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Brain correlates of uncertain decisions: Types and degrees of uncertainty

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Dedicated to my family

Contents

Chapter 1

Introduction

In order to decide, judge;
in order to judge, reason;
in order to reason, decide.
(what to reason about)

(Johnson-Laird, & Shafir, 1993, p.1)

Several years ago a specific win-a-car show was very popular. The show-master presented three doors to the candidate and asked him “Behind one of these doors there is a car you can win. Behind the others there are goats. What is your choice?”. The candidate made his choice (e.g., door no.1) and the show-master opened one of the two doors remaining - with a goat behind (e.g., door no.3). After the door was opened the show-master asked “Do you still go for the same door or do you want to revise your choice ?”.

What would you do? How would you decide?

Aside from probabilistic deliberations which could enhance your winning probability, the win-a-car show is nevertheless a game of chance. The possibility to win the car is not controllable by the person him-/herself, rather are external events or the will of the fairy godmother decisive.

At present the show “Who wants to be a millionaire?” is very popular. The procedure is as follows. The show-master asks you a more or less difficult question and gives you four possible answers. Your task is to choose the correct answer out of four presented ones. For example, the show-master would have asked you "What was the research ship of Charles Darwin called? Dolphin, Calypso, Beagle, or Dove?". What would you guess? Or would you know? (In case you are curious about the name of the research ship of Darwin, Beagle is the correct answer.) In contrast to the win-a-car show, the outcome of this game is controllable by the player him-/herself as the amount of money is directly related to one's knowledge.

Recently, there are numerous copycats of the millionaire show. This might be due to the factor *controllability* or *attribution of uncertainty*. If people conceive of uncertainty as being due to coincidental chance events in the world which are not controllable, uncertainty is attributed to external factors. Hence, when people play the win-a-car show uncertainty will be attributed to external factors and the outcome will be conceived of as being entirely determined by lucky guessing. In contrast, if people conceive of uncertainty as being due to a lack or insufficiency of their own knowledge, uncertainty is attributed to internal factors which are, in principle, controllable. Hence, when people play the millionaire show uncertainty will be attributed to internal factors and the outcome will be conceived of as being entirely determined by their own knowledge base. This entails that success will also be attributed to oneself. Probably, this is why these shows became so popular recently.

1.1 Decisions under uncertainty

1.1.1 Types of uncertainty

In order to decide favorably it is important to anticipate consequences associated with different options or actions. Anticipations of future outcomes can only be precise if the world would work entirely deterministic. However, this is not the case since there are events and circumstances in life that can influence the outcome of a decision. Thus, as consequences are logically and empirically junior to a decision they are uncertain by nature. Generally, uncertainty is a mental state described from a subjective point of view and is thus difficult to quantify. Therefore, classification of decision problems are usually approached by the required coping strategies or by the required cognitive effort in order to resolve uncertainty (for the latter see 1.1.2).

From a deterministic point of view uncertainty is always due to a lack of knowledge. However it has been shown that it makes a significant difference whether people think of a lack of determination as being a part of the external world or whether uncertainty is more attributed to internal states of knowledge and belief (Teigen, 1994). Depending on the perceived cause of uncertainty different coping strategies are implemented. The terms *internal* and *external* uncertainty were introduced by Howell and Burnett (1978) to refer to events that an individual can or cannot control.

A more general distinction is made by Kahneman and Tversky (1982) who also discriminated variants of uncertainty according to the perceived cause of uncertainty, i.e., *externally attributed uncertainty* and *internally attributed uncertainty*. The authors subdivided the former into uncertainty based on frequencies and uncertainty based on propensities, the latter into uncertainty based on arguments and uncertainty based on introspective confidence, i.e., knowledge.

To refer to uncertainty as external, the perceived cause that influences the decision in an uncontrollable way is located in the external world. Exemplifying downhill skiing that may considered as being very risky since external uncontrollable factors like avalanches can turn an enjoyable event into a nightmare. However, by learning about specific situation-consequence-cohesions, predictions could be made which help coping with the situation. According to the principle of frequency, the more often two events co-occur, the more strongly they would be associated. Generally, a typical coping strategy with externally attributed uncertainty is to rate the relative frequency of such events. Hence, in contrast to predictions that we make in guessing or gambling situations, those usually depend on extensive experiences and memories of event frequencies (Kahneman & Tversky, 1982).

In contrast, to refer to uncertainty as internal, the perceived cause of uncertainty is located in the person himself/herself. Imagine being asked whether New

York is located south of Rome and you would not know the answer, uncertainty is not due to a lack of determination in the external world, i.e., factors acting on the location of the two cities, but due to your poor geographical knowledge (Teigen, 1994). Hence, whenever the predictability of events depends on the inexperience with the specific decision problem or on the short duration of problem solving, uncertainty is caused by internal circumstances. However, according to the principle of contiguity, specific situation-consequence-cohesions could be learned by forming associations between temporally and/or spatially co-occurring events. Generally, a typical coping strategy with internally attributed uncertainty is an intensive memory search, most likely in combination with the attempt to get missing information from valid external sources (Kahneman & Tversky, 1982; Teigen, 1994).

In decision research it is debated whether the present division parallels the distinction between aleatory and epistemic probability (Glimcher, 2003; Jungermann, Pfister, & Fischer, 1998). Aleatory probability (from the Latin “aleator” meaning “the gambler”) represents the likelihood of future events whose occurrence is governed by some random physical phenomenon like tossing dice, i.e., externally attributed uncertainty in present terms. In contrast, epistemic probability represents uncertainty about propositions when one lacks complete knowledge of causative circumstances, i.e., internally attributed uncertainty in present terms. It is an open question whether aleatory probability is reducible to epistemic probability based on one’s inability to precisely predict every force that might affect the roll of a die, or whether such uncertainties exist in the nature of reality itself, particularly in quantum phenomena governed by Heisenberg’s uncertainty principle. Although the same mathematical rules apply regardless of what interpretation is favored, the choice has major implications for the way people try to cope and resolve uncertainty. The argued epistemological question will be neglected in the following as it appears to be more important whereto uncertainty is attributed, i.e., subjective probability.

Affective states pertain to internal events as well. However, until now the role of feelings, emotions, and moods and their influence on thinking, judgments and decision making is largely unexplained (Forgas, 1992; Jungermann et al., 1998).

Thereby it is important to distinguish between moods and feelings that emerge independently from the actual decision problem and those emotions that are directly evoked by the evaluation of the possible consequences. The former ones have been shown to unspecifically influence decisions (Strack, 1992). In contrast, the latter ones are anticipated emotions which are evoked by a comparison between the actual and the expected consequences. By a comparison of “what would have been possible” to “what is actually achieved”, emotions are able to influence the evaluation of the decision (for an overview see *disappointment* or *regret theory*, e.g., Loomes, 1988; Loomes & Sugden, 1986, 1987).

1.1.2 Degrees of uncertainty

Besides the classification of uncertain decisions into externally attributed and internally attributed ones, uncertain decisions can also be differentiated by the amount of cognitive effort needed in the specific decision situation to resolve uncertainty. Decision problems ranged at a lower level in the hierarchy require little cognitive effort and are therefore less uncertain. The meta-cognitive question how one decides how to decide depends crucially on the representation of decision-relevant information. That way, it is assumed that uncertainty in decision making can be expressed to a greater or lesser extent. For example, there are situations in which decisions proceed rather automatically without much of cognitive effort in contrast to situations in which decision-relevant information has to be searched for and structured before arriving at a decision. Thus, there is evidence for a continuum of uncertain decisions depending on the amount and utilization of cognitive resources. The degree of cognitive effort is correlated with the degree of reflection and consciousness with which decisions are made. According to Svenson (1990) four levels of uncertain decisions can be distinguished.

One end of the continuum is spanned by *routinized decisions* in which the preference for one option or action is triggered automatically. This is the case when a situation resembles ones that were rewarded so far if we did action x. Decisions are then tightly linked to constant actions or options by highly habituated preferences. These decision heuristics reflect learned contingencies between aspects of the decision situation and the effort of a particular decision rule which are knit long ago (Payne, Bettman, & Johnson, 1993). A heuristic or a “rule-of-thumb”, respectively, can be described as the application of experience-derived knowledge to a problem most often providing a description of the successive stages of a decision process (Gigerenzer & Todd, 1999). Exemplifying habituated preferences, imagine the decision of what kind of car to buy that is determined by an earlier purchase decision. The decision maker could reason like follows: I will go and buy a Mercedes Benz like I had one before since it was such a reliable car and I had so much fun driving it.

The advantage of such routines is that decisions can be made very quickly without much of cognitive effort and subsequently cognitive resources are available for other activities. The disadvantage, however, is that comparatively little attention is provided to the decision situation and thus it is probable that events signaling for a behavioral change are ignored.

Stereotype decisions differ from routinized decisions in two ways. First, not the entire situation is determining the decision strategy but the alternatives. Accordingly, a simple pattern-matching process is not sufficient. Second, a minimal evaluation process is required by what stereotype decisions are conscious. To exemplify this sort of decisions, imagine to go out for food. Although the situation, i.e., the restaurant, is completely different, the options, i.e., the dishes, are derived from a well-defined set, i.e., the menu (Jungermann et al., 1998). Stereotype decisions require more behavioral flexibility than routinized ones. However, since the field of options is always well-defined, the evaluation of the options is only minimal and generally guided by memory-based schemas (Svenson, 1990).

In decision situations that are characterized by a lack of routinized or stereotype preferences for one option the decision maker is required to derive a preference by deeply exploring his value system, i.e., an intensive memory search, or by gathering information from valid external sources. Such decision processes require at least an accurate consideration of the available options before a decision is reached, postponed, or refused. Decisions on this level also use trade-offs between the attractiveness of aspects on different attributes. This kind of decisions is termed *reflective decisions* since the actor is faced with a decision problem of some novelty and complexity (Jungermann et al., 1998; Payne et al., 1993; Svenson, 1990). Exemplifying reflective decisions, imagine going to buy a house. The decision maker could reason like follows: I decided to buy this house as I find the differences in price not so important and I value its quiet surroundings so much that this outweighs the smaller garden.

The highest cognitive effort, however, is required when the decision maker faces a new and unfamiliar problem in which the alternatives are not sufficiently defined or even partly unknown. Yet, sometimes the underlying values determining decision strategies are undefined and have to be generated. Several real life situations are characterized by a lack of options, e.g., the decision what to study or which job to accept. Subsequently, alternatives have to be created and their associated consequences have to be evaluated in relation to one's value system. These decisions are termed *constructive decisions* . Interestingly, this kind of decisions has fairly been neglected in decision research so far (Fischhoff, 1996).

In parallel to the described classification of decisions, taxonomies of errors use the determination of cognitive effort to distinguish *mistakes* from *action slips* (Frese & Zapf, 1994; Reason, 1990; Zapf, Maier, Rappensperger, & Irmer, 1994). Taxonomies of errors mostly focus on the timepoint when exactly in the action process an error occurs. Rasmussen (1983) proposed three basic error types related to three performance levels, i.e., skill-based action slips, rule-based mistakes, and knowledge-based mistakes. A more coarse differentiation is between action slips and mistakes. The latter ones are planning failures, i.e., the action proceeds as planned, but the plans or goals are not appropriate to achieve one's goal. Whereas, action slips occur whenever the action goes wrong but the plans or goals are correct. Implicated in this definition is the amount of cognitive effort needed for action execution as well as the amount of (un-)certainty during action execution. On the skill-based level sensorimotor performance is accomplished without any conscious control and uncertainty is low since sensorimotor performance is highly routinized. For example, errors on the skill-based level can signal for movement errors or premature errors. In contrast, on the rule- or knowledge-based level performance is accomplished consciously, i.e., the development of goals and action plans as well as the design of a situational analysis. Uncertainty arises mainly as consequences of actions are not fully determined. For example, errors on the rule-based level or on the knowledge-based level signal for more complex errors that often can only be resolved with external help, e.g., judgment errors or errors in reasoning.

1.1.3 Decision heuristics and learning

Meta-cognitive decisions, i.e., decisions about how to decide in accordance with one's value system, are not that frequent. In fact, the association between situational properties, i.e., task and context factors, and the effectiveness and efficiency of different decision rules or strategies are learned over time (Payne et al., 1993). Particularly, decision heuristics and if-then-rules, which constitute the definition criterion of routinized and stereotype decisions, are developed via learning. Although it is rather challenging to define "learning", a simple definition could be "a change in behavior due to experience" (Lieberman, 1993, p.34). However, there are some changes in behavior due to experience what one would not conceive of as learning, especially with regard to the acquisition of decision rules, e.g., a change in behavior because someone has not eaten for very long. In fact, what is meant by learning is that experiences result in the storage of information in the brain. However, this is of little practical use since information which is stored in the brain is not directly accessible, but changes in overt behavior are. However, also with this thinking there is the problem that it is possible to learn something even if there is no visible change in behavior. That way, learning is not really the change in overt behavior but rather the process that led to it. Accordingly, learning can be defined as the change in the capacity for behavior due to particular kinds of experience (Lieberman, 1993).

Considering routinized and stereotype decisions, heuristics reflect the established change in behavior due to experience with similar decision situations. That way, people learn about the relationship between two events that occur together (Rescorla, 1988). This form of learning is termed *associative learning* and is subdivided into classical conditioning and instrumental conditioning. Both forms of learning are of particular interest if the second event is an important one and people need to be able to identify its causes in order to undertake appropriate actions in the future, e.g., in order to decide favorably (Lieberman, 1993). Forming associations between two co-occurring events enables one to anticipate and predict the occurrence of important (future) outcomes. In cases when the predicted outcome deviates from the actual outcome this so-called *prediction error* leads to learning or re-learning, respectively (Schultz & Dickinson, 2000).[1] Subsequently, prediction errors enables people to adapt their behavior to the predictive and causal structure of the environment. Accordingly, if outcomes can reliably be anticipated no behavioral modifications are required. In contrast, if the prediction error is not nil, behavioral adjustments are required. Consequently, feedback evaluation or prediction errors, respectively, allow to assess whether or not the undertaken action was appropriate in order to achieve the desired outcome.

Accordingly, the acquisition of decision rules can be investigated. By varying the prediction error, the magnitude of reward, or the temporal difference between the undertaken action and the delivered reward, the gradual modification of decision rules can be observed. Associated with the representation of decision-relevant information is uncertainty, as carried out above. If the representation implies that only action x (given situation y) leads to the favored outcome it is fairly trivial that no uncertainty will arise. In contrast, if there is no reliable representation of decision-relevant information, uncertainty how to decide and what to do will arise. By the time the predicted outcome is similar to the actual outcome, no more behavioral modifications are required and a useful decision-relevant information is gathered. That way, investigations of routinized and stereotype decisions are very well practical in order to discover rules of behavior in decision making. However, this kind of investigation does not seem to be highly promising. This is due to two objections, first, higher level decision problems are considered

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[1] Note that the role of the prediction error is mainly important for the investigation of temporal aspects of decisions in error-driven learning and less obvious in other forms of learning like in perceptual or declarative learning (Schultz & Dickinson, 2000).

as being more interesting and fundamental as lower level decision problems, and second, the latter decision problems are also included as sub-processes in higher level decisions (Svenson, 1990). That way, lower level decisions, like routinized and stereotype decisions, can be conceived of as replications of decisions which in the beginning were treated as higher level decision problems, like reflective and constructive decisions. Therefore, it will be focused on the higher level decisions in the following.

1.1.4 Decision making and problem solving

Decision situations that are characterized by a lack of stereotype preferences or decision routines require the actor to decide constructively. To approach a favorable solution the decision maker can either combine known simple and/or complex decision strategies or has to construct a new and appropriate one. This decision process can also be termed a constructive *problem solving process* (Huber, 1982; Payne et al., 1993). It has been argued that the established distinction between decision making and problem solving has to be given up due to the psychological description and explanation of the process of problem solving. The latter is defined as a broader concept than decision making and comprises several subprocesses one of which is decision making (Brander, Kompa, & Peltzer, 1985). The current definition of problem solving reads as follows: A problem is given if an unfavorable initial state is wished to transform into a favorable goal state , but the transformation is constricted by a barrier. That way, problem situations are defined by the fact that the means in order to reach the goal are unknown, or have to be combined in a so far unknown way. Yet another definition criterion is the alternative that the goal state is not clearly defined or known (Dörner, Kreuzig, Reither, & Stäudel, 1983, pp.302). To conceive of decision making as problem solving helps to understand the dynamics of decisions leading to new questions, e.g., at what point a decision is terminated (Huber, 1982).

In sum, a problem is determined by the initial state, the goal state, and the operations that have to be performed in order to successfully achieve the intended goal state (Dörner et al., 1983; Hussy, 1984; Jausovec, 1994). Therefore, decision problems of some novelty and complexity in which the amount of the means-end-related information is insufficient can also be conceived of as a problem situation. A well known classification of problems is the one into *well-defined* and *ill-defined* problems, which was presumably first introduced by McCarthy (1956) (Howard, 1983; Hussy, 1984). Are all three characteristics, that make up a problem, clearly specified, this is termed a *close problem* or well-defined problem. In contrast, are the three characteristics less clearly defined, this is termed an *open problem* or ill-defined problem. Although there are several problem taxonomies (Dörner, 1976), typically the characteristics of the goal state, which is also termed *solution situation* , and the operators , which is also termed *problem* , are dichotomously divided into open and closed conditions. By combining the two characteristics and the two conditions, a taxonomy of four different problem types emerges (Dörner, 1976; Jausovec, 1994; Wakefield, 1989) (see Table 1.1).

Table 1.1: *Taxonomy of problem types. Open: not clearly defined; closed: clearly defined.*

		Problem	
		open	closed
Solution situation	open	(3) dialectic problem	(4) divergent-production p.
	closed	(2) insight problem	(1) interpolation problem

1. Well-defined interpolation problems: closed problem and closed solution situation. The goal state as well as the operators are clearly defined but not their specific combination and/or sequence. Thus, it is called for logical reasoning. Established interpolation problems are chess or paradigms used in problem-solving-experiments, e.g., the “cannibal-and-missionary-problem”.
2. Ill-defined insight problems: open problem and closed solution situation. The goal state but not the operators are clearly defined. Thus, a correct

solution exists and subjects are required to deduce the appropriate operators. Established insight problems are mental exercise tasks like match-stick arithmetic tasks which require subjects to disengage from familiar strategies (e.g., Knoblich, Ohlsson, Haider, & Rhenius, 1999).

3. Ill-defined dialectic problems: open problem and open solution situation. Both, the goal state and the operators are not clearly defined. Thus, one correct solution does not exist and subjects are required to discover the problem. Exemplifying are political and career decisions.

4. Ill-defined divergent-production problems: closed problem and open solution situation. The operators are clearly defined but not the goal state. Thus, this type of problem resembles creative thinking problems which are characterized by their open-endedness of solutions. However, divergent-production problems are more specific with regard to the operators and knowledge which is needed to solve the problem.

The description of well-defined problems applies to a lot of laboratory situations in which participants are supplied with information about the initial state, i.e., the stimulus configuration, the goal state, which is usually indicated via positive feedback, and participants are supplied with information in what way they are supposed to arrive at the correct solution situation. For example, participants are required to conduct algebraic proofs such as the one “Prove the equivalence of expression A and B”. The initial state is determined by the expressions A and B, the goal state by the mathematical proof, and the operators by the valid algebraic operations. Important to note is the distinction between *problem* and *task*. As carried out above, a problem is defined by the requirement to transform an initial state into a goal state via a means-end-analysis. In contrast, as soon as the finding of the right path is obsolete and the correct action is pre-determined or can be retrieved from memory, it is conceived of as a task. Dörner (1983) defined a task as the accomplishment of self-evident operations in a known way that lead to intended outcomes. The distinction between well-defined problems and tasks could be reconciled with the classification of errors, such that action slips might occur with tasks and mistakes with problems. The former occur whenever the action goes wrong but the chosen operators were correct; whereas mistakes occur whenever the action goes as planned but the chosen operators proved not to be appropriate to achieve the goal. Note however, that the term *task* is ambiguous as it once can refer to the bare execution of known actions and otherwise to experimental performance. Therefore, the term *task* in the present work will be used to refer to experimental performance (e.g., experimental conditions employed in fMRI experiments), whereas *task* as it is used in problem solving literature will be referred to as *well-defined task* in the following.

In view of the described problem classification decisions cannot only be classified according to the cognitive effort they require but also in accordance with regard to the characteristics “name recognition of the operators” and “clearness of the goal state”. Routinized or stereotype decisions cannot be equated with well-defined problems since the former are guided by habituated preferences and the latter by memory-based schemas, rather could they be conceived of as well-defined tasks. Constructive decisions can be equated with ill-defined problems since the goal state is not clearly defined but rather characterized by the open-endedness of the solution. However, reflective decisions can be equated with well-defined problems since the initial state is determined by the available alternatives, the goal state by the intended consequences, and the operators by the allowed decision strategies. Yet, the combination and sequencing of decision strategies is not known.

