributes necessary to represent something as "social", as other attributes, e.g., "locomotion", "rearing behavior" or others, may be as relevant, or even more important. But we do claim that these three attributes *are* part of the attribute/value composition that forms the concept "social partner". The specific behavior of an actor rat towards its partner is mediated by the actor rat's representation of the other rat as either socially relevant, i.e. a real rat, or irrelevant, i.e., an inanimate object. This means that manipulating one of the attributes does not necessarily change the rats' social behavior directly, but only indirectly through changing the representation of the other object as socially relevant or inanimate. We will determine specific interactions between the three attributes, e.g. if the appearance value has an effect on social concept representations only if the odour attribute has a certain value, too.

In light of the evidence discussed above, we hypothesize the following:

- We predict monotonic changes (increase, decrease) in prosocial behavior in response to the modifications of the values of the attributes *vocalization*, *appearance* and *odor*.
- We plan to eliminate / mask different attributes / attribute values of the real partner rat (exps. 1-3). We expect that the rats' behavior will covary with the attributes as predicted by the frame account depicted in figure 1.
- We also plan to manipulate/add attributes to an inanimate object (toy rat; exp. 4). We expect that adding attributes to the toy rat promotes prosocial behavior. We further predict interactions between the attributes, again supporting our frame account.
- Because not all attributes are likely to be considered equally important, we predict a different weighting of the attribute values on prosocial behavior with non-monotonic changes of the attribute values, interactions and constraints between the different attributes (i.e. probabilistic constraints).

In reference to the evidence outlined above, we justify our hypothesis as follows:

- 50 kHz vokalizations seem to serve as social contact calls to (re)establish and maintain contact between conspecifics (Wöhr & Schwarting 2009; Wöhr et al. 2007) and correlates with the intensity of social interaction in a mutualistic cooperation task (Łopuch & Popik 2011).
- Conspecific vocalization in non-human primates elicited activity in neural networks which strongly corresponds to the network shown to support the representation of conspecifics and effective information in humans (Gil-da Costa et al. 2004). This suggests that a common architecture underlies the conceptual systems of different species (Barsalou 2005).
- The feature lists approach (1B) is not able to explain interactions between factors that go beyond an additive effect.

The prosocial choice task

Figure 2 sketches the main logic of the task. We will train two rats in a double T-maze consisting of a starting box connected to two decision chambers by two independently operated doors, each leading to a choice compartment (figure 3). Rats indicate their decision by entering one of the two compartments. One animal, dubbed the actor rat, will be paired with either a social stimulus (another partner rat) or a non-social, inanimate stimulus (puppet toy rat). The actor always moves first and can enter either compartment. The partner never has a choice, i.e., the experimenter always directs the partner to the compartment facing the actor. After entering either compartment, actors always receive an identical amount of reward (three sucrose pellets), delivered after always the same delay, thus controlling for magnitude and delay discounting effects. Entering one compartment ("both reward - BR" compartment) results in a reward delivery of the same magnitude and delay in both the actors' and partner's compartments, whereas choosing the alternative option (the "own reward - OR" compartment) results in reward delivery to the actor rat compartment only. Importantly, in this design, the actor's selfish motives to choose one compartment or the other are identical for both alternatives since they yield the same reward delivered with the same delay. Furthermore, since the partner cannot return the favor after generous choices, or retaliate after selfish choices, the actor's choices are not influenced by any action of the recipient, eliminating reciprocal (tit-for-tat) and other strategic motivations. Consistent with the definition of prosociality mentioned in the introduction, for choices made in the partner condition, we refer to BR and OR choices as "prosocial", and "selfish" respectively. In the toy condition, the partner is an inanimate toy rat of similar size and shape. The toy condition serves as a control for pellet delivery smell and sound and potential secondary reinforcement effects of the food delivery. Importantly, the choice-reward payoff structure is identical across partner and toy conditions, i.e., rewards are delivered to the toy rat compartment with the same magnitude and delay as in the partner condition. Thus, any difference in choice allocation between the partner and the toy conditions can be attributed to the influence of social context on the actor's decisions. To control for potential side biases, left and right compartments are pseudo-randomly assigned as BR or OR across rats and sessions; thus, BR and OR sides differ across rats and testing days. Moreover, all experiments are carried out in red light in a closed black curtain system, to minimize the influence of contextual cues on decision making. To control for social exploration motives, systematic approach/avoidance behavior as well as possible effects of closeness while eating, the partner is always directed into the compartment directly facing the compartment chosen by the actor, thus keeping the average distance between animals equal after every choice.

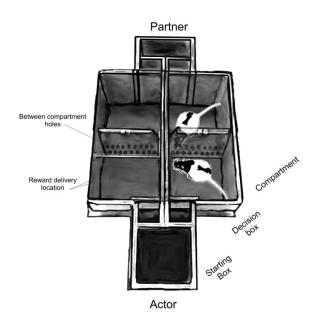


Figure 3: **Double T-Maze Apparatus**. Each T-maze consisted of a starting box connected to two decision chambers by two independently operated doors, each leading to a choice compartment. Rats indicated their decision by entering one of the two compartments via the respective decision box. In each session, compartments were pseudo-randomly assigned as either both-reward (BR) or own-reward (OR) compartment. Perforated and transparent walls were placed between compartments and between T Mazes to allow olfactory, auditory and visual communication between rats. A semi-automatic reward delivery system was placed at the intersection of each perforated wall, i.e., at the center of the maze (not shown on figure). Rewards were delivered to the rats' compartments.

Each session consists of 25 trials. A session begins with ten forced-choice trials (actors are forced to enter on or the other compartment in a pseudo-randomized order) in order to allow sampling of the compartment / outcome contingencies. The forced-choice trials are followed by fifteen free choice trials in which the actors can freely choose which compartment to enter. Each rat is tested in ten consecutive sessions in the partnercondition, and ten additional sessions in the toy condition. To control for potential order effects, half of the actors start training in the partner condition, followed by the toy condition, with the reverse order for the other half of rats. Actor and partner rats are never housed together. Actors are always paired with the same partner in the partner condition.

We plan to make a small modification to the original task described above: in order to control the putative motive to eat close to each other (Barnett & Spencer 1951), rewards will be delivered at the lateral sides of the respective compartments. Thus, rats consume their rewards with considerable spatial distance between them, eliminating social feeding motives.

Our currently used setup is manually operated, which only allows for measurement of one target rat at a time. In addition, the manual operation of the apparatus does not allow for precise timing of behavioral events, which is a problem for electrophysiological measurements (envisaged for the third phase of the CRC). An automated setup would allow for more precise timing. In addition, automated setups have the distinct methodological advantage of avoiding human contact during testing, and therefore eliminating putative experimenter and other effects that have to be painstakingly controlled in the manual version of the

task. Moreover, it would markedly reduce the manpower needed and therefore ultimately help saving on personnel costs. We therefore apply for funding to purchase two custom-made automated double T-maze setups.

Experiment 1: One possible attribute that rats use to represent something as a *social partner* is vocalization. We plan to test the impact of the vocalization attribute on perceiving someone else as a social partner. Partner rats will be classified according to their vocalization rate. Rats vocalize, among others, in the 50 kHz range. These vocalizations often occur in appetitive contexts and are believed to express positive emotional and/or motivational states of the rat (Wöhr et al. 2008, 2007). We therefore plan to categorize our rats into high- or low-vocalizers according to the rate of 50 kHz calls they emit. We will test if the vocalization rate predicts prosocial choices. The partner frame hypothesis predicts a monotonic increase in prosocial behavior with increasing vocalization rate.

Experiment 2: The partner rat's appearance may be another socially relevant attribute. In this experiment we plan to test its impact on prosocial choice. We have shown that actor rats discriminate between real and toy rat partners. If appearance plays a role in perceiving a conspecific as a real social partner, prosocial behavior should be modulated by changing the appearance of the partner rat. Therefore we want to use different rat strains as partner rats (Wistar vs. Long-Evans rats), and probe whether the actors' prosocial tendencies vary depending on the strain of the partner. The strains differ with respect to appearance (color of fur, color of eyes, posture, behavior). Simultaneously, we will record the ultrasonic vocalization rate of the animals to see if it covaries with appearance. An interaction of the attributes (e.g., vocalization has a stronger effect on prosocial choice if the partner rat's appearance is similar to the actor rat) would support the frame theoretical account.

Experiment 3: Another relevant attribute may be the partner rat's odor. We plan to test the impact of the odor attribute on perceiving someone else as a social partner. We will test if highly prosocial animals decrease their prosocial tendency if the odor cues of the partner rats are manipulated. Therefore we mask the natural odor of the partner rat with artificial odor (flower shop), sprayed in the partner compartments. Simultaneously, we will record the ultrasonic vocalization rates of the partners and actors to test if they covary with odor manipulation. Again, attribute interactions would support the frame theory account.