Reflective decision problems could be solved by an incremental solution approach consisting of the two sub-processes “difference reduction” and “subgoaling”. The former is accomplished by the selection of appropriate decision strategies that generate interim states similar to the goal state which depict subgoals. The basis of the selection is a predictive hypotheses about means-end-relations. As the term *prediction* implies, subjects first have to hypothesize about future events, i.e., they do not *know* about the consequences of specific actions. As a result, subjects will experience some sort of conflict about which decision strategy is to use when depicting an uncertain decision. Payne and colleagues (1993) proposed that subjects solve decision problems of some novelty and complexity by the generation of *if-then-rules*. That is, operators used to transform the initial state can be represented as the productions of the form “if condition x then action y” (e.g., “If there are more than four applicants, then exclude those who do not dispose of occupational experience“). These if-then-rules can be conceived of as *decision rules* .

Common to well-defined problems and reflective decisions, respectively, is the requirement to predict an event that is not fully determined. Preferences for specific operators are developed by testing preliminary working hypotheses generated on the basis of goal-directed ideas via close feedback evaluations. Consequently, by time valid decision rules will emerge.

1.1.5 A process model of decision making

Process models of higher level decisions or problem solving, respectively, are composed of different steps (Hogarth, 1980; Klauer, 1992; Svenson, 1990). These models describe the decision process as an orderly one, however, decision processes are sometimes chaotic. This is because the process of solving a decision problem involves continuous re-structuring and re-appraisal both before and after the decision has been made such that later steps in the process can alter earlier ones or that the goal of the decision process can change in the middle of the process. Therefore, these models serve as ideal type of process models.

1. Appearance of the decision problem. A careful analysis of the goal state as well as of the initial state is required in order to develop appropriate hypotheses or action plans, respectively.

2. Generation and production of appropriate action plans, including the prognosis of future events.

3. Evaluation of the action plans consisting in a comparison of promising alternatives with regard to usefulness, economy, and expected utility of the implementation.

4. Selection and decision of the preferred alternative from available ones.
5. Decision implementation. Execution and monitoring of the action.
6. Post-decisional processes consisting in feedback processing and evaluation with regard to the intended goal state.

Since a misfit between the goal of a decision process and the actual decision situation usually triggers the iteration of parts of the decision process, post-decisional processes will be described in more detail. In the post-actional phase, specific action outcomes are evaluated by comparing what has been achieved, i.e., the actual state , to what was initially wished to achieve, i.e., the target state. Usually, a re-evaluation of the initial situation is carried out consisting in re-adjustments of situational properties and their predictive values for future outcomes. The feedback can either be found out by the actor himself, through various kinds of self-monitoring, or by environmental cues indicating that something has gone astray. A third possibility of feedback signals are other people who know about the intended outcomes. They can notify the actor about a mismatch between the actual and the target state. This is especially the case when the actor is inexperienced and the other person is an expert in the field. Generally, feedback signals can either be positive (favorable) or negative (unfavorable), the latter often constitutes in an error. No matter of the valence of the feedback, its vital role is the information about how far the actor has progressed towards a specific goal. By nature, feedback is at the same time partly outside and partly inside the actor. Outside, as it gives information about the external world and the actual state. Inside, as the understanding and conceptualization of the feedback is only possible with a goal in mind. Thus, feedback, no matter whether it is positive or negative, is a relational concept (Frese & Zapf, 1994). Also on a temporal dimension the relational concept of feedback appears. The evaluation of feedback which takes place after the action execution directs people towards the past as well as to the future resulting in the generation of specific situation-consequence-cohesions. This evaluation process usually leads to a relatively stable change in behavior based upon experience which leads to the development of a decision heuristic.

Considering constructive decisions which are characterized by a lack of alternatives, it would be inadequate to start the description of a decision processe with the appearance of the decision problem. Heckhausen (Heckhausen, 1989, 1991) and Gollwitzer (Gollwitzer, 1991, 1996a,b) showed that initially there is a wish that has to be transformed into a want. If the the situation and time point appears to be appropriate, and if there is some priority and importance to act, the want is transformed into an intention which then acts as an action-guiding-goal. [2] While this is generally true for self-initiated actions and decisions that call for the generation of alternatives (like career decisions), the starting point for the remaining higher level decisions constitutes in the specific decision situation.

1.1.6 The real world in decision making. What is it good for?

Reflective decisions in general and constructive decisions in particular are not easy to investigate. In fact, constructive decisions like occupational or political decisions, which account for the most influential decisions in real life, were hardly ever object of investigation (Fischhoff, 1996; Jungermann et al., 1998). The experimental paradigms used are rather surrogates for complicated decisions and can take on lives of their own (Fischhoff, 1996). This could lead to the engagement in subtle variations within the experimental world and theoretical accounts could end up with the problem of extrapolation requiring a lot of conjecture.

This instance is due to the strategy in cognitive psychology to standardize situations of interest, so as to gain access to the ongoing decision process. Since descriptive decision research aims at the psychological description and explanation of decision making, its influencing factors and circumstances, it is important to provide for comparable decision situations, e.g., similarly uncertain decisions. As higher level decisions can be so unique that one cannot say how people generally behave in such situations it can be thought of observing decisions *in vivo* and eliciting concurrent verbal protocols. However, the reduction of the problems of standardization comes along at the price of incurring others. That is, the method

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[2] The implementation from a wish into a want is termed “to cross the Rubicon“ (Heckhausen, 1989, 1991).

of introspection appeared to be inappropriate and unreliable in order to describe cognitive processes in particular unconscious and subconscious processes (Zimbardo, 1988). At best, the careful observation of one's own mental processes can only provide limited account of why people behave the way they do. That way, in order to tell which factors influence decision behavior, it is inevitable to standardize experimental situations and measure reaction times (RT) and error rates. In doing so, it is attempted to earn something general by struggling with the particulars of specific decisions.

However, for a couple of phenomena it is not possible to distinguish cognitive processes on the basis of RT or error rates. For example, in order to distinguish externally from internally attributed uncertainty there is no reason why there should be a difference in RT for the one or other uncertainty. To keep at this example, the application of different coping strategies with different attributions of uncertainty can mainly be gathered via introspection.

An alternative way to try to disentangle different attributions of uncertainty has recently been established by the measurement of hemodynamic correlates. By using functional Magnetic resonance imaging (fMRI) it is possible to identify changes in neural activity with regard to specific (aspects of) cognitive processes. That way, the brain becomes an external criterion for the dissociation of different cognitive processes. Furthermore, the convergent results of imaging studies contribute to the knowledge of functional communality and thus make it possible to interpret the data in a parsimonious way, e.g., which kind of resources are used in order to reach or postpone a decision. Moreover, the method of fMRI can be used to test whether uncertainty is dealt with differently depending on the degree of uncertainty. For example, it could be assumed that by the time uncertainty is relatively high people would change to a qualitatively different coping strategy, a shift that does not need to be conscious. Thus, especially for the investigation whether externally and internally attributed uncertainty are qualitatively or quantitatively different and beyond whether uncertainty might be conceived of as a simple dual mode without any degrees in between, fMRI is suggested to be the dedicated method.

1.1.7 Real world decisions versus laboratory decisions

Regarding the structure of goal-directed actions or higher level decisions, respectively, a major distinction between real life and laboratory situations lies in the pre-decisional phase. The goal of the decision process refers to the representation of future states which are usually personally relevant. Needless to say that laboratory situations differ in this respect. Generally, goals are given by the experimental situation. By complying in participation subjects agree to carry out the task, i.e., transforming the external task to an internal one.

However, real world and laboratory situations resemble each other with respect to the remaining processes. The initial state has to be encoded. Since goals serve as anticipative cognitive structures guiding the action process, more or less elaborated action programs have to be generated. These action programs can be everything from a first idea how to approach the goal to elaborated blueprints. The developmental process from ideas to blueprints is a stepwise one whereby the goal serves as a comparison for the appropriateness of the action. This process is also called *hypotheses testing*. The actor decides for an option or an action according to a hypothesis binding a specific action to the initial situation or to a specific situational property. After action execution the actual state is evaluated in view of the target state. If the evaluation reveals shortcomings with respect to goal achievement another action will be executed according to a competing hypothesis. This process will be continued until a decision-rule remains leading to the intended target state with a high probability. That way, the initial situational properties will gain predictive values for a specific outcome in combination with the executed action. Note that this applies only to situations in which subjects are not supplied with a general rule system determining exactly how to respond given a specific initial situation. In contrast, routine situations supersede the testing of various decision-rules since an effective action is default.

The evaluation of the appropriateness of the executed action is done by means of feedback. That is, feedback plays a role for learning and motivation since it provides information about the consequences of actions as well as about the qualities of actions. Hence, feedback gives information about how far one has progressed towards the goal. Additionally, positive feedback and negative feedback serve as reinforcement, however, in opposite direction. Positive feedback serves as a keep-at-it-signal, whereas negative feedback indicates the converse of an efficient action and signals for an attitude change. Primarily in highly uncertain situations is it important to actively search for feedback, in order to be able to correctly predict future outcomes.

In order to stay in line with the concepts in cognitive psychology and cognitive neuroscience, the initial situation will be referred to as the *stimulus situation*, the undertaken action will be referred to as the *response*, and decision-rules will therefore be referred to as *stimulus-response-rules* (SR-rules) or *stimulus-response-associations*, respectively. Positive feedback can also be termed *reward* and negative feedback *punishment*.

1.2 Imaging data in uncertainty-related paradigms

To date there is a great number of studies investigating brain activations induced by well-defined problems including rule induction and application (Goel & Dolan, 2000; Goel, Gold, Kapur, & Houle, 1997), hypotheses testing (Elliott & Dolan, 1998), artificial grammar learning (Fletcher, Büchel, Josephs, Friston, & Raymond, 1999), anticipation of monetary gains and losses (Breiter, Aharon, Kahneman, & Dale, 2001), dynamical motion predictions (Ullsperger & von Cramon, 2003), sequence-based stimulus predictions (Schubotz & von Cramon, 2002), uncertainty in risky decisions (Critchley, Mathias, & Dolan, 2001), reward prediction (Critchley et al., 2001; Elliott, Newman, Longe, & Deakin, 2003), reward anticipation (Knutson, Fong, Adams, Varner, & Hommer, 2001; Knutson, Fong, Bennett, Adams, & Hommer, 2003), and risky choices (Critchley et al., 2001; Rogers et al., 1999). Common to all these paradigms is the prediction of uncertain events. Successful predictions are based on an appropriate rule system that has to be set up by means of a careful feedback evaluation. In order to arrive at a generally valid rule system, participants have to sample feedback information across the experimental session to attain a working hypotheses. Over time, preferences for specific options or SR-rules, respectively, are developed by testing these preliminary working hypotheses.

There is yet another group of studies investigating uncertainty-related processes like guessing (Elliott, Frith, & Dolan, 1997; Elliott, Rees, & Dolan, 1999) and gambling (Bechara, Tranel, Damasio, & Damasio, 1996; Breiter et al., 2001; Monchi, Petrides, Petre, Worsley, & Dagher, 2001). Although they resemble well-defined problems in the way that participants are required to find the right path in the problem space, guessing and gambling does not allow for learning and adaptation processes, i.e., the impossibility to use feedback information in order to successfully predict future events. However, it has been shown that people try to use feedback information in order to predict future events even in gambling situations, i.e., the so-called "gamblers fallacy" (Tversky & Kahneman, 1974). This fallacy is referred to as the inability to comprehend statistical independence of events, e.g., that subjects incorrectly assume an increased probability of black on the roulette wheel after a long run of red. Consequently, by using frequency information subjects incorrectly believe that their prediction ability improves. Several erroneous beliefs underly the gamblers fallacy , i.e., the "misperception of randomness" (Bar-Hillel & Wagenaar, 1987) and the "law of small numbers" (so termed by Tversky & Kahneman, 1971). The former is described by the belief that randomness is characterized by certain patterns according to which randomness can be determined. The latter is the belief that small samples are highly representative of the population. Both erroneous beliefs lead to an inadequate use of feedback information sampled across trials which is thought to be be used for future predictions. However, in very specific gambling situations it is yet worthwhile to sample frequency information. For example, when subjects are required to predict events of a defined sample with known stimulus properties like predicting the color of a playing card but the cards must not be placed back into the pack, the observation of relative frequencies can be used for future predictions, i.e., a probability matching approach.

Findings common to studies investigating uncertainty-related paradigms are brain activations within frontomedian areas corresponding to Brodmann Area 6, 8, 9, and 10 (see Figure 1.3). Activation within the dorsal part of the anterior cingulate cortex (ACC) or BA $32'/24'$, respectively, and within the orbitofrontal gyrus (OFC) are often reported when guessing or gambling behavior or the representation of reward and punishment is investigated. However, before describing the imaging data in detail, the anatomical location of the different brain regions within the frontomedian wall will be described.

1.2.1 Anatomy of the frontomedian cortex

In order to agree on a uniform identification of anatomical content as well as to perform multi-subject analyses a standard nomenclature is needed. As an international convention the “Brodmann map” which is based on comparative cytoarchitectonics of the cortex defined in Brodmann Areas (BA) (Brodmann, 1909) and the three-dimensional stereotactic “Talairach atlas”, which is based on an orthogonal grid-system (Talairach & Tournoux, 1988), are used. Since it is widely accepted that the functional differentiation of the cerebral cortex into areas is reflected by specific laminar patterns, it is a proximate strategy to establish boundaries between areas at the point where laminar patterns change. A century ago, Brodmann argued that the human cortex is organized anatomically in the same way as the cortex of all other mammals. He showed that the cortex in animals and humans consists of six layers, and, on the basis of anatomical differences in these layers, he developed a numbering system which has become a standard basis for designating areas of the cortex (see Figure 1.1). The classical map by Brodmann (1909) divided the frontal lobe into 13 cytoarchitectonic areas, the so-called Brodmann Areas. That is on the lateral surface BA 4, 6, 8, 9, 10, 44, 45, and 47; on the medial surface BA 4, 6, 8, 9, 10, 11, 12, 25, and 32. The second international convention is the Talairach stereotactic atlas which retained the classical areas of Brodmann. A proportional grid makes this atlas (although derived from one particular brain) applicable to all other brains. The origin of the coordinate system is represented by the upper boundary of the anterior commissure (AC). The y-axis is defined as a straight line through the upper boundary of AC and the lower boundary of the posterior commissure (PC). A horizontal line through AC perpendicular to the AC-PC line is defined as the x-axis. A straight line perpendicular to both, the x-axis and the y-axis, passing through AC is defined as the z-axis (see Figure 1.2). A general morphology regardless of the brain under consideration is given by major lines of cortical enfolding, e.g., the central sulcus is consistently found between the vertical lines through AC (VCA) and PC (VPC) and the VCA line separates the anteriorly located pre-supplementary motor area (pre-SMA) from the posteriorly located supplementary motor area (SMA). If individual data sets are aligned with the Talairach coordinate system activation foci can be reported in Talairach coordinates and BA's thereby allowing for a concordant spatial localization.

In the following only BA's will be described that showed to be crucial for uncertainty-related paradigms, i.e., BA 6, 8, 9, 10, and $32'/24'$. Cytoarchitectonically these areas differ such that mesial BA 8, 9, and 10 belong to the *granular prefrontal isocortex* defined by a well developed inner granule cell layer IV. In contrast, BA 6/BA $24'$ and BA $32'$ belong to the *agranular* and *dysgranular* frontal cortex, respectively. Both cortices are defined by the lack of a broad layer IV, whereby the insertion of layer IV starts within the agranular cortex.

The superior frontal gyrus therewith the frontomedian wall is traditionally subdivided into the areas BA 6, 8, 9, and 10 in a caudorostral (posterior-anterior) direction (see Figure 1.3) (Petrides & Pandya, 1999). Based on anatomical and functional data BA 6 on the medial wall of the prefrontal cortex is subdivided into the SMA in the caudal portion of BA 6 and in the pre-SMA in the rostral portion (Picard & Strick, 2001). A kind of border between these two motor areas is provided by a perpendicular line cut through the anterior commissure (AC), i.e., the VAC-line (see Figure 1.3). The caudal border of BA 6 to BA 4 (primary motor cortex) on the lateral surface is located in the anterior bank of the central sulcus, the anterior border of BA 6 to BA 8, however, is not as clearly defined. In fact, due to missing anatomical landmarks BA 8 and pre-SMA are difficult to distinguish. The same applies to the distinction between BA 8 and the ventrally located BA $32'/24'$. The latter area is also referred to as the "dorsal division of the ACC" which is composed of areas $24b'$-c' and $32'$ contrary to the rostral-ventral

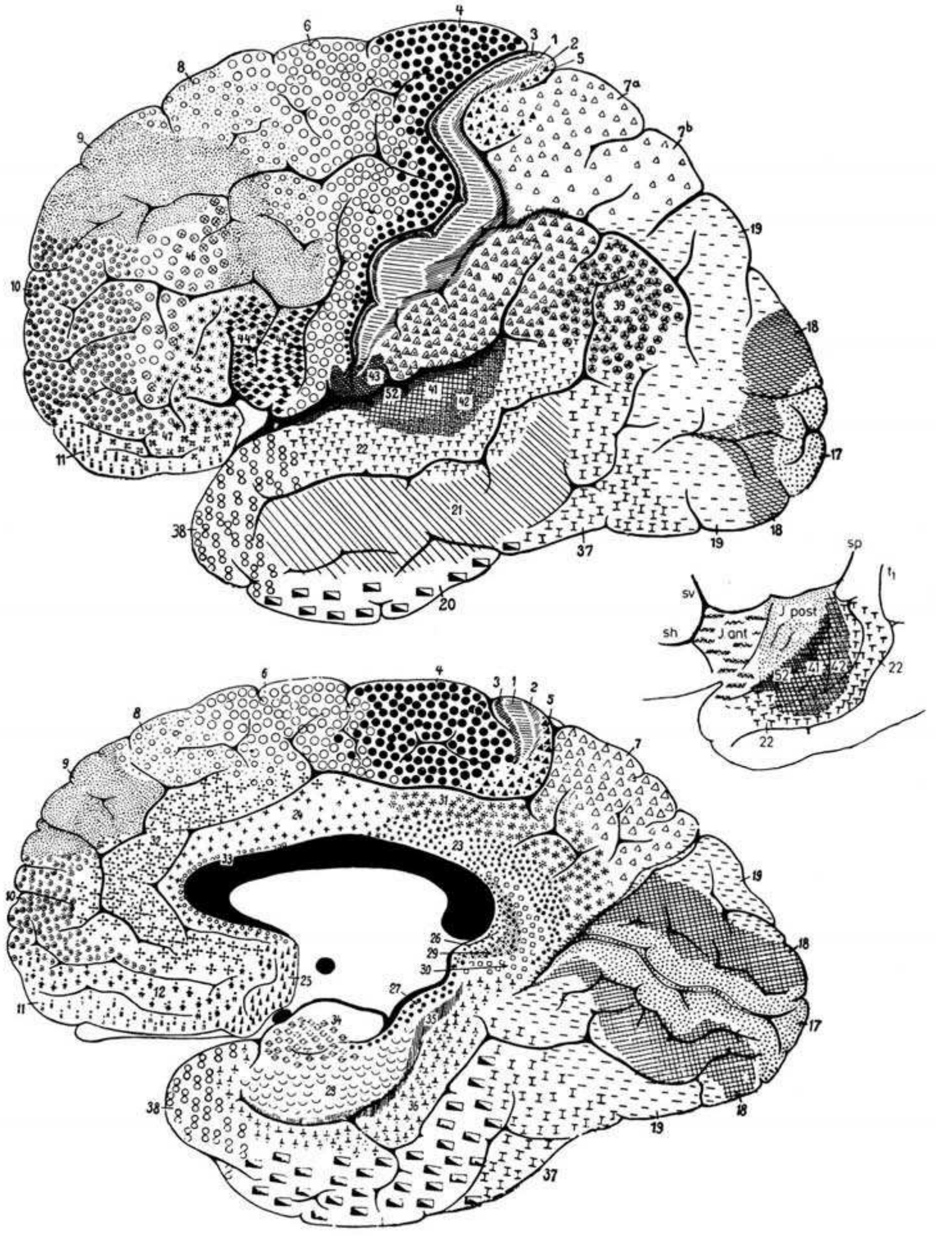

Figure 1.1: *The basis of Brodmann's cortical localization is its subdivision into areas with similar cellular and laminar structure. Brodmann undertook a systematic study of the cells of the cerebral cortex, using sections stained with the then new method of Nissl. Depicted are a lateral and medial view of Brodmann's cytoarchitectonic atlas as well as a view of the insular cortex (from Brodmann, 1909).*