Experiment 4: In experiments 1-3, we intend to eliminate single attribute values, and probe the effects of attribute-value presence vs. absence on prosocial choice. In experiment 4, instead of eliminating attribute values, we plan to add different attributes to the inanimate toy object. The goal is to test which attribute, or which combination of attributes and attribute values, are needed to turn a puppet into a recognized social partner. As in experiments 1-3, we focus on the attributes vocalization (experiment 4a), odor (experiment 4b) and appearance (experiment 4c). In Experiment 4a) we will add a recorded playback of 50 kHz vocalization to an inanimate object and test whether the actors' prosocial tendencies increase. In Experiment 4b) we will add rat urine odor to an inanimate toy and probe whether the actors' prosocial tendencies increase. In Experiment 4 c) we will use a true-to-life taxidermy of a Long Evans rat, and/or combinations of the attributes vocalization, odor and appearance. Again, attribute interactions would support the frame theory account.

3.4.2 Work packages (48 months)

Work package (WP) 1: months 1-7 We allow for an initial preparation and setup period of about seven months. We will set up the T-maze system, the vocalization system and staff will be trained on the software and general animal work. Furthermore, we will develop and test the general procedure and task variables.

PI: preparation and administration of the grant and research; post-doc: conducting the research, setting up the systems, training the SHKs; 2 SHKs: setting up the system and procedures

WP2: months 8-13 Following the preparation and setup period, we will conduct experiment one, as described above. We expect the data collection and analysis to take six months. This includes the measurement and analysis of ultra-sound vocalizations. The remaining time will be used for statistical analyses, writing and publishing results.

PI: administration, supervising data analysis, preparing publications; postdoc: animal training, statistical analysis, preparing publications; 2+2 SHKs: animal husbandary and training, training of additional 2 SHKs for WP3

WP3: months 14-19 We will conduct experiment two with a new batch of rats and two different rat strains. During six months, we will test if appearance plays a role in perceiving the counterpart as a social partner as described above. The time estimation includes the measurement and analysis of ultra-sound vocalizations. This time frame provides sufficient flexibility to account for unforeseen delays and unexpected interruptions.

The remaining time will be used for statistical analyses, writing and publishing results. Staff/work allocation as in WP2.

WP 4a: months 20-26 Experiment 4a will take approx. seven months, including habituation times and animal training. In addition this time frame provides sufficient flexibility to develop the ultrasonic playback system to add a recorded playback of 50 kHz vocalization to an inanimate object and probe whether the actors' prosocial tendencies increase. The remaining time will be used for additional statistical analyses, writing and publishing results. Staff/work allocation as in WP2.

WP 4b: months 27-33 Following experiment 4a, we will conduct experiment 4b in which we will add odours (i.e. rat urine) to an inanimate object and probe whether the actors' prosocial tendencies increase. Duration: seven months. Staff/work allocation as in WP2.

WP 4c: months 34-40 We will conduct experiment 4c in which we probe the attribute *appearance* by using a true-to-life taxidermy of a Long Evans rat as a partner object. Duration: seven months. Staff/work allocation as in WP2.

WP 5: months 41-48

In the last work package we plan to test several combinations of attributes values *vocalization, odor* and *appearance*. In addition, this time frame provides sufficient flexibility to analyse data and account for unforeseen delays and unexpected interruptions. Duration: eight months.

3.5 Role within the Collaborative Research Centre

This project is admittedly the odd-ball in the CRC because of the usage of animal models. However, we consider this fact a particular strength rather than a weakness, and believe that our project can make significant contributions to the success of the CRC. Despite the non-linguistic and abstract social concept approach, our study provides the empirical and experimental basis to adjust the theoretical formalization of frames studied in other projects. We will closely interact with project **A01** (Petersen) to embed our empirical findings in the theoretical frame context. More specifically, in interaction with project **A01**, we plan to lay the experimental basis to formalizing constraints of an attribute/value structure of social cognition. We consider our interaction with project **A01** important since our project is unique in the collaborative research center in actually testing the interactions and constraints between concepts in an abstract frame.

Furthermore, we will also collaborate with project **B06-C** (Zielasek, Vosgerau). In the next funding period, project B06-C will put stronger emphasis on the social component in psychiatric classification. Although our planned experiments do not have direct implications for neuropsychiatric classification, we will collaborate with B06-C to address the principal question if, and to what extent, frame theory can be applied to formalize social problems. The insights gained from our projects will inspire efforts to use frame theory for the neuropsychiatric classification of social disorders, or social aspects thereof, such as social deficits in schizophrenia, sociopathy, or autism-spectrum disorders.

Our project entails analysis of our rats' ultrasonic vocalization (USV) behavior. We plan to go beyond standard USV analyses of simple decomposition into frequency components, and aim to look at vocalization behavior from a novel angle. To this end, we will interact with project **D05-N** (van de Vijver). Ruben van de Vijver is a phonologist with expertise in the analysis of prosodic means of phonological expressions. We plan to apply analytical tools that have been developed to examine phonological phenomena in humans, such as motherese, to characterize the USV emission patterns of our rats.

Bibliography

Alba, J. W. & L. Hasher. 1983. Is memory schematic? *Psychological Bulletin* 93(2). 203–231. doi: 10.1037//0033-2909.93.2.203.

Barnett, S. A. & M. M. Spencer. 1951. Feeding, social behavior and interspecific competition in wild rats. *Behavior* 3. 229–242.

Barsalou, L. W. 1992. Frames, concepts, and conceptual fields. In A. Lehrer & E. F. Kittay (eds.), *Frames, Fields, and Contrasts: New Essays in Semantic and Lexical Organization*, 21–74. Hillsdale: Lawrence Erlbaum Associates.

Barsalou, L. W. 2005. Continuity of the conceptual system across species. *Trends in cognitive sciences* 9(7). 309–311. doi: 10.1016/j.tics.2005.05.003.

Barsalou, L. W. 2008. Grounded cognition. *Annual review of psychology* 59. 617–645. doi: 10.1146/annurev.psych.59. 103006.093639.

Bartal, I. B.-A., J. Decety & P. Mason. 2011. Empathy and pro-social behavior in rats. *Science* 334(6061). 1427–1430. doi: 10.1126/science.1210789.

- Birrell, J. M. & V. J. Brown. 2000. Medial frontal cortex mediates perceptual attentional set shifting in the rat. *The Journal of neuroscience : the official journal of the Society for Neuroscience* 20(11). 4320–4324.
- Blanchard, D. C. & R. J. Blanchard. 1990. Behavioral correlates of chronic dominance-subordination relationships of male rats in a seminatural situation. *Neuroscience and biobehavioral reviews* 14(4). 455–462.
- Blanchard, R. J., K. J. Flannelly & D. C. Blanchard. 1988. Life-span studies of dominance and aggression in established colonies of laboratory rats. *Physiology & behavior* 43(1). 1–7.
- Gil-da Costa, R., A. Braun, M. Lopes, M. D. Hauser, R. E. Carson, P. Herscovitch & A. Martin. 2004. Toward an evolutionary perspective on conceptual representation: Species-specific calls activate visual and affective processing systems in the macaque. *Proceedings of the National Academy of Sciences* 101(50). 17516–17521. doi: 10.1073/pnas.0408077101.

Crockett, M. J., B. R. Braams, L. Clark, P. N. Tobler, T. W. Robbins & T. Kalenscher. 2013. Restricting temptations: neural mechanisms of precommitment. *Neuron* 79(2). 391–401. doi: 10.1016/j.neuron.2013.05.028.