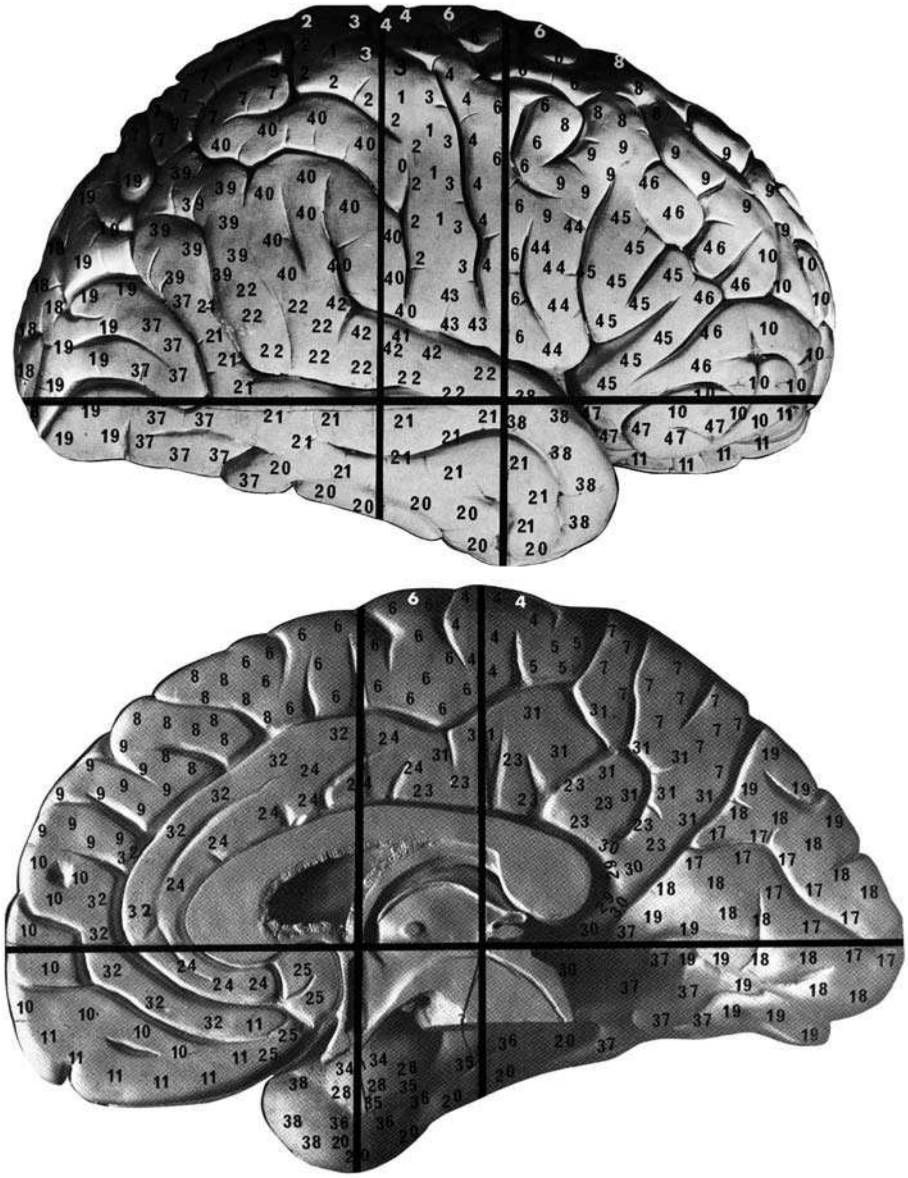

Figure 1.2: *The upper panel depicts the right hemisphere shown from the lateral surface, the lower panel the right hemisphere shown from the midline, both with Brodmann Areas and basal lines by Talairach and Tournoux (1988). The horizontal line defines the y-axis through the upper boundary of AC and the lower boundary of PC. The vertical line through AC (VCA) constitutes the z-axis, the vertical line through PC is termed the VCP line. (adapted from Talairach & Tournoux, 1988)*

division which is composed of areas 24a-b, 32, and ventral areas 25 and 33 (Bush, Luu, & Posner, 2000; Vogt, Nimchinsky, Vogt, & Hof, 1995). This subdivision is based on differences in cytoarchitectonics, patterns of projection, and function. Following anatomical findings from primates, Picard and Strick (2001) proposed an even finer subdivision of the ACC, namely into caudal cingulate zone (CCZ) and anterior and posterior rostral cingulate zone (RCZa, RCZp). According to the authors, the subdivision of the RCZ, which lies rostral to the VCA line, is supported by studies suggesting a functional dissociation of RCZa and RCZp.

Adjacent to BA 8 in caudorostral direction borders BA 9 and BA 10. The mesial portions of BA 9, 10, and 32 (sometimes including BA 8) are referred to as the anterior medial prefrontal cortex (aMPFC) (Gusnard, Akbudak, Shulman, & Raichle, 2001; Zysset, Huber, Samson, Ferstl, & von Cramon, 2003). Based on anatomical studies in non-human primates, it is agreed upon a dorsal-ventral distinction of the aMPFC (Morris, Petrides, & Pandya, 1999; Petrides & Pandya, 1999). The dorsal aMPFC is suggested to include mesial parts of BA 9 and 10, whereas the ventral aMPFC is suggested to include pre- and subgenual parts of BA 10 and 32 (Petrides & Pandya, 1994). The anterior-most part of the prefrontal cortex is usually referred to as the frontopolar cortex. Often, all activation foci falling into BA 10 are classified as frontopolar. In contrast, Christoff and Gabrieli (2000) regard the anterior parts of the middle and superior frontal gyri as frontopolar cortex. This classification approach stems from the observation that medial, lateral, and orbital surfaces of BA 10 vary in terms of cytoarchitecture and functional connectivity (Pandya & Barnes, 1987; Petrides & Pandya, 1994).

The OFC, as the name implies, is located above the eye socket which is called “orbita”. The rectal gyrus, also called the medial orbital gyrus, the anterior, lateral, and posterior orbital gyri all belong the superordinate concept OFC.

1.2.2 Uncertainty and the brain

Decisions get uncertain whenever the predicted consequences of actions are not fully determined by specific stimulus-consequence-cohesions or decision rules, respectively. Prototypical are situations in which people are either unfamiliar with

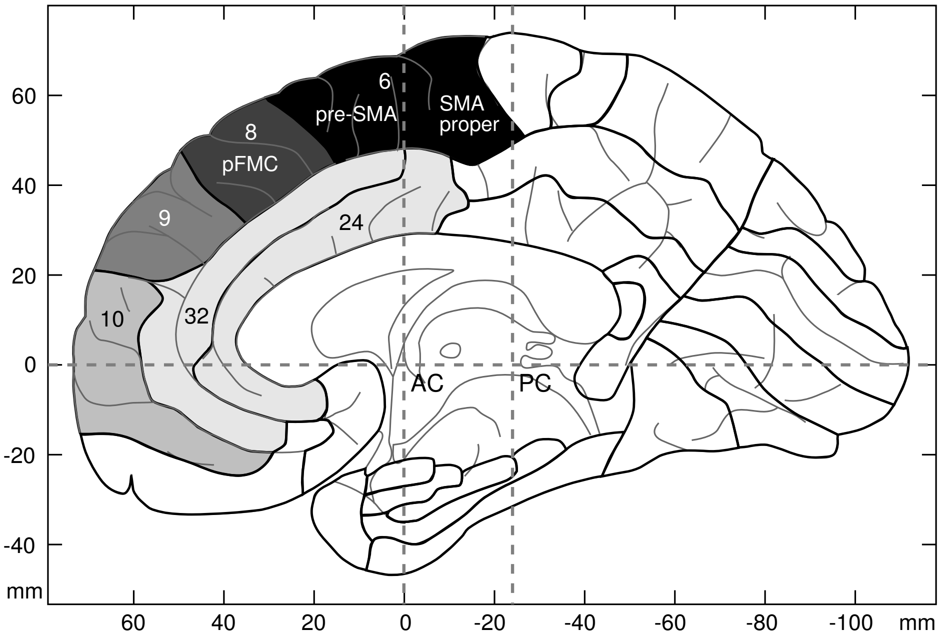

Figure 1.3: *Sketched is the right hemisphere shown from the midline. The outer frame shows coordinates from Talairach and Tournoux (1988). The crosshairs cut through the anterior and the posterior commissure (AC-PC), with vertical orientation lines (VAC-VPC) perpendicular to AC-PC, respectively. Brodmann Areas 6, 8, 9, 10, 24, and 32 are outlined and illustrated in grayscales (adapted from Talairach & Tournoux, 1988).*

the decisive specialties of the initial state or with the means-end-relations or both.

Being undecisive which action to choose is given in paradigms investigating neural correlates of hypotheses testing, rule induction, artificial grammar learning, and motion or sequence predictions. Different from guessing and gambling paradigms in which a probability matching approach might be a successful coping strategy, the specified paradigms call for the set-up of a general rule-system via feedback evaluation. The posterior frontomedian cortex showed to be involved in hypotheses testing compared to guessing (Elliott & Dolan, 1998), in rule induction compared to deduction (Goel et al., 1997), and in learning arbitrary grammar rules (Fletcher et al., 1999). Interestingly, the study by Elliott and Dolan (1998) revealed that it seemed not to be decisive whether a rule system actually exists rather it seemed to be crucial that participants believed in the existence of a detectable rule system.

Increased activation within pre-SMA extending into mesial BA 8, has also been observed whenever conflicts arose about the correspondence between a perceived event and the appropriate action selection (Ullsperger & von Cramon, 2001). Participants had to perform a speeded modified flankers task. Brain activation within BA 6/8 that was related to response competition was taken to be reflected by the contrast incompatible correct trials versus compatible correct trials. Likewise, activation within mesial BA 8 near the border to BA 6 was found when participants had to predict serial events in increasingly complex stimulus trains (Schubotz & von Cramon, 2002).

Being undecisive which action is to choose may also be due to imperfectly known rules, e.g., complex categorization rules. Distinct to paradigms requiring the set-up of a rule system, specified paradigms rather call for an accurate definition of the rules (e.g., necessary or sufficient rules). For example, in the study by Goel and Dolan (2000) a concrete stimulus property was linked to a specified response, in form of an if-then-rule. Required was a same/different response and the rule was “if the animals have the same tail and abdomen conditions, then they are the same type of animal” (Goel & Dolan, 2000, p.110). Participants were confronted with a variety of animals holding different tails and abdomen. Uncertainty in response selection was due to a insufficient description of the “same-set” and the “different-set”. Yet, the task was soluble by carefully monitoring and evaluating the feedback information. Application of arbitrary and insufficiently known SR-rules (compared to baseline condition) elicited activation within the mesial prefrontal cortex (BA 8) (Goel & Dolan, 2000).

The finding that BA 8 seemed to be involved in uncertain decisions is confirmed by the neuropsychological interpretations of lesions to the frontomedian cortex. Patients with lesions to the frontal cortices between both hemispheres showed severely impairment both in coping with routine actions as well as in the production of goal-directed ideas in novel situations (von Cramon & Matthes-von Cramon, 1994). The latter aspect is a crucial requirement for the generation of predictive and preliminary working hypotheses in order to solve problems (Hussy, 1984). Patients with lesions to the frontomedian wall, whose occurrence is often resulting from anterior cerebral artery infarction, are characterized by hypobulia, i.e., cessation of movements despite intact locomotor system, and an increased dependence on external stimulation (von Cramon & Matthes-von Cramon, 1994). Accordingly, it could be assumed that lesions to the frontomedian cortex lead to a lack of internal stimulation, i.e., the production of goal-directed ideas, resulting in an inability to cope with problem solving situations or decision situations, respectively.

Together, activation within the posterior frontomedian cortex was elicited whenever uncertainty arose which action has to be chosen. However, the specified studies manipulated uncertainty mainly via the increased complexity or via the insufficiency of knowledge, i.e., via internally attributed uncertainty. But, which brain areas would be involved in externally attributed uncertainty, e.g., with probabilistic learning tasks?

The investigation of neural correlates with externally attributed uncertainty is just emerging and results are relatively diverse (e.g., Cools, Clark, Owen, & Robbins, 2002; Elliott et al., 1999; Nieuwenhuis et al., 2003; Poldrack et al., 2001). Probabilistic learning tasks are characterized by probabilistic cue-outcome relations based on trial-by-trial feedback (Poldrack et al., 2001).

A recent fMRI study by (Nieuwenhuis et al., 2003) using a probabilistic learning task revealed an area at the border between BA 8 and BA $32'$ to be significantly activated for response errors and negative feedback, i.e., more activation following incorrect responses than correct responses and more activation following negative feedback than positive feedback. The activation is suggested to be involved whenever events are worse than expected. Activation within BA 8 has also been found with probabilistic reversal learning tasks (Cools et al., 2002). The authors found more activation following final reversal errors than correct responses. A final reversal error in their paradigm constitutes in the time point at which participants started to respond to the previously irrelevant stimulus-reward association, i.e., the time point at which the evaluation of the feedback signaled for a rule change. The probabilistic weather prediction task by Poldrack and colleagues (2001) contrasted against baseline revealed the basal ganglia (nucleus caudatus) to be significantly activated and a “widespread activation of cortical regions” (Poldrack et al., 2001, p.547). The task of the participants was to predict rain or sunshine depending on a particular set of cards.

An extreme form of probabilistic contingencies is represented in guessing situations. Guessing is characterized by the fact that the relationship between the response and the desired outcome is entirely determined by chance. Elliott and co-workers (1999) described the process of guessing as “making choice responses under incompletely specified situations” (Elliott et al., 1999, p.403). The task employed in this guessing study required a prediction of either the color or the suit of a playing card. Note that cards were not placed back into the pack, so that the observation of the relative event frequencies was a successful coping strategy (Ayton, Hunt, & Wright, 1991). Accordingly, if distributions of stimulus properties are known, e.g., the rates of suits and colors, the best way to deal with uncertainty in such guessing tasks is to adopt a probability matching approach. The observation of relative frequencies resulting in the translation into valid probability metrics implies a constant evaluation of feedback across the entire experimental session. Since single trials in such guessing tasks do not imply any information about performance a cross-trial processing of feedback information is required. Accordingly, Elliott and co-workers (1999) inferred from their results that the medial orbitofrontal cortex is dealing with the process of extracting information across a number of trials, i.e., feedback evaluation in guessing or gambling paradigms. Guessing compared to reporting was associated with significant activations within the OFC, the ACC, and medial prefrontal cortex inter alia (Elliott et al., 1999). In accordance with these results, Bechara, Damasio, Tranel, and Andersen (1998) suggested the medial orbitofrontal cortex (the authors refer to this area as the ventromedial cortex, i.e., BA 25, lower, 24/32, medial aspects of 11, 12, and 10) to be involved in the process of forming an association between a stimulus and its averaged reward value. The authors used the Iowa Gambling Task in which participants are required to figure out the advantageous stimulus which is possible via cross-trial evaluation of feedback information, i.e., via reward and punishment. Likewise, significant activations within OFC and ACC were found when investigating outcome anticipation in a reward-related gamble, i.e., the prediction about the most likely event. The two brain areas OFC and ACC showed to be modulated as a function of outcome uncertainty (Critchley et al., 2001). In this study playing cards were used numbered from 1 to 10 and participants had to predict whether the next playing card would be higher or lower than the previous card. That way, cards of value 1 or 10 elicited certain responses, while remaining values carried different degrees of uncertainty, i.e., the probability of being higher or lower approximated the true likelihood for a random set.

Anticipation and experience of monetary gain and losses investigated by Breiter and colleagues (Breiter et al., 2001) was accompanied by significant activations within the OFC and a sub-cortical network including the ventral tegmental area (VTA) and the ventral striatum or nucleus accumbens, respectively. Activation within the ventral striatum was also found by Knutson and co-workers (Knutson et al., 2003) who investigated the anticipation of increasing monetary rewards. Moreover, the authors found the mesial prefrontal cortex to be significantly responsive when reward has been successfully obtained, suggesting the mesial prefrontal cortex to be involved in tracking rewarding outcomes.

Note, however, that the strategy of monitoring cross trial feedback information cannot be successful in “true” gambling tasks, e.g., playing roulette. This is because event probability is the same on each trial independent from event occurrence on the previous trial, thus, the sampled feedback information cannot improve performance (compare 1.2). Yet, the employed tasks in the cited gambling studies mostly did not use such “true” gambling tasks.

1.3 Open questions

The synopsis about recent imaging studies revealed the posterior frontomedian cortex around mesial BA 8 to be central in cognitive processes involved in uncertain decisions. By contrasting hypothesis testing with response selection, rule learning with item learning, guessing with reporting, inductive reasoning with deductive reasoning, receiving monetary reward with anticipating reward, response conflict with no conflict, or final reversal errors with correct responses, these studies suggest a general difference between processes under uncertainty and those which are quite certain. However, wherefrom uncertainty arises is neglected so far, likewise is the mode of assessing uncertainty in decision making. To date, there are no studies directly comparing the neural correlates of externally attributed and internally attributed uncertainty neither in cognitive psychology nor in cognitive neuroscience.

Hence, it would be interesting to compare these two variants of uncertainty and test whether this concept describes psychological states only or whether it will correspond to distinct brain networks. Thus, it is not clear whether or not variants of uncertainty differ on the cerebral level. The question remains whether externally attributed uncertainty would elicit brain activation within the same brain networks as internally attributed uncertainty.

On the one hand it could be assumed that the reason of uncertainty would not matter and activation would be found within the same brain areas as uncertainty is always due to a lack of knowledge. This assumption is supported by Bereby-Meyer, Meyer, and Budescu (2003) who concluded from their behavioral studies that the same cognitive principles govern choice behavior in the presence of both externally and internally attributed uncertainty. Moreover, the finding of BA 8 activation with probabilistic learning tasks would argue for a common cortical substrate.

On the other hand, it could be assumed that the reason of uncertainty would matter and activation would be found within different brain areas as the perceived cause of uncertainty determines the coping strategy. This assumption is supported by Huber, Wider, and Huber (1997) who found that the requirement to actively search for information, i.e., the coping strategy specific for internally attributed uncertainty, was found to reduce the interest in probability information, i.e., the coping strategy specific for externally attributed uncertainty. This finding suggests that the strategies involved in the former and latter variant of uncertainty are somehow negatively correlated. Moreover, since the perceived controllability has been shown to constitute an important factor for psychological health (Hatfield et al., 2002; Zimbardo, 1988) it is reasonable to assume that uncertainty due to external factors would constitute a completely different psychological state than uncertainty due to internal factors. In the latter situation people know that they are generally empowered to resolve the uncertainty. The distinction of uncertainty into external versus internal, made by many authors in decision research (e.g. Budescu & Wallsten, 1987; Heath & Tversky, 1991; Kahneman & Tversky, 1982; Teigen, 1994), emphasizes the assumption of different cerebral correlates.

In view of the given literature it could be expected that uncertainty, no matter of the reason, would be reflected by brain activations within frontomedian areas around mesial BA 8. As strikingly similar frontomedian activations were found by many different paradigms, all reflecting uncertainty in the one or the other way, both, externally as well as internally attributed uncertainty, could be expected to be reflected by activation within BA 8 in the same way with respect to activation intensity or extension. This assumption implies that uncertainty is a mode of the brain and not specific for the one or other variant of uncertainty. However, since different variants of uncertainty have not been compared systematically within the same paradigm, it may also be that the two are distinguishable according to activation intensity or/and the extension of the involved brain networks. If this holds true, externally attributed uncertainty is expected to correspond to stronger frontomedian activations similar to guessing situations whereas internally attributed uncertainty may induce additional activation within brain areas reported to subserve working memory functions, i.e., lateral prefrontal cortex and posterior brain areas (Fletcher & Henson, 2001; Owen, 2000) Aside from the question of neural correlates of variants of uncertainty it is not clear whether or not different degrees of uncertainty would draw a distinction on the cerebral level. Everyday verbal protocols suggest that people are used to differentiate between subtle degrees of uncertainty. Examples of qualitatively expressed uncertainty are “probably”, “maybe”, “certainly”, or “I am not sure whether..”. Sometimes people also use words referring to frequencies with which events occur like “never”, “frequently”, “rarely”. These fine graduations in language suggest a difference between almost certain or fairly certain situations. Thus, it would be very interesting to investigate whether or not different degrees of uncertainty would be reflected by modulations within the involved brain areas. For example, would it make a difference on the cerebral level when subjects say that they are certain with 60% or with 100%? It is expected that decisions under higher uncertainty are reflected by an increase in activation within the involved brain areas. This is not at all hackneyed, since being more or less (un-)certain might as well be conceived of as a simple dual mode in the brain with with no degrees in between.