- Edwards, W. J., R. Newman, K. Snapper & D. Seaver (eds.). 1982. *Multiattribute Evaluation*. Thousand Oaks, CA: SAGE Publications, Inc. doi: 10.4135/9781412985123.
- Fehr, E. & U. Fischbacher. 2003. The nature of human altruism. *Nature* 425(6960). 785–791. doi: 10.1038/nature02043. Fehr, E. & S. Gächter. 2002. Altruistic punishment in humans. *Nature* 415(6868). 137–140. doi: 10.1038/415137a.
- Fiske, S. T. & S. E. Taylor. 1984. Social Cognition. Reading and MA: Addison-Wesley Publishing.
- Glas, A. L. & K. J. Holyoak. 1975. Alternate conception of semantic memory. *Cognition* 3. 313–339.
- Hampton, J. A. 1979. Polymorphous concepts in semantic memory. *Journal of Verbal Learning and Verbal Behavior* 18(4). 441–461. doi: 10.1016/S0022-5371(79)90246-9.
- Hernandez-Lallement, J., M. van Wingerden, C. Marx, M. Srejic & T. Kalenscher. submitted. Rats act generously in a Pro-social Choice Task .
- Kalenscher, T. & C. M. A. Pennartz. 2008. Is a bird in the hand worth two in the future? The neuroeconomics of intertemporal decision-making. *Progress in Neurobiology* 84(3). 284–315. doi: 10.1016/j.pneurobio.2007.11.004.
- Kalenscher, T., S. Windmann, B. Diekamp, J. Rose, O. Güntürkün & M. Colombo. 2005. Single units in the pigeon brain integrate reward amount and time-to-reward in an impulsive choice task. *Current biology : CB* 15(7). 594–602. doi: 10.1016/j.cub.2005.02.052.
- Kalenscher, T. & M. van Wingerden. 2011. Why we should use animals to study economic decision making A perspective. *Frontiers in Neuroscience* 5. 1–11. doi: 10.3389/fnins.2011.00082.
- Kalenscher, T. 2007. Decision making: don't risk a delay. Curr. Biol. (17). 58-61.
- Kalenscher, T., C. Lansink, L. J.V. & P. C.M. 2010. Reward-associated gamma oscillations in ventral striatum are regionally differentiated and modulate local firing activity. *J. Neurophysiol.* (103). 1658–1672.
- Kunda, Z. 1999. Social Cognition: Making Sense of People Bradford Bks. Cambridge and Mass: MIT Press.
- Lakshminarayanan, V. R. & L. R. Santos. 2008. Capuchin monkeys are sensitive to others' welfare. *Current Biology* 18(21). R999–R1000. doi: 10.1016/j.cub.2008.08.057.
- Łopuch, S. & P. Popik. 2011. Cooperative behavior of laboratory rats (Rattus norvegicus) in an instrumental task. Journal of comparative psychology (Washington, D.C. : 1983) 125(2). 250–253. doi: 10.1037/a0021532.
- Mackintosh, N. J. 1965. Selective attention in animal discrimination learning. *Psychological bulletin* 64. 124–150.
- Niedenthal, P. M., L. W. Barsalou, P. Winkielman, S. Krauth-Gruber & F. Ric. 2005. Embodiment in attitudes, social perception, and emotion. *Personality and Social Psychology Review* 9(3). 184–211. doi: 10.1207/ s15327957pspr0903_1.
- Rosch, E. & C. B. Mervis. 1975. Family Resemblances: Studies in the internal structure of Categories. *Cognitive Psychology* 7(4). 573–605.
- Rutte, C. & M. Taborsky. 2007. Generalized reciprocity in rats. *PLoS Biology* 5(7). e196. doi: 10.1371/journal.pbio. 0050196.
- Rutte, C. & M. Taborsky. 2008. The influence of social experience on cooperative behaviour of rats (Rattus norvegicus): direct vs generalised reciprocity. *Behavioral Ecology and Sociobiology* 62(4). 499–505. doi: 10.1007/s00265-007-0474-3.
- Sutherland, N. S. & N. J. Mackintosh. 1971. *Mechanisms of Animal Discrimination Learning*. New York: Academic Press.
- Wöhr, M., B. Houx, R. K. W. Schwarting & B. Spruijt. 2008. Effects of experience and context on 50-kHz vocalizations in rats. *Physiology & behavior* 93(4-5). 766–776. doi: 10.1016/j.physbeh.2007.11.031.
- Wöhr, M. & R. K. W. Schwarting. 2009. Ultrasonic communication in rats: effects of morphine and naloxone on vocal and behavioral responses to playback of 50-kHz vocalizations. *Pharmacology, biochemistry, and behavior* 94(2). 285–295. doi: 10.1016/j.pbb.2009.09.008.
- Wöhr, M., R. K. W. Schwarting & T. Bussey. 2007. Ultrasonic communication in rats: Can playback of 50-kHz calls induce approach behavior? *PLoS ONE* 2(12). e1365. doi: 10.1371/journal.pone.0001365.
- Wyer, R. S. & D. E. Carlston. 1994. Associated Systems Theory: A Systematic Approach to Cognitive Representations of Persons, vol. 7 Advances in social cognition. Hillsdale and N.J: L. Erlbaum Associates.