As carried out above, it could be argued that from a deterministic point of view uncertainty is always due to a lack of knowledge. It follows from that the the search for domain-specific information could lower uncertainty by reducing the range of all possibilities to the relevant alternatives. Generally, the preference for one option develops over time by comparing what has been achieved to what was initially wished to achieve. That way negative and positive feedback signals for an attitude change or for an attitude maintenance, respectively. Thus, only with the knowledge of results is learning and performance improvement possible. As the amount of positive feedback increases so does knowledge about the adequate solution strategy. Hence, the two factors, increasing amount of positive feedback and the increasing amount of relevant knowledge, are confounded by nature. However, if uncertainty actually depends on relevant knowledge, then solely an increase of relevant knowledge, indicated by positive feedback, should lower uncertainty. In contrast, an increase of exclusively positive feedback should not lead to a reduction in uncertainty. Thus, the question arises whether activation in areas modulated by uncertainty of knowledge, which are hypothesized to be frontomedian areas, is reduced only by increasing the amount of knowledge or whether an increase of positive feedback simulating a pseudo-learning process would also reduce activation within frontomedian areas. Is it the case that uncertainty of knowledge depends on the relevant knowledge, then an increase of positive outcomes should not lower frontomedian activation and thus should lead to different cerebral effects than an increase of relevant knowledge.

1.4 Implementation

Open questions are: (1) whether or not externally and internally attributed uncertainty differ on the cerebral level; (2) whether or not higher and lower degrees of uncertainty draw differently on the involved brain areas; and (3) whether or not an activation reduction within the involved brain areas can exclusively be achieved by a real learning process. The present studies set out to investigate brain correlates of uncertainty in decision making using fMRI. Young healthy adults performed a forced choice task in which they had to predict which of two concurrently presented stimuli would win in a virtual competition game. By varying the pre-experimental instruction, training, trial cues, and the determination of event occurrence different types and degrees of uncertainty in decision making were induced.

Externally attributed uncertainty, i.e., uncertainty of frequency, was induced by varying the winning probabilities according to specified winning rules. To each stimulus combination a specific winning probability was assigned ranging from $p=.6$ to $p=1.0$ that did not change during the experiment. Therewith, different degrees of externally attributed uncertainty were induced.

Internally attributed uncertainty, i.e., uncertainty of knowledge, was induced by varying the degree of instructed knowledge about winning rules. This was achieved by using the task instruction and trial cues to generate distinct degrees of knowledge uncertainty. The task instruction corresponded to knowledge about differently well known valid decision rules, whereas the trial cues corresponded to knowledge about the valid decision rule within a specific situation. Accordingly, decisions differed in terms of the necessity to apply, test or search the valid decision rules, thereby inducing different degrees of knowledge uncertainty.

The factor *variants of uncertainty* was varied between subjects, i.e., one group of participants thought of a lack of determination of event occurrence as being part of the external world (Experiment 1, Exp.1) whereas another group attributed uncertainty to internal states of knowledge and belief (Experiment 2, Exp.2). The factor *degree of uncertainty* was varied within subjects and variants of decision.

In both experiments a control condition was employed in which participants knew exactly which stimulus would win since an external cue indicated the winning one. Thus, participants decided with absolute certainty. Cognitive processes related to perception, general attention, or motor output, that were of no interest in the present experiments, were intended to be subtracted out by keeping their influence constant over all compared conditions. Hence, perceptual stimulation, trial structure, and motor requirements were the same within all conditions.

The third experiment (Experiment 3, Exp.3) set out to investigate whether activation within brain areas modulated by knowledge uncertainty was exclusively reduced by increasing the amount of relevant knowledge or whether an increase in positive outcomes was comparatively powerful. The same experimental paradigm was used as in Exp.1 and 2. By employing two learning conditions, the validity of the supplied feedback was manipulated. In the case of valid decision rules, participants were supplied with feedback dependent on their response, thereby reducing knowledge uncertainty due to a set-up of relevant knowledge. In contrast, in the case of invalid decision rules, participants were supplied with feedback independent from their response. In fact, the feedback was modeled by a pre-determined learning curve derived from pilot data. That is, participants were supplied with increasing positive feedback but they had no chance to build up a relevant knowledge base. By doing so, it was intended to separate the effects due to increasing knowledge from effects due to increasing positive feedback.

Chapter 2

Methods

In order to investigate the relation between cognitive processes and the underlying brain areas, dedicated methods are developed during the last decades. For example, functional neuroimaging methods like positron emission tomography (PET) and fMRI made it possible to identify changes in neural activity with regard to specific aspects of cognitive processing in particular within parts of the human cerebral cortex.

During the last two decades fMRI has rapidly become the method of choice to study neural correlates of behavior. The reason why cognitive scientist became so enthused about fMRI are its prominent advantages. Namely, fMRI does not require injections of radio-isotope (as compared to PET) and is non-invasive in other respects. The spatial resolution is unexelled at about 2 to 3mm and the temporal resolution is about 1s. Due to the spatial resolution and in contrast to other imaging techniques, it is possible to look at deep sub-cortical structures. Importantly, repetitive measurements are possible, i.e., the possibility to rescan a single subject as often as desired. Furthermore, by using fMRI it is possible to conduct single-subject analyses. And last but not least, it is possible to use already existent MRI scanners.

In general, fMRI creates digital images displaying local changes in blood flow, i.e., hemodynamic measures. The physiological parameter changes in blood flow are conceived of as an indicator for neural activity. Therefore, fMRI represents an eminent dedicated method to generate maps of cognitive activities.

However, it would be insufficient to leave it with a numeration of solely advantages of fMRI. Also fMRI comes along with some disadvantages. The method has to deal with the problem of susceptibility artifacts. That is the problem of signal loss in brain regions adjacent to air filled cavities which posses different magnetic properties than brain tissue not bordering such cavities, e.g., air sinuses (see below). The crucial question whether the activated area is causal (necessary) for the investigated function (or whether it is just a co-activation) can only be answered for particular regions (e.g., primary visual cortex). However, in order to investigate whether or not specific activations depict an epiphenomenon, additional information is needed to be integrated, e.g., data from drug related changes in activation, patient data, or data from virtual lesions by using transcranial magnetic stimulation (TMS). The allegation of “neurophrenology” may be met by the approach to measure functional integration in terms of effective connectivity. The underlying assumption is that each function is determined by its connections. By manipulating the interregional interactions, based on anatomical connections, information about co-activations and necessity of activations could be gathered. However, this approach is yet limited to regions whose anatomical connections and function are sufficiently determined and remains to future studies.

In the following the physical as well as the physiological basics of (functional) MRI will be explained. Further on, the different steps of the data processing and the statistical evaluation of functional magnetic resonance images which were conducted in the present experiments will be described in detail (for an overview about fMRI see for example Bandettini & Moonen, 1999; Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997). Completing, the risks of participating in a fMRI study will shortly be mentioned.

2.1 Physical basics of MRI

Already for a couple of years the method of magnetic resonance imaging (MRI) has been used in the clinical domain in order to visualize anatomical structures.

(f)MRI is based on the fact that the protons of the water molecules possess a spin, i.e., a rotation around their axis. As the protons possess an electrical charge the rotation causes an electrical circular flow which produces a magnetic dipole moment. If a water probe (e.g., water of the human brain) is exposed to an external constant magnetic field $\vec{B}_0$ of a MRI scanner, it gets magnetized. The net magnetization (sum of the magnetic dipole moments) increases with the strength of the external constant magnetic field and is directed towards $\vec{B}_0$ which is called the longitudinal direction. If the magnetization is not balanced in direction of $\vec{B}_0$, the orthogonal (transversal) component of the magnetization is precessing in the transversal plane to $\vec{B}_0$. The frequency ω of the precessing magnetization, the so-called Larmorfrequency, is given by $\omega = \gamma B_0$. γ is the gyromagnetic ratio of the protons, which is different for different materials, and describes the coupling of the spin and the magnetic dipole moment. Generally, the precession frequency increases with the strength of the external magnetic field.

If the magnetization is balanced in direction of $\vec{B}_0$, no signal is measurable. However, in order to receive a measurable signal, transversal magnetization has to be produced. This is done by exposing the water probe to a brief radio-frequency (RF) pulse. The RF impulses must have the same frequency ω as the precessing magnetization so that the protons can receive part of the RF energy. This phenomenon is termed *resonance*. In sum, the RF impulse results in a decline of the longitudinal magnetization and in a generation of the transversal magnetization. Past the excitation the signal decays freely. This is termed the free induction decay (FID), which is determined by the relaxation parameters of T1, T2, and T2* which will be explained more detailed in the following. The parameter T1 describes the relaxation of the transverse magnetization towards the longitudinal axis. As this process is induced by the interaction of the magnetization with the surrounding lattice, it is called the spin-lattice relaxation. The progression of the longitudinal relaxation is slow so that the parameter T1 is usually used for anatomical measures. The transverse relaxation of the magnetization is described by the parameters T2 and T2*. The T2 process describes the coherence loss of the spins due to spin-spin relaxation, while T2* covers the effect of magnetic field inhomogeneities which are caused by physiological parameters like the blood oxygenation. The latter effect is essential for fMRI. It is important to note that deoxyhemoglobin is paramagnetic (i.e., possesses magnetic properties) as compared to oxyhemoglobin. The latter does not differ in magnetic susceptibility from other tissue or water, thus, resulting in a homogeneous local magnetic field. Accordingly, oxyhemoglobin accounts for the longevity of the signal. In contrast, the presence of paramagnetic deoxyhemoglobin results in an increase of local inhomogeneity which in turn makes the nuclei to precess at slightly different frequencies. Hence, the higher the level of deoxyhemoglobin the faster the signal decays. By changing the oxygenation state of the blood, changes in MRI image contrasts can be obtained. The detection of **b**lood **o**xygen **l**evel **d**ependent changes in the MRI signal is done via the internal contrast agent deoxyhemoglobin. This method is termed *BOLD contrast* (see 2.2).

In order to define the origin of the signal, a spatial encoding is necessary. In order to achieve this information another magnetic field is superimposed onto the external magnetic field. By doing so, the external magnetic field varies linear in space. Hence, the application of gradients in three dimensions allows for a localization of the measured signal (for example, D'Esposito, Zarahn, & Aguirre, 1999; Orrison, Lewine, Sanders, & Hartshorne, 1995)

2.2 Physiological basis of fMRI and the BOLD effect

The most common method of fMRI is BOLD contrast imaging (first demonstrated by Ogawa & Lee, 1990), which will be explained in detail in the following. Is a population of neurons active, their metabolism is enhanced, i.e., the consumption of oxygen and glucose is increased. As a result, neural events are followed by an increase in regional cerebral blood volume (rCBV) and in regional cerebral blood flow (rCBF). This mechanism is termed *neurovascular coupling* (Roland, 1993). The supply of oxygen is exceeding the consumption such that the concentration of oxygenated hemoglobin increases whilst the concentration of deoxyhemoglobin decreases. By virtue the rate of oxygenated and deoxygenated hemoglobin is changed. By using the magnetization difference between oxy- and deoxyhemoglobin a fMRI signal is created. If the rate of oxygenated and deoxygenated hemoglobin is changed subsequent to a neural response, a decrease in spin dephasing within the involved brain area appears and subsequently an increase in the fMRI signal. The change in the rate of oxy- and deoxygenated hemoglobin is taken as an indicator for increased regional cerebral blood flow, which in turn is assumed to indicate neural activity. That way, a brief increase in neural activity results in a slow time course of the fMRI signal change, i.e., the hemodynamic response. The sluggish nature of the fMRI signal change results in a limited temporal resolution of the signal to a few seconds (D'Esposito et al., 1999).

The BOLD signal has several key determinants. Namely, after a delay of approximately 2s neural activity triggers an increase in signal intensity. The maximum of signal intensity occurs after 4-6s. Within 5-10s after neural activity the signal falls to circa 10% of its basis value and fades away after 10-12s. Often a subsidence of signal intensity below the basic value is observed and that is called an undershoot. In general, the hemodynamic response is subject to variability due to several different sources, e.g., intra- and inter-individual variations as well as physiologically related variations (such as caffeine, nicotine, or hormone level). The latter is met by standardization of experimental implementation. Within one participant during one experimental session no significant variability in multiple hemodynamic responses is reported. Likewise, no significant or if significant but only small variability effects within one participants across experimental sessions over several days are observed. Yet, significant variability effects between participants within the same brain area are reported (Aguirre, Zarahn, & D'Esposito, 1998).

Using the BOLD contrast, neural activity is measured indirectly via its assumed hemodynamic correlate. However, recently Logothetis, Pauls, Augath, Trinath and Oeltermann (2001) could show that the BOLD response directly reflects an increase in neural activity, i.e., the neural response to a stimulus. By the simultaneous acquisition of fMRI and electrical data in monkeys the authors found that the BOLD signal reflects synaptic activity, i.e., the local input and intra-cortical processing of a population of neurons in a given area, rather than the spiking activity. Yet, it is suggested that the BOLD contrast underrates neural activity (Bandettini & Ungerleider, 2001).

2.3 Potential risks of participation in fMRI experiments

Despite the classification of fMRI experiments as harmless there are some aspects to consider. Participants are brought into a very high magnetic field usually 1.5 or 3 Tesla.[1] Therefore, it is immense important to exclude subjects with pace makers or with other metalloid objects inside their bodies from participation. For the same reason, participants are searched for metalloid items which could could cause serious injuries if brought into a high magnetic field. Beyond, the diameter of the magnetic resonance tomograph accounts only for approx. 60cm. Some people might perceive this as too constricted, especially people with claustrophobia. Those people also have to be excluded from participation. The application of the gradients result in a great noise exposure of around 120dB without ear protection. Thus, participants must wear ear plugs. In order to ensure optimal security, participants' pulse is monitored during the whole experimental session. Furthermore, participants have the possibility to communicate via an intercommunication system or in serious cases can operate an alarm. Above all, each fMRI experiment has to be designed according to ethical guidelines and each fMRI experiment has to be approved by the local ethics committee of the respective university.

2.4 Analysis of fMRI data

The result of a fMRI study is a time sequence of digital (2D) images taken every n seconds within each defined cubical measuring unit which is termed a *voxel* (volume element). An image matrix in the present experiments contains 64x64 voxels that have a spatial within-plane resolution of 3x3mm with an inter-slice distance

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[1] The strength of a magnetic field is measured in Tesla (T) or Gauss (G), whereby $1T = 10.000G$. Comparative, the strength of the earth magnetic field accounts for 0.3-0.7 G.

of 2mm and a slice thickness of 5mm. The main objective of fMRI studies is to obtain a statistical parametric map (SPM) that depicts brain areas significantly responding to a specific experimental condition. This requires several preprocessing and evaluation steps that will be described in the following. All evaluations are conducted by using the software package LIPSIA (Leipzig Image Processing and Statistical Inference Algorithms) by Lohmann and co-workers (Lohmann et al., 2001).

2.4.1 Preprocessing

Several preprocessing steps are required prior to statistical evaluation to improve the data quality and remove artifacts due to motion, slice acquisition, and low frequency drifts (which are due to physiological or technical reasons). Scarcely anything can be done to correct for artifacts due to susceptibility gradients, i.e., the material dependent property of being magnetized in an external magnetic field. Susceptibility gradients occur specifically in tissues bordering air-filled cavities, e.g., in the orbitofrontal or anterior temporal cortex. Affected areas should be excluded from investigation or interpretation.

In all present experiments time sequences of 2D images were taken every 2.5s. Functional data were corrected for 2D motion artifacts using a matching metric based on a linear correlation. This means that the 2D images were geometrically rotated and shifted until a satisfactory match with a reference scan was acquired. The slices acquired in the fMRI studies were naturally not measured simultaneously but sequentially. This offset in slice acquisition may affect the statistical analysis and was therefore corrected. A sinc-interpolation based on the Nyquist-Shannon-Theorem was applied to correct for the temporal offset between the slices acquired in one scan. In the course of fMRI studies slow signal-drifts may occur due to physiological (e.g., blood pulsation, respiration) or technical reasons (e.g., lower signal values on average at the beginning of a scan than towards the end). Changes in the average signal intensity, i.e., baseline drifts, were corrected by using a temporal highpass filter. The underlying assumption is that the signal fluctuations are best described as low frequency components of the signal. Additionally, noise within the data can be lessened by performing spatial smoothing using a Gaussian filter kernel. In all present experiments a temporal highpass filter with a cut-off frequency of 1/170 Hz was used for the baseline correction of the signal and a spatial smoothing using a Gaussian filter kernels with 5.65mm FWHM was applied.

2.4.2 Spatial transformations

Generally, images have to be preprocessed so that they are geometrically aligned with each other and conform to a standard anatomical space, e.g., the Talairach stereotactic space (Talairach & Tournoux, 1988) (see 1.2.1). Hence, in order to warrant comparability between subjects and subsequently to submit a group analysis the fMRI data of all subjects were rotated and scaled such that the data sets were geometrically aligned with each other. As a standard stereotactic coordinate system the Talairach-space (Talairach & Tournoux, 1988) was used in all present experiments, therefore, local maxima were reported with their respective Talairach-coordinates and Brodmann Areas. In a separate session 3D high resolution T1-weighted images were acquired for each subject. In the experimental session 2D anatomical slices were acquired using a MDEFT (Modified Driven Equilibrium Fourier Transform) sequence. These slices were co-registered with the 3D full brain scan that resided in the stereotactic coordinate system and then transformed by linear scaling to a standard size $(135x175x120mm)$. The transformation parameters obtained from this step were subsequently applied to the functional slices so that the these were also registered into the stereotactic space. The last step of the preprocessing consisted in the transformation of the 2D functional data into the three-dimensional space. Accordingly, slice-gaps were scaled using a trilinear interpolation, generating output data with a spatial resolution of $3x3x3mm(27mm^3)$ per voxel. In order to improve the described linear normalization a subsequent preprocessing step was conducted performing an additional non-linear normalization: Each anatomical 3D data set was deformed such that it matched a 3D anatomical data set that served as a model image. The result was a deformation field describing where each pixel in one data set should move so that it matched a corresponding pixel in the model data set. This deformation field was then applied to the results obtained from the statistical analysis (contrast images), i.e., linearly normalized 3D contrast images. In LIPSIA the non-linear normalization is based on an algorithm invented by Thirion (1998).

2.4.3 Statistical evaluation

The main objective of the statistical evaluations is to find and depict areas that are significantly responding to a specified experimental condition via the attainment of a SPM. In short, this is achieved by calculating an analysis of variance (ANOVA) separately at each voxel. Voxel-wise, t-statistics from the results of the ANOVA are generated. Subsequently, t-statistics are converted into z-scores. The resulting SPM$\{Z\}$ are then superimposed on an anatomical high resolution image so as to visualize the functional data (see 2.5).

The measured fMRI signal could best be expressed by the convolution of the stimulus (described by the stimulus function) and the hemodynamic response function. The hemodynamic response function itself was expressed by basis functions. In the present event-related designs the hypothetical hemodynamic response function was explicitly modeled for each stimulus. Generally, the number of employed basis functions influences the parameter estimation. Usually, only the amplitude of the function, expressed in the first basis function, is tested. However, by using more than one basis function, i.e., its first and second derivative, both stimulus-dependent as well as regionally specific aspects of the response can be taken into account. Therefore, the design matrix was generated utilizing a synthetic hemodynamic response function and its first and second derivative (Friston et al., 1998) and a response delay of 6s. [2]

In the present proceeding, the statistical analysis was based on a least-squares estimation using the general linear model (GLM) for serially autocorrelated ob-

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[2] In order to account for serial autocorrelation, the model equation, including the observation data, the design matrix and the error term, were convolved with a Gaussian kernel with a dispersion of 4 $sec.\ FWHM$. The effective degrees of freedom were estimated as described in Worsley and Friston (1995) and in Seber (1977).

servations (random effects model) (Aguirre, Zarahn, & D'Esposito, 1997; Friston, 1994; Worsley & Friston, 1995; Zarahn, Aguirre, & D'Esposito, 1997). This means, it is assumed that the variation of the measured signal (Y) could be explained in terms of a linear combination of the explanatory variables (experimental conditions, $X\beta$) and an error term (ε): $Y = X\beta + \varepsilon$. This linear combination is called a fitted response. The parameters (betas) corresponding to each of the predictors were unknown and had to be estimated based on a least-squares estimation. Errors were assumed to be independent and identically normally distributed with a mean of zero.

In the following, contrast maps, i.e., estimates of the raw-score differences between specified conditions, were generated for each session and subject. As the individual functional datasets were all aligned to the same stereotactic reference space, a group analysis could be performed. For multi-session analysis, specific hypotheses were tested by using a t-statistic and a weighted linear combination of the effects which is also called a contrast vector. The resulting t-values indicated the significance of a certain effect voxel-wise, i.e., whether parameters differed significantly (Holmes & Friston, 1998; Worsley & Friston, 1995). Subsequently, t values were transformed into z-scores resulting in a statistical parametric map (SPM$\{$Z$\}$) indicating the statistical significance voxel-wise. In order to minimize the probability of false positives (type I error) only voxels with a z-score greater than 3.09 ($P < 0.001$ uncorrected) and with a volume greater than 225 mm^3 (5 voxels) were considered as activated voxels. In all three experiments group analyses were calculated by using a voxel-wise random effects model with subject serving as the random effect, i.e., allowing for the expression of each subjects' activation to be modeled as a random variable. By comparing the average activation to the variability of the activation over subjects it is possible to make inferences about the population where the sample is drawn from (Friston, Holmes, & Worsley, 1999).

2.5 Visualization

The resulting SPMZ were superimposed on an anatomical high resolution image and for a good perceptibility z-values were color-coded. The functional data from the present studies were all superimposed onto the same anatomical image. The chosen anatomical image was an individual brain showing a fairly prototypical course of gyri and sulci (see Figure 2.1). In the following results sections various views from the superimposed functional and anatomical images were generated to illustrate the results. By using a specific threshold for the z-values it was possible to mask only those voxels that are below the chosen threshold. The threshold of z-values was color-coded such that values of $Z = 3.09$ were displayed as crimson and the higher the z-value the brighter the color (up to bright yellow) (see Figure 2.2).

Figure 2.1: *Left, median, and top view of the anatomical image which was used as a reference image.*

Figure 2.2: *Displayed is the color ramp which is used to indicate significantly activated z-values. The crimson end of the scale refers to z-values of* $Z = 3.09$.

2.6 Procedure of the fMRI

In the following the technical details will be reported applying to all three fMRI experiments which were conducted at the Max-Planck-Institute of Cognitive Neuroscience in Leipzig, Germany.

Imaging was performed at 3 Tesla on a Bruker Medspec 30/100 system equipped with the standard bird cage head coil (SGRAD MkIII 580/400/S, MAGNEX Scientific Ltd., Abingdon, UK). Slices were positioned parallel to the bi-commissural plane (AC-PC) with 16 slices (thickness 5mm, spacing 2mm) covering the whole brain. A set of 2D anatomical images was acquired for each participant immediately prior to the functional experiment, using a MDEFT sequence (256x256 pixel matrix). Functional images in plane with the anatomical images were acquired using a single-shot gradient EPI sequence (TE=30ms, 64x64 pixel matrix, flip angle 90°, field of view 19.2cm) sensitive to BOLD contrast. During each trial, 2 images were obtained from 16 axial slices at the rate of 2.5s. In a separate session, high resolution whole brain images were acquired from each participant to improve the localization of activation foci using a T1-weighted 3D segmented MDEFT sequence covering the whole brain.

Participants were instructed immediately before the MRI experiment. In the MRI session, subjects were supine on the scanner bed with their right and left index finger positioned on MRI-suitable response buttons. In order to prevent postural adjustments, the subject's arms and hands were carefully stabilized by tape. In addition, form fitting cushions were used to prevent arm, hand and head motion. Participants were provided with earplugs to attenuate scanner noise. Visual stimuli were presented with VisuaStim (Magnetic Resonance Technologies, Northridge, USA), consisting of two small TFT-monitors placed directly in front of the eyes, simulating a distance to a normal computer monitor of about 100cm. In the case of ametropia participants used either their own lenses or were supplied with appropriate ones. Participants were excluded from the studies in the case of color-blindness. After participants were welcomed at the laboratory they received an instruction about the procedure and the task of the specific experimental session. Immediately prior to the functional imaging session, subjects spent twenty five minutes in the scanner, so that they could acclimate to the confinement and sounds of the MR environment. Past the experiment participants were debriefed and thanked for their participation.

2.7 Design of fMRI experiments

Generally, there are two design classes in fMRI, blocked and event-related designs (Frackowiak et al., 1997). Blocked fMRI designs are characterized by a blocked presentation of experimental trials, e.g., block of trials condition A, block of trials condition B, etc. Blocks usually last for 40-60s. Using this kind of presentation design it it possible to dissociate hemodynamic responses associated with the repeated presentation of stimuli or the constant performance of one task, respectively. The advantage of blocked designs consists in the great amount of repetitions resulting in high statistical power. However, this design class comes along with several disadvantages. Namely, a constricted randomization of conditions, the risk of possible confounds due to processes like maintenance of a particular attentional set, or the impossibility to dissociate signal changes within blocks. Moreover, due to the predictable arrangement of conditions participants usually know beforehand what kind of task they would have to perform next. Also the temporal structure of the experimental session becomes predictable after a while. Both factors could give rise to anticipation and habituation effects.

The advent of event-related designs allows to overcome some of these shortcomings. This design class allows to characterize and compare hemodynamic responses to single stimuli or events independently from the context in which the stimuli are presented. Most importantly, event-related designs allow to randomize stimuli/events so that evaluations are unaffected by possible confounds due to processes like maintenance of particular attentional sets. Randomization and coevally balancing transition probabilities allow to exclude effects due to anticipation and habituation. Due to unrestricted randomization and relatively fast presentation of events, fMRI experiments differ hardly anymore from behavioral or electrophysiological experiments. This offers a great possibility to investigate the functional relationship with behavioral measures, e.g., using error rates or RT as parameters or the investigation of post-hoc selected events based on participants' performance (Burock, Buckner, Woldorff, Rosen, & Dale, 1998). Note, although the hemodynamic responses add up linear it is possible to dissociate responses to events that are only separated by 2s (Clark, Maisog, & Haxby, 1998).[3] Not less important is the improvement of the temporal resolution. This can be achieved by varying the phase of the event relative to the data acquisition and by making repeated measurements such that being in synchrony with the data acquisition is not required. For each stimulus/event the measured signal is described by a convolution of the temporal stimulus distribution and the hemodynamic response function. In all present experiments event-related designs were employed.

The specification of different contrasts allows to test for a variety of effects which can be categorized into three broad classes, i.e., subtractive, parametric, and factorial designs. In general, the analysis of fMRI data follows the method of cognitive subtraction (Friston et al., 1996). That means, cognitive-behavioral differences are correlated with brain activation by means of a comparison between tasks that differ in only the cognitive process of interest but not in sensory, motor or cognitive requirements. The method of cognitive subtraction holds the assumption of pure insertion. This means, it is assumed that the addition of a cognitive process to a preexisting set of processes does not affect them. Generally, the method of cognitive subtraction is simple and offers a very effective way to map functional anatomy (Friston, Price, Buechel, & Frackowiak, 1997). For example, the null hypothesis that there are no cerebral differences between uncertain and certain decisions could be rejected, if the main effect of type of task would be significant.

In contrast, parametric designs are required if the main focus lies on the investigation of brain regions that vary *systematically* with the degree of cognitive processing. Parametric designs are used to investigate the relationship between experimental parameters and the hemodynamic response. Thus, the crucial difference between subtractive and parametric designs is that the latter ones imply the

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[3] This is achieved by partialing out the overlap of hemodynamic responses.

assumption that the cognitive process (of interest) can be expressed to a greater or lesser extent (Friston et al., 1997). Accordingly, cognitive processes are not regarded as categorical invariants but rather considered as dimensions or attributes that can be expressed more or less. For example, amongst other things, the present experiments aimed to investigate activation changes subject to the degree of uncertainty in decision making. That means, by a parametric variation of the degree of uncertainty it was investigated whether the involved brain regions vary systematically with the degree of uncertainty. In general, one advantage of parametric designs is that no appropriate control condition has to be employed and additionally only the changes due to the experimental parameters of interest are measured. However, in all present experiments an appropriate control condition was employed in order to additionally test for the main task effects.

In order to complete the overview of different experimental designs in fMRI, factorial designs will shortly be mentioned as they were not realized in the present experiments. If the focus of research lies on the assessment of the effects of one manipulation on the effects of another manipulation, neither subtractive (categorical) nor parametric (dimensional) designs are appropriate. Designs associated with this kind of research questions are factorial (interaction) designs. In this case the two factors of interest are combined in the same experiment.

2.8 Design of the present fMRI studies

In the following, a short description of the design in the present experiments is given. However, a more detailed elaboration is carried in the respective chapters.

The first experiment (Exp.1) aimed to investigated brain correlates of externally attributed uncertainty, i.e., uncertainty of frequency. By using a parametric design it was tested whether different degrees of uncertainty of frequency are reflected by modulations of the involved brain areas. An expected slow learning effect in the course of the experiment was controlled and additionally it was tested whether the same brain areas are affected or not.

The second experiment (Exp.2) aimed to investigate brain correlates of internally attributed uncertainty, i.e., knowledge uncertainty. By using a parametric design it was tested whether different degrees of knowledge uncertainty are reflected by modulations of the involved brain areas. Comparable to the first experiment, a slow learning effect in the course of the experiment was expected and therefore controlled. Additionally it was tested whether the same brain areas modulated by knowledge uncertainty are affected or not.

In order to compare brain activations induced by externally attributed uncertainty (Exp.1) to brain activations induced by internally attributed uncertainty (Exp.2), a group comparison was calculated. This means, the resulting two sets of contrast images from Exp.1 and Exp.2 were compared voxel-wise using a two-sample t-test to examine the hypothesis that the mean contrasts of the two groups differ significantly.

The third experiment (Exp.3) aimed at the investigation of uncertainty reduction given internally attributed uncertainty. That way, it was tested whether activation within areas shown to be modulated by knowledge uncertainty is solely reduced by increasing the amount of relevant knowledge (real learning) or whether an increase in solely positive outcomes (pseudo learning) is comparatively powerful. By using a subtractive design both main task effects and a direct contrast between the two learning conditions were calculated.

Chapter 3

Experiment 1

3.1 Introduction

In real life situations predictions are made on the basis of expectations about which event is the most probable to come up. Dependent on the frequency with which we experienced that an event *e* has followed the type of situation we face again, predictions are made with more or less certainty. In order to come up with a stable representation about event frequencies we therefore have to face the same type of situations over and over again, i.e., within a so-called *natural sampling* (Gigerenzer, 1994; Hasher & Zacks, 1979; Kleiter et al., 1997). The acquired representation of probabilities of event occurrence is applied to external stimulus properties, so that a distinction between differently probable events is possible. The high accuracy of frequency estimations observed in humans confirm the vital meaning of correct estimation of event frequencies in many adaptive behaviors (Betsch, Plessner, Schwieren, & Gütig, 2001; Sedelmeier, 1999). Like guessing and gambling, probability-based predictions are charged by externally attributed uncertainty. In contrast to internally attributed types of uncertainty in decision making, externally attributed uncertainty occurs whenever we think that it is caused by events in the world that we cannot control (Howell & Burnett, 1978; Kahneman & Tversky, 1982). The typical coping strategy used in such situations is to rate the relative frequency of such events. Brain correlates of this externally attributed uncertainty have been investigated in guessing paradigms confronting subjects with two or more events of equal probability (Elliott & Dolan, 1998; Elliott et al., 1999; Paulus et al., 2001). However, in many real life situations we do not expect one out of several events to occur with the same probability. Rather, we describe situations as indicating varying event probabilities, for instance when saying *"I am very certain that it will rain tomorrow"* or *"I am quite certain that Peter will be late.*". Hence, in contrast to predictions that we make in guessing or gambling situations, our real life predictions usually depend on extensive experiences and memories of event frequencies. Accordingly, Exp.1 set out to investigate whether activations induced by uncertainty in a natural sampling prediction would be different from or similar as those induced by uncertainty in guessing or gambling. A similarity is suggested by the fact that both types are so-called externally attributed types of uncertainty. A difference is suggested by the fact that predictions that base on a natural sampling refer to a learning process, whereas guessing and gambling do not.

FMRI was used to investigate the neural correlates of predictions based on a virtual natural sampling. Participants were presented with stimulus combinations that determined the probability of a subsequently following event which occurred with a probability of $p = .6, .7, .8, .9$, or 1.0. Using a parametric design, the hypothesis was tested whether brain activation within the region of interest, i.e., frontomedian areas, would increase with decreasing event probability. Many different tasks that require decisions or overt responses under uncertainty are known to draw on frontomedian areas (Bechara et al., 1996; Critchley et al., 2001; Elliott & Dolan, 1998; Elliott et al., 1999; Goel & Dolan, 2000; Paulus et al., 2001, 2002; Rogers et al., 1999). However, uncertainty is reported to be reflected within posterior frontomedian areas, including mesial BA 8 or anterior BA 6, corresponding to pre-SMA, and BA$32'/24'$, i.e. the dorsal part of the ACC. Accordingly, though the engagement of frontomedian areas in behaviors under uncertainty is clearly indicated in the literature, we are ignorant about the correlates of uncertainty that we typically face in everyday behavior, i.e., natural samplings. One central aim of Exp.1 was therefore to clarify the anatomical location within the posterior portion of the frontomedian wall that co-varies positively with increasing uncertainty in predictions in a natural sampling. In addition to posterior frontomedian areas, orbitofrontal areas are known to be engaged in uncertain decisions, particularly those induced by reward expectancy, and depending on varying task-corresponding emotional attitudes (Breiter et al., 2001; Critchley et al., 2001; Elliott et al., 1999; O'Doherty, Kringelbach, Rolls, Hornack, & Andrews, 2001; Rogers et al., 1999). However, due to technical restrictions of the T2* sequence in a 3T NMR system that usually causes signal voids (Norris, Zysset, Mildner, & Wiggins, 2002), medial orbitofrontal activations could not be detected in Exp.1 (see also 2.4.1). The focus of the present study is therefore on posterior frontomedian areas, including mesial BA 6, mesial BA 8, BA $32'$, and BA $24'$. The cognitive representation of event frequencies (like "2 out of 10") are reported to differ crucially from those of event probabilities (like "20%") (Gigerenzer, 1994; Gigerenzer & Hoffrage, 1995). As worries came up that strategies like coding event frequencies by event probabilities could emerge after extensive behavioral training, it was decided to dismiss a training. Without a pre-session training, however, slow learning effects during the course of the experimental session were expected, and therewith a slow decrease of general uncertainty. As the main focus of Exp.1 was the investigation of probability-dependent uncertainty varying between blocks, it was clearly needed to control for this slow learning effect. This was done by the implementation of an additional statistical regressor that modeled learning effects (see also 3.2).

3.2 Method

3.2.1 Stimuli and task

The task of the participants was to predict which of two concurrently presented stimuli would win in a virtual competition game. Uncertainty of frequency was manipulated by varying the winning probabilities between experimental conditions (ranging from 60% to 100%). The winning probabilities depended on a specific stimulus feature (as explained below).

Stimuli consisted of comic pictures showing UFO's differing in color, shape, and a figure seated within the UFO. Four different colors, shapes, and comic figures (in the following referred to as A, B, C, and D) were employed respectively. Participants were instructed to attend to one specific stimulus feature, i.e., the figure dimension. The stimulus properties color and shape varied randomly across figures. Within each trial, two stimuli were presented concurrently, one on the right and one on the left side of the screen. Within the stimulus dimension, six possible pairings were generated by combining the four different figures (e.g., A-B, A-C, A-D, B-C, B-D, and C-D). Participants had their index fingers on a left and a right response button, corresponding to the stimulus presentation positions on the screen.

In the prediction conditions, each of five pairings of figures was systematically associated with a particular winning probability, and these associations were consistent throughout the experiment. Accordingly, depending on the pairing in the uncertain prediction condition, the feedback showed one of both figures with a mean probability of .6 (that D wins against C), .7 (that D wins against B), .8 (that B wins against C), .9 (that C wins against A), and 1.0 (that A wins against D), respectively (see Table 3.1). The figure combination (A-B) was used as control condition in which an external cue indicated the winning stimulus.

Table 3.1: *Listed are the stimulus combinations and the assigned winning probabilities.*

Stimulus combination	*winning probability*
D trumps C	0.6
D trumps B	0.7
B trumps C	0.8
C trumps A	0.9
A trumps D	1.0

In the five prediction conditions ($p = .6, .7, .8, .9, 1.0$), participants were instructed to press the response button spatially corresponding to the stimulus they excepted to win, i.e., to bet on the winner (e.g., after stimulus presentation, if figure A will win against figure D, or conversely). In the control condition (A-B) three arrows in the middle of the screen indicated which of these two stimuli would win. Participants were asked to simply indicate the stimulus that was indicated by the arrows. The three arrows indicating the winning stimulus pointed to A and to B equally often, i.e., A won against B with a probability of .5. Average winning probabilities were almost balanced between the four figures (A: .533 , B: .533, C: .500, and D: .433). By balancing the probabilities in this way, it was aimed to avoid cross-talk between pairings and subsequent effects like latent inhibition to operate between blocks.

3.2.2 Experimental design

A blocked presentation design was used, with probabilities varying between each block ($p = .6, .7, .8, .9, 1.0$). Each of these blocks as well as blocks of the control condition consisted of five subsequently presented trials showing the same figure pairing (for instance, A plays five times against B). Within each trial, one pair of stimuli was presented for 2s during which participants' response was recorded. Presentation was followed by a feedback presented for 1.5s, showing the winner if the prediction was correct, or showing a masking of both stimuli if the prediction was incorrect (see Figure 3.2). The inter-block-interval was 5s. Overall, 10 blocks were presented for each of the five probabilities and the control condition, resulting in 60 blocks or 300 trials altogether. Blocks were presented in randomized order, and the order was also randomized and balanced between participants. The frequency of block-block transitions was balanced across the experimental session. The order of blocks was balanced between participants, such that the group-averaged event probability was .80 at each time during the course of the entire experimental session (see also comments on the regressor modeling slow learning effects). That is, participant 01 started for instance with the block order .7, .6, 1.0 and so on, whereas the participant 02 started with .1, .8, .6 and so on (see Figure 3.1).

An enhancement of the BOLD signal was achieved by employing a jittering

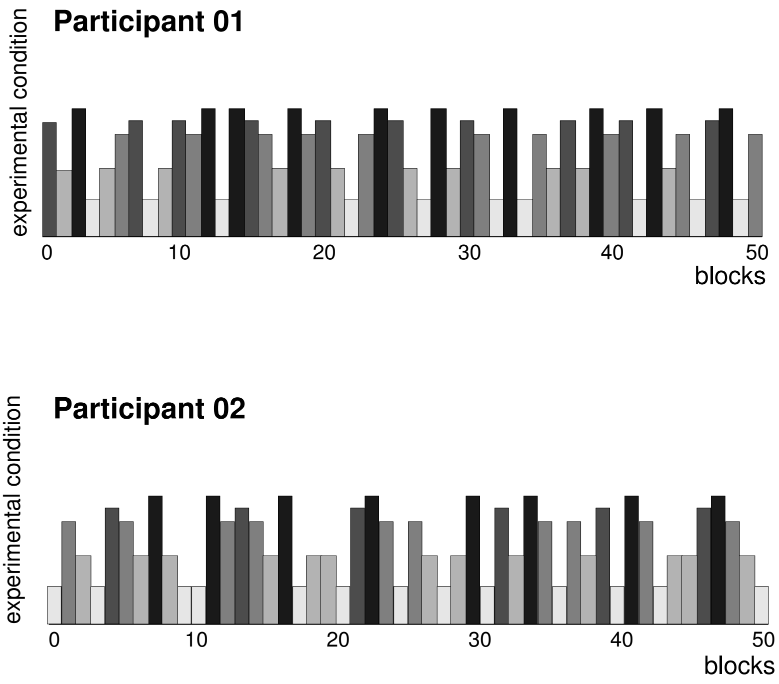

Figure 3.1: *Example of the distribution of the experimental conditions. Each participant had another distribution such that the group-averaged event probability was* $p = .80$ *at each trial over the course of the entire experimental session.*

which allowed the assessment of the BOLD-response at different times relative to the event onset. Both the beginning of each block as well as the inter-trial-interval was jittered. Accordingly, while trial duration (3.5s) and trial asynchrony (5s) were kept constant, the inter-trial-interval (mean duration of 1.5s) varied by a jittering of 0, 500, 1000, or 1500ms, respectively, assigned randomly to the trials.

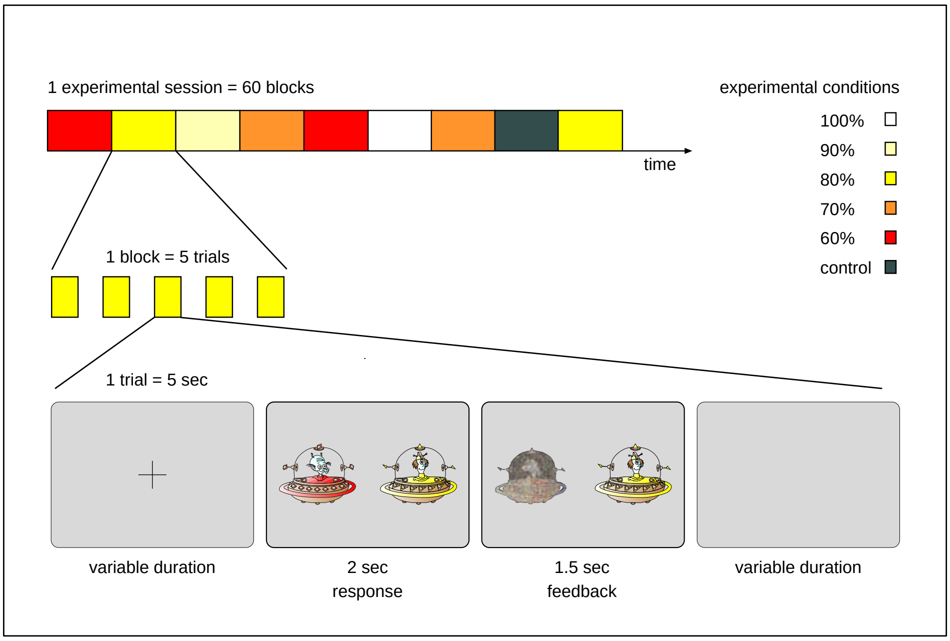

Figure 3.2: *Example of the stimulation. One experimental session consisted of 60 blocks, i.e., 300 trials. Blocks with different winning probabilities (color-coded) and the control condition were presented in (pseudo-)randomized order. One block consisted of 5 trials showing the same stimulus combination. Stimuli were presented for 2s during which participants' response was recorded followed by a feedback of 1.5s. In the present example a positive feedback is shown.*

3.2.3 Participants

Sixteen right-handed, healthy volunteers (5 female, mean age 24.9, range 21-35 years) participated in Exp.1. After being informed about potential risks and screened by a physician of the institution, subjects gave informed consent before participating. The experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.

3.2.4 Procedure

The procedure was conducted as described in chapter 2.6.

3.2.5 Data analysis

Effects of increasing externally attributed uncertainty were analyzed by using a parametric design with two regressors (Büchel, Wise, Mummery, Poline, & Friston, 1996; Büchel, Holmes, Rees, & Friston, 1998; Lange, 1999). So as to model the effects of externally attributed uncertainty independent from the cause but as a measure of performance a regressor was used that consisted in the average prediction error per probability of event occurrence, i.e., the average prediction error for each experimental condition. This regressor is referred to as "condition-regressor" in the following. Within the same model it was tested for slow unspecific learning effects by the use of a second regressor, consisting in the group averaged error score for each trial. This regressor is referred to as "learning-regressor" in the following. Note that such a second regressor can only be useful if it models a different source of variance than the first regressor and this is blocked-dependent uncertainty. The statistical independence of the group-averaged learning effect from the block-wise variation of uncertainty was achieved by balancing the order of event probabilities between subjects so that the group-averaged event probability was the same at each trial, i.e., $p = .80$. The condition-regressor (group-averaged error score for each condition) and the learning-regressor (group-averaged error score for each trial) were thereby statistically independent in each subject. That is, none of the correlations were significant (two subjects $r = -0.11$, three subjects $r = 0.10$, two subjects $r = -0.17$, three subjects $r = -0.04$, three subjects $r = 0.02$, three subjects $r = 0.13$). Both regressors referred to the same sample of trials, including all uncertain prediction conditions, but not the control condition. Absolute certain predictions, i.e., the control condition, were modeled as a separate onset vector within the same model. By including both regressors within one statistical model, contrast maps could be generated that extracted the three effects of interest independently from each other. Three contrast maps were generated from that statistical model:

Firstly, all uncertain prediction blocks were collapsed and contrasted against certain predictions, i.e., the control condition. Thereby, it was tested for the main task effect. Second, the effects of probability-dependent uncertainty in prediction were tested by using the condition-regressor. And third, the effects of time-dependent uncertainty were tested by using the learning-regressor.

3.2.6 MRI data acquisition

The acquisition of the MRI data was conducted as described in chapter 2.6. One functional scan consisted of 723 images and each image of 16 slices.

3.2.7 MRI analysis

All preprocessing and evaluation steps were calculated by using the software package LIPSIA (Lohmann et al., 2001) as described in chapter 2.4.

3.3 Results

3.3.1 Behavioral data

Performance was measured by the rate of erroneous predictions and reaction times of correct predictions. A repeated measures ANOVA with the 5-level factor uncertainty ($p = .6, .7, .8, .9, 1.0$) yielded a significant main effect for both erroneous predictions ($F(4,60) = 54.5; p < .0001$) and reaction times ($F(4,60) = 6.0; p < .001$) (see Table 3.2). As participants did not make any erroneous responses in the control condition, a repeated measures ANOVA with the 2-level factor uncertainty (all uncertain conditions collapsed, control condition) was not feasible neither for erroneous predictions nor for reaction times. A one-sided Pearson-correlation between erroneous predictions and time was found to be significantly negative ($r = . - 19; p < .001$). Likewise, reaction times got significantly shorter in the course of the experiment, as indicated by a significantly negative one-sided Pearson-correlation ($r = -.43; p < .0001$). Together, decreasing rates of both erroneous predictions and reaction times indicated significant slow learning effects over time.

Table 3.2: *Error rates (mean and SD in percent) and reaction times (mean and SD in ms) for all conditions during the fMRI scanning (*n*=16).*

Condition	Error rates (%)	Reaction times (ms)
$p = .6$	52.5 (3.8)	1095.5 (153.7)
$p = .7$	47.2 (9.7)	1030.4 (168.6)
$p = .8$	41.2 (8.2)	1026.0 (177.8)
$p = .9$	29.4 (9.2)	1004.9 (150.7)
$p = 1.0$	14.3 (7.8)	997.5 (125.2)
control	0	932.0 (203.5)

3.3.2 MRI data

Main task effect

In order to test for the main task effect, all 5 levels of uncertain predictions were collapsed and contrasted against certain predictions, i.e., the control condition. As listed in Table 3.3 and shown in Figure 3.3 significant activations were elicited within the right posterior frontomedian cortex (mesial BA 8/6), the right anterior insula, the cuneus, the cerebellar vermis extending laterally into the paramedian portion of the left cerebellar hemisphere, and within a sub-cortical network, including the ventral striatum, the thalamus, and the right midbrain area (VTA).

Parametric effect of externally attributed uncertainty

When testing for the parametric effect of externally attributed uncertainty positively co-varying voxels were found to be located within the right posterior frontomedian cortex (mesial BA 8), the right thalamus, the right anterior insula, and the left cerebellar cortex (see Table 3.4 and Figure 3.4). Hence, the right mesial BA 8 was the only cortical area that was found to be activated both in contrast to the control condition (main task effect) and in the parametric modulation of probability-dependent prediction uncertainty (parametric effect). Some areas that

Table 3.3: *Anatomical specification, hemisphere, Talairach coordinates* (x,y,z)*, and maximal z-scores (Z) of significantly activated voxels in prediction under uncertainty (all levels collapsed) in contrast to prediction under certainty (control condition).*

Area	Hemisphere	x	y	z	***Z***
Frontomedian Cortex (BA 8/6)	R	8	18	46	**4.4**
Ventral striatum	L	-12	12	-3	**4.5**
	R	21	15	-6	**4.0**
Thalamus	L	-15	-18	12	**3.4**
	R	8	-17	6	**4.2**
Midbrain area	R	8	-17	-6	**3.9**
Anterior insula	R	40	19	6	**4.1**
Cerebellum	R	1	-68	-23	**4.7**
Cuneus	R	4	-71	14	**4.1**

were activated significantly in the main task effect did not co-vary positively with increasing uncertainty. Additional activations were located within the right middle frontal gyrus and superior frontal sulcus, and the mid-portion of the right intraparietal sulcus. Though these areas were also slightly activated in the main task effect, maximal *z*-scores remained below the statistical threshold.

Parametric effect of slow learning

Finally, it was tested for voxels that co-varied positively with decreasing uncertainty due to slow learning effects in the course of the experimental session (see Table 3.5 and Figure 3.5). As a result, significant activations within only two areas were found. Namely, one activation located at the junction of the right inferior pre-central sulcus and the right inferior frontal sulcus (inferior frontal junction area, IFJ), the other within the left posterior parahippocampal gyrus. Hence, there was no area that was commonly activated by probability-dependent uncertainty in

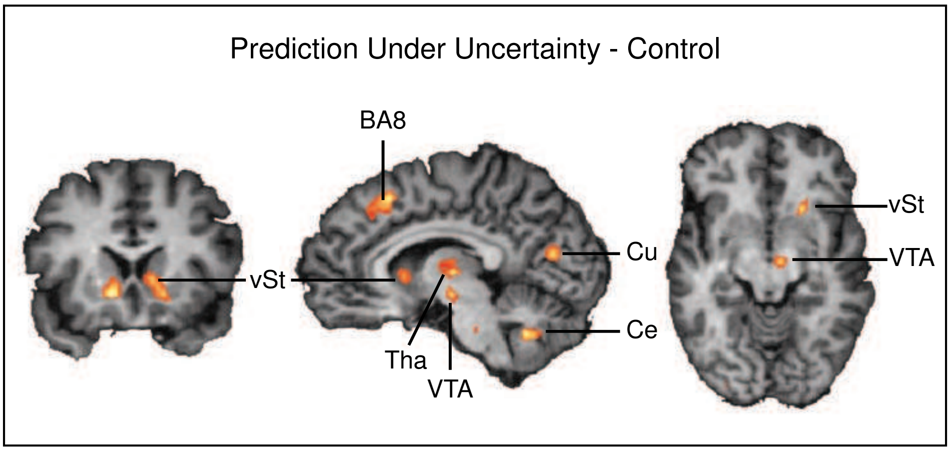

Figure 3.3: *Main task effect (Z* > 3.09*) for prediction under uncertainty versus control condition. Group-averaged activations are shown on coronal (y=12), sagittal (x=8), and axial (z=-6) slices of an individual brain normalized and aligned to the Talairach stereotactic space. For activation coordinates, see Table 3.3. Abbreviations: vST, ventral striatum; BA8, mesial Brodmann Area 8; Tha, thalamus; VTA, midbrain area; Cu, cuneus; Ce, Cerebellum.*

prediction and by decreasing uncertainty due to slow learning effects.

3.4 Discussion

Exp.1 investigated brain areas particularly within the frontomedian cortex that co-varied positively with a parametric modulation of prediction uncertainty in a virtual natural sampling approach. To that end, different degrees of prediction uncertainty were induced by different probabilities of event occurrence. In contrast to a control condition that allowed a certain prediction on the basis of external cues, prediction under uncertainty engaged the mesial BA 8. Though the maximally activated voxel of the frontomedian activation was located on the border between BA 6 and BA 8, closer inspection revealed voxels activated above the statistical threshold were only found anteriorly to the activation maximum, that is within BA 8, but not within BA 6. This was further supported by the para-

Table 3.4: *Anatomical specification, hemisphere, Talairach coordinates* (x,y,z)*, and maximal z-scores (Z) of voxels co-varying positively with increasing prediction uncertainty.*

Area	Hemisphere	*x*	*y*	*z*	***Z***
Frontomedian Cortex (BA 8)	R	4	30	46	**3.9**
Thalamus	R	8	-11	9	**3.4**
Anterior insula	R	37	12	-3	**3.6**
Cerebellum	L	-18	-71	-29	**4.0**
Superior frontal sulcus	R	17	3	46	**3.6**
Middle frontal gyrus (MFG)	R	37	21	36	**3.7**
Inferior parietal lobule	R	46	-53	38	**4.0**

Table 3.5: *Anatomical specification, hemisphere, Talairach coordinates* (x,y,z)*, and maximal z-scores (Z) of voxels co-varying positively with decreasing prediction uncertainty in the course of the experiment.*

Area	Hemisphere	*x*	*y*	*z*	***Z***
Inferior frontal junction area (IFJ)	R	43	0	26	**3.5**
Posterior parahippocampal gyrus	L	-18	-44	-3	**4.1**

metric analysis. When testing for voxels that co-varied positively with increasing uncertainty in prediction as measured by the mean prediction error across blocks, activation was found to be clearly located within mesial BA 8.

3.4.1 Increasing uncertainty reflected within mesial BA 8

Uncertain versus certain prediction elicited activation within mesial BA 8. The maximally activated voxel was located at the border to mesial BA 6, i.e. the pre-SMA, whereas the parametric effect of increasing uncertainty induced maximal activation anteriorly within mesial BA 8. Though this outcome raises the question of functional differences and similarities between anterior mesial BA 6/pre-SMA and mesial BA 8, these are difficult to determine in the literature. On the one hand, the pre-SMA role in higher movement organization is long established, as in contrast to hierarchically lower movement output organization attributed to the posteriorly adjacent SMA proper (Picard & Strick, 1996, 2001; Shima & Tanji, 1998). Specifically, the pre-SMA receives converging and rich input from all lateral prefrontal areas, which in turn are target regions from sensory cortices (Bates & Goldman-Rakic, 1993; Luppino, Matelli, Camarda, & Rizzolatti, 1993). The pre-SMA is therefore suggested in *cognitive* rather than motor aspects of voluntary behavior, particularly in the anticipatory processing of sensory (visual) information in view of a potential decision making or motor selection (Ikeda et al., 1999; Picard & Strick, 2001). On the other hand and in contrast to the pre-SMA, less is known about the functional profile of the anteriorly adjacent mesial BA 8. Projections between the monkey homologue of the pre-SMA, area F6 (Matelli, Luppino, & Rizzolatti, 1985), and anteriorly adjacent areas of the frontomedian wall suggest a close functional relationship (Luppino et al., 1993). Tracer studies in the monkey do not explicitly differentiate between mesial BA 6 and adjacent 8, but in contrast point out that rich prefrontal projections target the rostral SMA so anteriorly, that this target area may include Walker's medial area 8b (Bates & Goldman-Rakic, 1993). In accordance with fronto-parietal projections investigated in the monkey, right frontal and parietal areas together with mesial 8 were found to be increasingly activated by increasing prediction uncertainty . Also in imaging studies, mesial BA 8 and pre-SMA are often reported to be engaged in the same task and contrast. For instance, mesial BA 8 and pre-SMA together show increased activation whenever conflicts arise about the correspondence between perceived events and appropriate motor selections (Ullsperger & von Cramon, 2001). Likewise, predicting serial events in increasingly complex stimulus trains increased pre-SMA activation near the border or even including a portion of mesial BA 8 (Schubotz & von Cramon, 2002). More clearly separated from BA 6 are functions of the mesial BA 8 in hypothesis testing (Elliott & Dolan, 1998) and rule application (Goel & Dolan, 2000). Elliott and Dolan discuss mesial BA

8 activation in terms of a response selection guided by mnemonic representations of adaptive SR-mappings, rather than by internally guided guessing. Similarly, Goel and Dolan (2000) refer to the anticipatory functions of BA 8, suggesting that subjects anticipate stimuli in view of activated response rules for these stimuli. Note, however, that these authors refer to mesial BA 8 as pre-SMA. Indirect evidence for a functional difference between mesial BA 8 and pre-SMA may come from findings that indicate the pre-SMA does not co-vary with the amount of errors made in a visuo-manual learning paradigm (Sakai et al., 1999). In contrast, mesial BA 8 activation was found to co-vary with errors in the present experiment. A cautious suggestion may therefore be that BA 6 (pre-SMA) and mesial BA 8 are both involved in the acquisition of stimulus-response associations, with the latter to modulate this learning process by error evaluation.

3.4.2 Uncertain predictions based on natural samplings as in contrast to other types of decisions under uncertainty.

The aim of the present study was to figure out whether predictions based on a natural sampling induce similar or different frontomedian activations as other externally attributed types of uncertainty, particularly guessing or gambling. When comparing activations from the present study with those of other types of uncertainty-inducing tasks, two different activation clusters emerge. As plotted in Figure 3.6, activations reported in guessing paradigms (Elliott et al., 1999), error detection (Ullsperger & von Cramon, 2001), and risky choice (Critchley et al., 2001; Rogers et al., 1999) elicited activations within BA $32'/24'$. In contrast, activation within Exp.1 was found to be located similar to those of hypothesis testing (Elliott & Dolan, 1998), response competition (Ullsperger & von Cramon, 2001), rule application (Goel & Dolan, 2000), and sequence-based stimulus prediction (Schubotz & von Cramon, 2002), i.e., within mesial BA 8 and 6. This comparison indicates that activations induced by uncertainty in a natural sampling prediction are indeed different from those induced by uncertainty in guessing, although both types are so-called externally attributed variants of uncertainty. As suggested in the introduction, differences in frontomedian correlates may instead reflect that predictions that base on a natural sampling refer to a learning process and memory, whereas guessing and gambling do not. In comparison to further activations induced by decision under uncertainty, a common characteristic of tasks that elicit similar activations like the present natural sampling approach may be that uncertainty is reduced in the long run. They involve the setting up of a model that is tested and that helps us to adapt our behavior stepwise and in a cumulative manner. In contrast, guessing and risky choices involve a short-term error processing, but no long-term behavioral adaptation to valid stimulus-response rules. Accordingly, the main difference between tasks activating BA $32'/24'$ and those activating BA 8/6 may be that the former do not allow for learning and adaptation processes, but function more as an alerting system. This difference may include also emotional processes, which should have higher impact on fast behavioral adaptations rather than on long-lasting learning. Accordingly, BA $32'/24'$ is suggested in the integration of cognitive processing of uncertainty with corresponding adaptive changes in bodily states (Critchley et al., 2001) or evaluative processes related to the emotional consequences of a (risky) choice (Elliott & Dolan, 1998). Together with results discussed in the literature, the present findings can be taken to indicate that mesial BA 8 is particularly engaged in feedback-based testing models or hypothesis on valid SR-associations that lead to long-lasting behavioral modifications. In contrast, BA $32'/24'$ appears to be rather engaged in the fast correction of response errors, including or modulated by a short-term emotional evaluation.

3.4.3 Sub-cortical activation

In contrast to the control condition, predictions under uncertainty induced also activations within a sample of sub-cortical areas, including several foci within the midbrain (ventral tegmental area, VTA), the ventral striatum (nc. accumbens), and the dorsal thalamus. These structures belong to a striatal-thalamo-cortical network basically prominent in reward-based learning functions (Breiter et al., 2001; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Elliott, Friston, & Dolan, 2000; Graybiel, 2000). As in the presently employed natural sampling approach, such types of learning are typically characterized by a slow delayed acquisition rate of implicit SR-associations. In particular, the nc. accumbens is taken to support the ability to work for delayed rewards (Cardinal, Parkinson, Hall, & Everitt, 2002). It is suggested that erroneous predictions function as a *teaching signal* for phasic changes in dopaminergic activity (Hollermann & Schultz, 1998; Schultz, 1998; Schultz & Dickinson, 2000). Thereby, dopaminergic projections from the VTA through the ventral striatum and the frontomedian cortex (Williams & Goldman-Rakic, 1998) provide phasic signals to modify and update SR-mappings (Inase, Tokuno, Nambu, Akazawa, & Takada, 1999).

Activations that were found within these areas can be reconciled with the idea of a summative, value-based attitude formation in natural samplings (Betsch et al., 2001). This approach assumes that, in natural samplings, the responses evoked by perceptual events are automatically recorded and summed up. Subsequently, these summary evaluations can serve as a basis for predictions and corresponding behavioral responses. However, it has also to be considered that uncertainty was not the only aspect to vary between conditions. Rather, the expectancy and the experience of positive and negative prediction outcome varied too. Since a positive prediction outcome could be seen as a kind of reward, a related issue here is whether expectancy and experience of reward can be dissociated on the brain level. Recent imaging studies have indicated that expectancy and previous experience mostly share common neural substrates (Breiter et al., 2001), as already suggested by the work of Mellers and colleagues (Mellers, Schwartz, Ho, & Ritov, 1997; Mellers, Schwartz, & Ritov, 1999). Accordingly, the frontomedian areas found to be activated in Exp.1 could be differently modulated by either the expectancy or the experience of positive prediction outcomes.

3.4.4 Decreasing uncertainty by slow learning effects over the course of the experimental session

Slow learning effects during the course of the experimental session were expected due to decreasing uncertainty related to knowledge. Learning effects were controlled for by modeling a second regressor using the group-averaged error score for each trial. In addition, however, it was also looked directly for the effects of the learning-regressor in order to confirm non-overlapping brain activations for slow learning and frequency-dependent uncertainty. As a result, significant activations were found only within two regions, the right IFJ and the posterior parahippocampal gyrus. Activations within the posterior fronto-lateral cortex have been reported in shifting cognitive set, i.e., the switching from one response tendency based on previous experiences to a currently more suitable one (Brass & von Cramon, 2002; Monchi et al., 2001; Nakahara, Hayashi, Konishi, & Miyashita, 2002). According to this view, decline in IFJ activation would reflect decreasing requirements on switching between different stimulus-response associations. With increasing familiarity with the stimulus pairings and their probabilistic meaning, the requirements on behavioral switching and flexibility may decline during the course of the experimental session. This would also apply to decreasing activation within parahippocampal sites, which show slow sustained modulations during new stimulus-response learning (Cahusac, Rolls, Miyashita, & Niki, 1993). However, the crucial implication of this finding is that slow learning effects and the reduction of prediction uncertainty draw on different, non-overlapping brain areas, so that learning effects did not distort the activation pattern which was in the focus of interest.

3.4.5 Conclusion

Findings from Exp.1 indicated that frequency-based prediction uncertainty elicited frontomedian activation that resemble those induced in long-term stimulus-response adaptation processes such as hypothesis testing, as in contrast to those engaged in short-term error processing such as guessing.

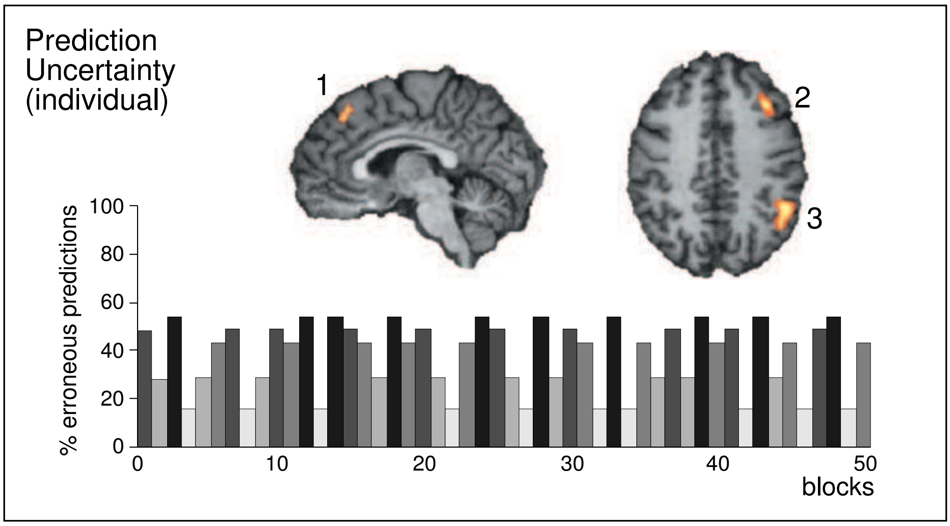

Figure 3.4: *Parametric effects of prediction uncertainty. The upper panel shows the group-averaged activations on a sagittal (x=4), and an axial (z=36) slice. Voxels co-varying positively with prediction uncertainty were located within mesial BA 8 (1), the middle frontal gyrus (2), and the inferior parietal lobule (3). Coordinates of further activations are given in Table 3.4. An example for a regressor for one participant is plotted on the lower panel. Regressors were determined individually, depending on the presentation order of blocks. The level of uncertainty was modeled by the mean prediction error made for each of the five probabilities. Bars for each experimental block are shown in different intensities of gray. Note that the ten blocks of the control condition did not enter the parametric analysis and are therefore not shown in the figure.*

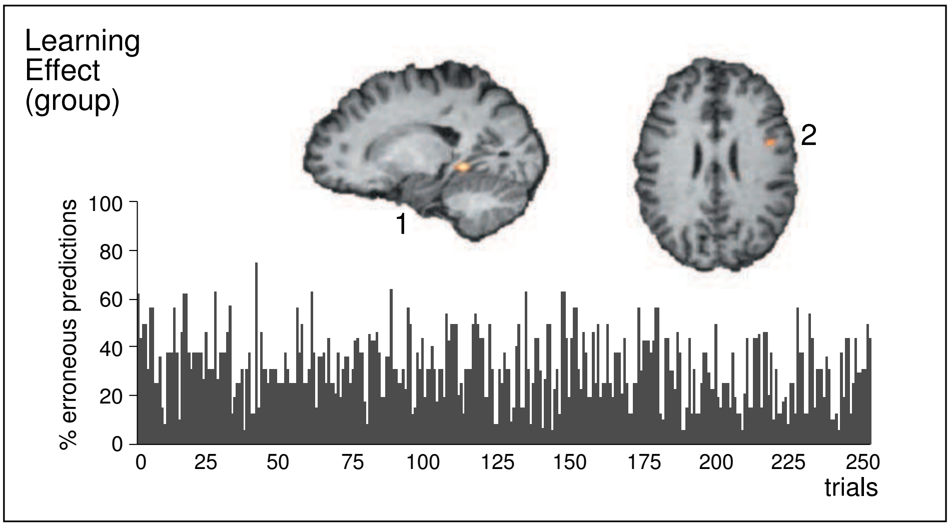

Figure 3.5: *Parametric effects of learning. The upper panel shows the group-averaged activations on a left sagittal slice (x=43) and an axial slice (z=3). Voxels co-varying positively with the decreasing error rates in the course of the experimental session were found within the left posterior parahippocampal gyrus (1) and within the right inferior frontal junction area (2). The lower panel shows the regressor that modeled decreasing uncertainty due to slow learning effects across participants (gray bars). The regressor was based on the group-averaged mean prediction error for each trial of the experimental condition (5 trials per block, 50 blocks = 250 trials). The 50 trials of the control condition are not plotted as they did not enter the parametric analysis.*

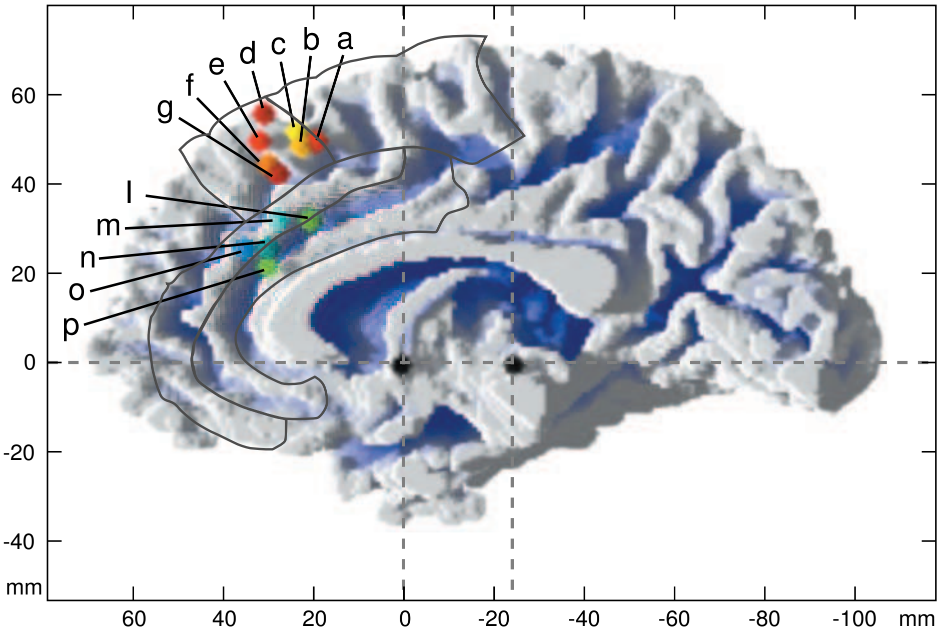

Figure 3.6: *Comparison between frontomedian activations of Exp.1 (a, e) and those of other studies on decisions under uncertainty. The right frontomedian wall of a white matter segmented individual brain is shown from the midline. The outer frame shows coordinates from Talairach and Tournoux (1988). The crosshairs cut through the anterior and the posterior commissure (AC-PC), with vertical orientation lines (VAC-VPC) perpendicular to AC-PC, respectively. Brodmann Areas 6, 8, 24, and 32 are outlined. Red-yellow spheres refer to activation foci within mesial BA 8, green-blue spheres to those within BA $32'/24'$. The red sphere a corresponds to the main task effect of prediction uncertainty compared to the control condition (see Figure 3.3). The sphere e corresponds to the parametric effect of increasing prediction uncertainty (see Figure 3.4). Other letters and spheres correspond to the following studies: b, Schubotz & von Cramon, 2002 (prediction difficulty); c, Elliott & Dolan, 1998 (hypothesis testing); d and g, Goel & Dolan, 2000 (rule application); f, Ullsperger & von Cramon, 2001 (response competition); l, Ullsperger & von Cramon, 2001 (error detection); m, Elliott & Dolan, 1998 (committing oneself to choice); n, Critchley et al., 2001 (uncertainty and arousal); o, Elliott et al., 1999 (guessing); and p, Rogers et al., 1999 (risky choice).*

Chapter 4

Experiment 2

4.1 Introduction

From a deterministic point of view, uncertainty is always caused by a lack of knowledge. Nevertheless, we are used to attribute our uncertainty to different causes, and these different causes are reflected in the way we try to resolve our uncertainty, i.e., by our coping strategies. A phenomenological analysis by Kahneman and Tversky (1982) distinguished between external attribution of uncertainty (see Exp.1) and internal attribution of uncertainty in decision making, a distinction also made by other authors (e.g., Howell, 1971; Teigen, 1994). External attribution of uncertainty occurs whenever we think that our uncertainty is due to coincidental chance events in the world which we cannot control. As a prominent coping strategy, then, we try to rate the probability of external events (e.g., “There is a sixty percent chance for rain tomorrow”). Internal attribution of uncertainty, in contrast, occurs whenever we think that our uncertainty is due to a lack or insufficiency of knowledge, i.e., to internal factors in ourselves which in principle we could control. A successful coping strategy in this case is an intensive memory search, most likely in combination with the attempt to get missing information from valid external sources (e.g., “I am quit sure that possums are mammals, but I don’t know exactly”).

In the second experiment (Exp.2) it was aimed to investigate the neural correlates of internally attributed uncertainty and beyond in as much they differ from those induced by externally attributed uncertainty (Exp.1). Thus, it was investigated whether the two variants of uncertainty, which we are used to distinguish in every day life, can be dissociated on the brain level. Using the same experimental paradigm as in Exp.1, internally attributed uncertainty was induced by varying the degrees of instructed knowledge about the winning rules. Parallel to Exp.1, where six levels of externally attributed uncertainty were induced, five levels of internally attributed uncertainty were induced in Exp.2.

For externally attributed uncertainty (Exp.1) mesial BA 8 was found to reflect uncertainty of frequency and furthermore to co-vary positively with increasing uncertainty. Using the same parametric approach as in Exp.1, it was investigated whether internally attributed uncertainty is also reflected by frontomedian activations (main effect), and if so, whether this brain activation also increases with increasing uncertainty of knowledge (parametric effect). Hence, it was tested whether mesial BA 8 activation reflects increasing uncertainty, regardless of the reason of uncertainty. In a subsequent group comparison (between-subjects design) it was investigated whether the co-activated networks underlying internally and externally attributed uncertainty differ significantly from each other. Particularly, since storage and retrieval of acquired visuomotor associations are required for the suggested coping strategy in decisions under internally attributed uncertainty (Kahneman & Tversky, 1982), fronto-parietal activations in networks that sub-serve working memory functions were expected (Fletcher & Henson, 2001; Owen, 2000).

Since the manipulation of knowledge uncertainty made a pre-experimental training of the winning rules impossible, slow learning effects during the course of the experimental session were expected, and therewith a slow decrease of general uncertainty. As the main focus of Exp.2 was the investigation of knowledge-dependent uncertainty varying between blocks, it was clearly needed to control for slow learning effects during the experimental session. This was done by the implementation of an additional statistical regressor that modeled learning effects (see also 3.2).

4.2 Method

4.2.1 Stimuli and task

In order to allow for a comparison between Exp.2 and the preceding Exp.1, only few features of the experimental paradigm were modified. As before, participants had to predict which of two concurrently presented stimuli would win in a virtual competition game. The crucial difference between the two paradigms was that uncertainty in Exp.1 was manipulated by varying winning probabilities between experimental conditions (from 60% to 100%), whereas uncertainty in Exp.2 was manipulated by varying the degree of knowledge that participants were provided with regarding 15 winning rules, each of which determining a 100% winning probability as dependent on stimulus features (as explained below). The second difference between Exp.1 and 2 was that experimental conditions were announced by task cues in the present study.

The same stimulus material was used as in Exp.1.

Stimuli consisted of comic pictures showing UFO's differing in color, shape, and a figure seated within the UFO. Four different colors, shapes, and comic figures were employed, respectively. Within each trial, two of these stimuli were presented concurrently, one on the right and one on the left side of the screen. Within each stimulus dimension, five possible pairings were generated by combining the four different levels (e.g., within the color dimension, the pairings red-yellow, red-blue, yellow-blue, yellow-green, and blue-green were presented; the sixth pairing, here red-green, was generally skipped in order to restrict rule complexity (see below)). Participants had their index fingers on a left and a right response button, corresponding to the stimulus presentation positions on the screen.

In the prediction conditions, each stimulus dimension (color, shape, figure) represented a rule group consisting of five different sub-rules specifying the correct feedback , as listed in Table 4.1. These 15 rules were valid throughout the experiment, that is, yellow always trumped blue and so on. In order to induce different levels of uncertainty of knowledge, participants were provided with different amounts of information about these rules. One rule group was trained up to optimal performance prior to the fMRI session (*trained rules condition*). A second rule group was verbally instructed at the end of this training session, but not practiced (*learned rules condition*). The third rule group was neither trained nor verbally instructed, so that participants were initially ignorant about this set of rules (*explored rules condition*). In a fourth prediction condition, participants were asked to test which one out of two rule groups, i.e., the trained or the learned rule group, was valid within a given block (*tested rules condition*). The assignment of stimulus dimension to rule group was balanced between participants.

Table 4.1: *Listed are the three rule groups which consisted of five different and intransitive sub-rules.*

Rule group	*Color*	*Comic figure*	*Shape*
Sub-rules	yellow trumps blue	A trumps B	circle trumps triangle
	blue trumps red	B trumps C	triangle trumps quadrat
	green trumps blue	D trumps B	ellipse trumps triangle
	red trumps yellow	C trumps A	quadrat trumps circle
	yellow trumps green	A trumps D	circle trumps ellipse

In the four prediction conditions (trained, learned, explored, and tested), participants were instructed to press the response button spatially corresponding to the stimulus they excepted to win (e.g., after the task cue “color rules are valid”, if the red stimulus will win against the blue, or conversely). In the control condition, pairings showed two identical stimuli (same color, shape, and figure). Three arrows in the middle of the screen indicated which of these two stimuli would win. Participants were asked to simply indicate the stimulus that was indicated by the arrows.

4.2.2 Experimental design

The experimental design was identical to Exp.1 with regard to presentation, time flow, randomization, and jittering. The only difference to Exp.1 was the presenta-

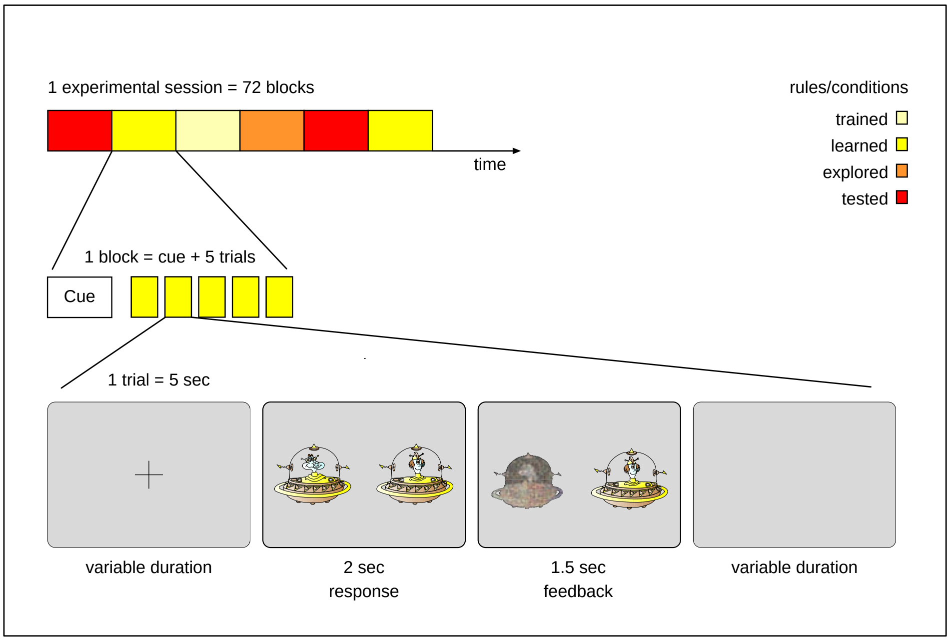

Figure 4.1: *Example of the stimulation. One experimental session consisted of 72 blocks, i.e., 360 trials. Blocks with differently well known winning rules (color-coded) and the control condition were presented in (pseudo-)randomized order. One block consisted of 5 trials showing the same stimulus combination. Stimuli were presented for 2s during which participants' response was recorded followed by a feedback of 1.5s. In the present example a positive feedback is shown.*

tion of a verbal cue at the beginning of each block which announced the respective experimental condition (see Figure 4.1). Overall, 15 blocks were presented for each of the four prediction conditions, and 12 for the control condition, resulting in 72 blocks or 360 trials altogether. Blocks were presented in randomized order, and the order was also balanced between participants.

4.2.3 Participants

Twelve (7 female, mean age 25.1, range 20-31 years) right-handed, healthy volunteers participated in Exp.2. After being informed about potential risks and screened by a physician of the institution, subjects gave informed consent before participating. The experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.

4.2.4 Procedure

The procedure was conducted as described in chapter 2.6. However, different to Exp.1, participants performed a training session immediately prior to the functional imaging session. The training session lasted twenty five minutes during which the anatomical images were taken.

4.2.5 Data analysis

Effects of levels of prediction uncertainty were analyzed using a parametric design that paralleled that of Exp.1 (Büchel et al., 1996, 1998; Lange, 1999). In order to model the effects of prediction uncertainty as a measure of performance, a regressor was used consisting in the group-averaged prediction error per experimental condition (trained, learned, explored, and tested). Parallel to Exp.1, this regressor is referred to as “condition-regressor” in the following.

Within the same model, it was also controlled for slow unspecific learning effects, that is, for the reduction of *condition-independent* uncertainty. This was done by introducing a second regressor referred to as “learning-regressor” in the following. Note that the learning-regressor could not be modeled individually, because learning depended systematically on knowledge, and therefore on the individual presentation order of experimental conditions. In order to avoid modeling of two statistically interdependent regressors (individual condition-regressor and individual learning-regressor), the learning-regressor consisted in the group-averaged error score for each trial. Since the order of conditions was balanced inter-individually, regressors were statistically independent. By this design, unspecific learning effects could be controlled for.

Both condition-regressor and learning-regressor referred to the same sample of trials, including all prediction conditions, but excluding the control condition. The control condition was modeled as a separate onset vector within the same model. By including both regressors within one statistical model, contrast maps could be generated that extracted three effects of interest, independently from each other:

Firstly, the main task effect was investigated by building the contrast between all collapsed prediction conditions and control condition. Second, the parametric effect of levels of prediction uncertainty was tested by using the condition-regressor. Third, the parametric effect of slow condition-independent uncertainty reduction was tested by using the learning-regressor. Finally, in order to investigate whether internally attributed uncertainty differed significantly from externally attributed uncertainty (group comparison between Exp.1 and 2), contrast images were compared voxel-wise using a two-sample t-test to examine the hypothesis that the mean contrasts of the two groups differ. The resulting image contains z-values indicating the degree of significance of the group difference.

4.2.6 MRI data acquisition

The acquisition of the MRI data was conducted as described in chapter 2.6. One functional scan consisted of 1010 images and each image of 16 slices.

4.2.7 MRI analysis

All preprocessing and evaluation steps were calculated by using the software package LIPSIA (Lohmann et al., 2001) as described in chapter 2.4.

4.3 Results

4.3.1 Behavioral data

Performance was measured by the rate of erroneous predictions and reaction times of correct predictions. A repeated measures ANOVA with the 2-level factor uncertainty (all uncertain conditions collapsed, control condition) yielded a significant main effect both for error rates ($F(1,5) = 35.2, p < .002$) and for reaction times ($F(1,5) = 61.1, p < .001$). A repeated measures ANOVA with the 4-level factor uncertainty (trained, learned, tested, and explored rules) yielded a significant main effect for error rates ($F(3,36) = 14.0, p < .0001$) but not for reaction times ($F(3,36) = 2.2, p = .11$) (see Table 4.2).

Table 4.2: *Error rates (mean and SD in percent) and reaction times (mean and SD in ms) for the different conditions during the fMRI scanning (*n*=12).*

Rule group	Error rates (%)	Reaction times (ms)
trained	6.6 (6.9)	881.2 (149.4)
learned	15.7 (12.5)	901.2 (228.3)
explored	16.8 (6.8)	878.6 (185.4)
tested	23.4 (13.8)	1005.2 (198.9)
control condition	0	617.8 (95.3)

A slow learning effect was not significant as measured by error rates (one-sided Pearson-correlation between erroneous predictions and time: $r = -.01; p = .40$), but as decrease in reaction times in the course of the experiment (one-sided Pearson-correlation between reaction times and time: $r = -.23; p < .001$). Errors dropped from the first to the last quartile by 4.7%, as compared to 5.5% in Exp.1.

4.3.2 MRI data

Main task effect

Corresponding to the behavioral analysis, the main effect of task was tested by collapsing all uncertain prediction blocks and contrasting them against the control condition (absolute certain prediction). Significant activations were found within the right posterior frontomedian cortex (mesial BA 8), bilaterally within inferior prefrontal areas (inferior frontal junction area (IFJ), i.e., at the cross-section of the inferior frontal sulcus and the inferior pre-central sulcus); mid-portions of the middle frontal gyrus (MFG) along the inferior frontal sulcus (IFS), the antero-superior insula, posterior parietal cortices (along the banks of the intraparietal sulcus (IPS)), within pretectal areas, and extra-striate visual cortices (see also Table 4.3 and Figure 4.2).

Table 4.3: *Anatomical specification, hemisphere, Talairach coordinates* (x,y,z)*, and maximal z-scores (Z) of significantly activated voxels in prediction under uncertainty (all levels collapsed) in contrast to prediction under certainty (control condition).*

Area	Hemisphere	*x*	*y*	*z*	***Z***
Frontomedian Cortex (mesial BA 8)	R	4	21	47	**4.5**
Frontomedian Cortex (anterior BA 8)	R	1	33	41	**4.2**
Inferior frontal junction area (IFJ)	L	-38	9	32	**3.8**
	R	40	13	32	**3.7**
Middle frontal gyrus (MFG)	L	-44	25	23	**4.4**
	R	37	27	26	**4.4**
Antero-superior Insula	L	-26	24	6	**4.5**
	R	28	22	9	**4.0**
Intraparietal sulcus (IPS)	L	-26	-62	50	**3.8**
	R	31	-53	47	**4.6**
Pretectal area	L	-5	-29	0	**3.8**
	R	4	-26	0	**3.3**
Extra-striate visual cortex	L	-35	-54	-9	**4.3**
	R	31	-50	-8	**4.3**

Effects of levels of uncertainty

Effects of knowledge-dependent (internally attributed) uncertainty were tested using the condition-regressor (group-averaged prediction error per experimental condition). As listed in Table 4.4 and shown in Figure 4.3, significant activations were elicited within the right frontomedian cortex (anterior portion of mesial BA 8), the left IJF, the right mid-portion of MFG, and bilaterally within posterior parietal cortices along the banks of the anterior portion of the IPS. Note that trials with correct and incorrect responses were collapsed, because excluding the trials with negative feedback did not change the overall activation pattern, except for a little

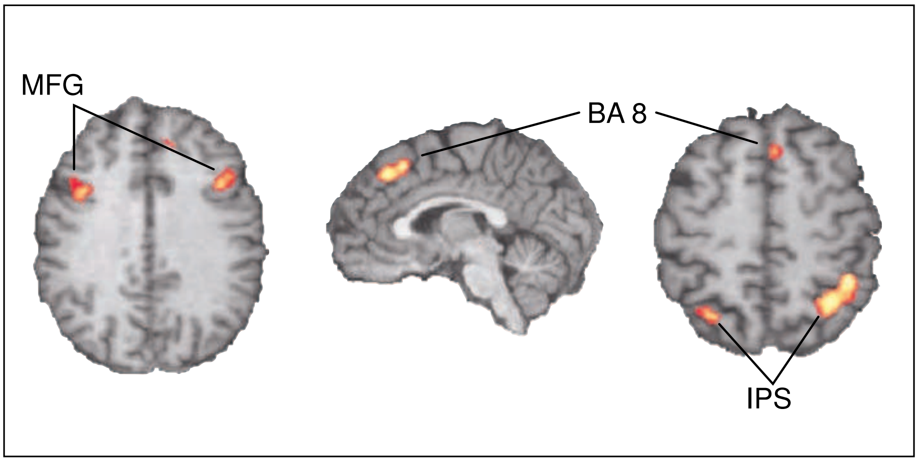

Figure 4.2: *Main task effect (Z* > 3.09*) for knowledge uncertainty versus certainty (control condition). Group-averaged activations are shown on axial (z=32;50) and sagittal (x=3) slices of an individual brain normalized and aligned to the Talairach stereotactic space. For activation coordinates see Table* **??**. *Abbreviations: BA 8, mesial BA 8; MFG, middle frontal gyrus; IPS, intraparietal sulcus.*

worse signal-to-noise ratio. Moreover, when using reaction times as values for the condition-regressor, the same cerebral network was found to be activated. In this case, the overall signal-to-noise ratio was lower than in the error-based analysis.

Slow learning effects

It was tested for slow learning effects on the BOLD contrast by using the learning-regressor (group-averaged error score for each trial). Activations were found within the right IFJ (Talairach coordinates: $x = 46, y = 7, z = 35; Z = 4.0$), the right inferior frontal sulcus (Talairach coordinates: $x = 43, y = 15, z = 26; Z = 3.8$), the left dorsal thalamic system (Talairach coordinates: $x = -14, y = -27, z = 0; Z = 3.7$), and within the right insula (Talairach coordinates: $x = 40, y = -5, z = -6; Z = 3.6$) (see also Figure 4.4).

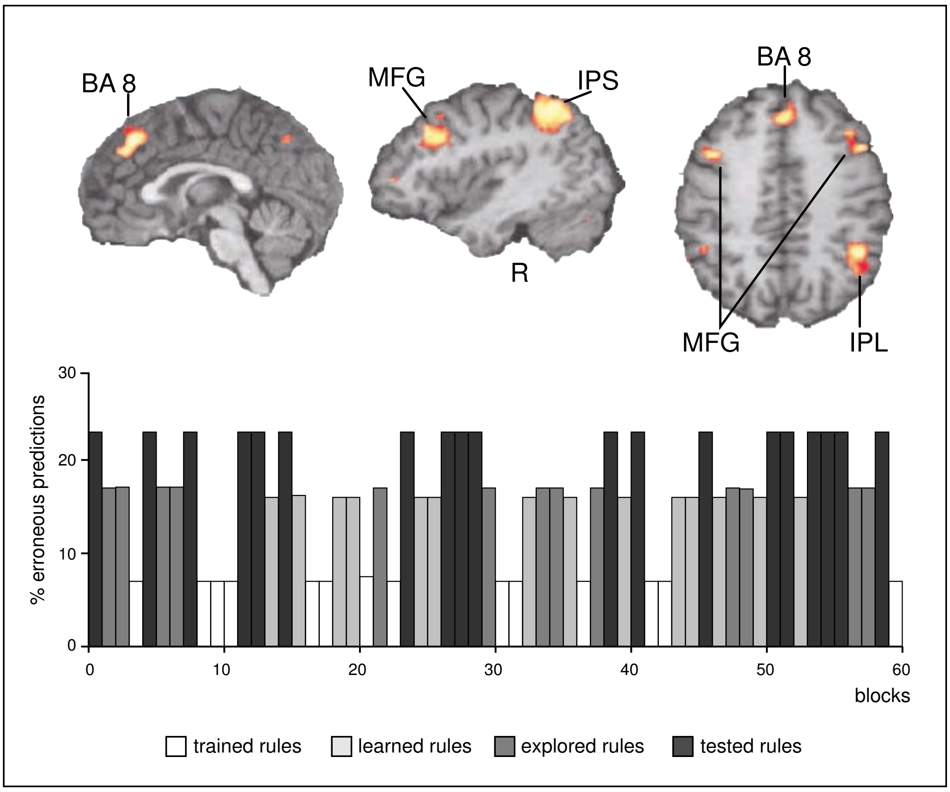

Figure 4.3: *Parametric effects of knowledge uncertainty. Group-averaged activations of voxels co-varying positively with erroneous predictions are shown on sagittal (x=1;40) and axial (z=38) slices. For activation coordinates see Table 4.4. Abbreviations: BA 8, mesial BA 8; MFG, middle frontal gyrus; IPS, intraparietal sulcus; IPL, inferior parietal lobe.*

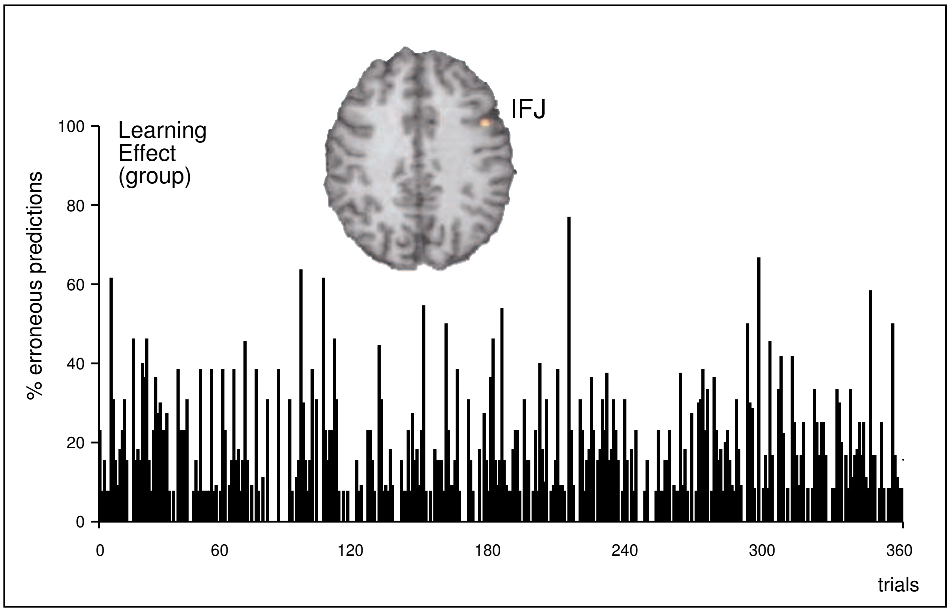

Figure 4.4: *Parametric effects of slow decreasing uncertainty. Group-averaged activation of voxels co-varying positively with the error rates in the course of the experiment is shown on an axial (z=35) slice. For activation coordinates see results section. Abbreviation: IFJ, inferior frontal junction area.*

Table 4.4: *Anatomical specification, hemisphere, Talairach coordinates* (x, y, z)*, and maximal z-scores (Z) of voxels co-varying positively with increasing prediction uncertainty.*

Area	Hemisphere	x	y	z	**Z**
Frontomedian Cortex (anterior BA 8)	R	1	33	41	**4.3**
Inferior frontal junction area (IFJ)	L	-44	12	38	**4.0**
Middle frontal gyrus (MFG)	R	40	24	35	**4.2**
Inferior parietal sulcus (IPS)	L	-38	-42	44	**4.1**
	R	40	-53	50	**4.2**

Comparison between externally and internally attributed uncertainty

Subsequently, it was tested whether networks underlying externally attributed uncertainty and those underlying internally attributed uncertainty differ significantly. A between-subjects group comparison was calculated using a two-sample t-test, i.e., the two sets of contrast images from Exp.1 and Exp.2 were compared voxelwise (Lohmann et al., 2001). The resulting image (see Fig. 4.5) contains z-values that indicate significant group differences of the main effects of uncertainty. According to the initial hypothesis, it was focused on three regions of interest: the mesial BA 8, fronto-lateral and posterior parietal areas. As expected, the inferior frontal cortex (IFJ bilaterally; mid-portion of left MFG/IFS) and posterior parietal cortices correlated positively with uncertainty when internally attributed. Talairach coordinates were nearly identical to coordinates of the main effect (see Table 4.5). The number of significantly activated voxels indicating a difference within the anterior portion of mesial BA 8 was negligible (11 voxels) and restricted to the most anterior part of this region.

Table 4.5: *Anatomical specification, hemisphere, Talairach coordinates* (x, y, z), *and maximal z-scores (Z) indicating the degree of significance of the group difference for internally attributed uncertainty.*

Area	Hemisphere	x	y	z	Z
Frontomedian Cortex (anterior BA 8)	L	-2	31	47	**4.0**
Inferior frontal junction area (IFJ)	L	-41	18	35	**4.2**
	R	40	13	32	**3.8**
Middle frontal gyrus (MFG)	L	-41	25	23	**4.2**
Inferior parietal sulcus (IPS)	L	-29	-62	50	**3.8**
	L	-47	-44	50	**4.0**
	R	31	-53	47	**4.7**

4.4 Discussion

Exp.2 was designed to investigate whether different causes of uncertainty in a prediction task are reflected within the same brain areas. By using a parametric approach and inducing different degrees of uncertainty, it was aimed to identify and compare the brain correlates of internally attributed uncertainty, i.e., uncertainty of knowledge (Exp.2), with those of externally attributed uncertainty, i.e., uncertainty of frequency (Exp.1). As a common cortical substrate of uncertain predictions, regardless of uncertainty attribution, mesial BA 8 was found to be significantly activated. In contrast, activation within other brain areas differed significantly between the two types of uncertainty. A direct comparison showed that internally attributed uncertainty specifically engaged a fronto-parietal network bilaterally. In the following, both commonly activated brain areas as well as areas that were exclusively activated for internally attributed uncertainty will be discussed.

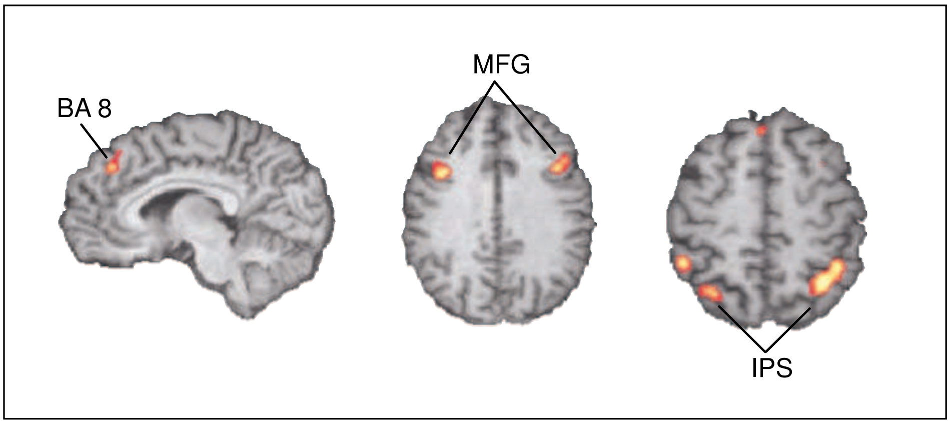

Figure 4.5: *Group comparison between the two types of uncertainty. Significant differences in activation strength are found within the anterior portion of mesial Brodmann Area 8 (BA 8), the posterior middle frontal gyrus (MFG), and within posterior parietal areas bordering the intraparietal sulcus (IPS). For activation coordinates see Table 4.5.*

4.4.1 Types of uncertainty - or ways of learning, rule validity, and coping strategies?

First, the argument has to be considered that Exp.1 and Exp.2 differed not only with regard to differently attributed uncertainties, but also with regard to different types of learning, and also with regard to differently valid SR-rules. As will be argued in the following, however, neither of these two potential confounds can explain the differences between the experiments.

Considering the learning characteristics, uncertainty of frequency (Exp.1) is observed in situations in which we typically cannot learn up to optimal performance, whereas uncertainty of knowledge (Exp.2) emerges if we can, and hence is a transient phenomenon as in contrast to the former. In order to balance this inherent difference between both types of uncertainty, learning requirements were manipulated in a way that Exp.2 was too short to allow for learning up to optimal performance. Data support that this manipulation was successful: Errors decreased from quartile 1 to quartile 4 by 5.5% in Exp.1, and 4.7% in Exp.2.

Both learning effects were not significant ($F(3,45) = 2.9; p = .05$ respectively $F(3,33) = 1.7; p = .18$). Therefore, it can be assumed that differences between Exp.1 and 2 cannot be reduced to remaining uncertainty in the latter and non-remaining uncertainty in the former.

Considering the second potential confound, rule validity was necessarily the instrument to implement different levels of uncertainty of frequency in Exp.1, as in contrast to Exp.2. Following, the average rule validity differed between Exp.1 (80%) and 2 (100%). However, if differences between Exp.1 and 2 were caused by differently valid rules, then one would also expect for the same reason that, firstly, WM networks should not co-vary parametrically with levels of uncertainty in Exp.2, because they all refer to the same (100%) rule validity; and secondly, that the very same WM networks should be activated and co-vary parametrically with levels of uncertainty in Exp.1, because they differ with regard to rule validity (60%, 70%, 80%, 90% and 100%). As evident from the data, however, neither is the case. Therefore, rule validity cannot be the cause for systematic differences between Exp.1 and 2.

In contrast, it is of course correct to say that the studies differed with regard to the coping strategies they induced, and that these different strategies are reflected by different cerebral activations. Behaviorally, different coping strategies have been suggested to be an indicator for different attributed uncertainties (Kahneman & Tversky, 1982). The term “variants of uncertainty” is meant to refer to exactly this definition, i.e., different ways to try to resolve decision uncertainty and hence different strategies to avoid future errors or achieve future rewards. Note that the performance scores in both experiments confirmed that participants tried to perform well. This of course had to be prooved statistically in particular for Exp.1, where expected maximal performance were below 100% correct responses. To this end, the discrimination index P_r by $P_r = hit - falsealarm$ (Snodgrass & Corwin, 1988) was calculated. This index allows to correct performance scores for guessing tendencies in all response classes. As a result, all conditions showed to be significantly different from chance level (100%: $t_{(15)} = 37.7$, $p < 0.001$; 90%: $t_{(15)} = 22.3$, $p < 0.001$; 80%: $t_{(15)} = 16.4$, $p < 0.001$; 70%: $t_{(15)} = 7.8$, $p < 0.001$;

60%: $t_{(15)} = 2.2$; $p = 0.04$). Therefore, it can be exclude that differences between Exp.1 and 2 were caused by guessing tendencies in the former as in contrast to the latter.

Finally, it is important to note that present Exp.2 as well as preceding Exp.1 were not designed to differentiate pre- and post-feedback processes. Activations therefore reflect uncertainty as especially emerging in the pre-feedback phase, together with processes that start in the post-feedback phase. However, although uncertainty may be reduced due to feedback evaluation in the latter phase, it is unlikely to vanish entirely. Moreover, expectancy and previous experience were found to mostly share common neural substrates (Breiter et al., 2001), as already suggested by behavioral data (Mellers et al., 1997, 1999).

4.4.2 Attribution-independent activation of uncertainty: mesial BA 8

Both internally as well as externally attributed uncertainty elicited activation within mesial BA 8 (Talairach coordinates in Exp.1: $x = 8, y = 18, z = 46$). A group comparison revealed no significant difference in the mean activation value within the posterior part of mesial BA 8. Internally attributed uncertainty elicited activation within a larger area than externally attributed uncertainty, extending into anterior mesial BA 8 and reaching the border of mesial BA 9. However, this difference was probably caused by a slightly larger activation in Exp.2, and may reflect quantitative rather than qualitative differences.

Like adjacent mesial areas BA 6 (pre-SMA) and adjacent portions of BA $32'/24'$, mesial BA 8 has been repeatedly found in tasks that induce uncertainty (see also Figure 3.6). In this context, BA $32'$ (together with BA $24'$) is usually referred to as the anterior cingulate cortex (ACC). Since the anatomical and functional organization of mesial BA 8 has begun to be focused on only recently, empirical evidence for a functional distinction between these three areas is still weak. Moreover, activations within mesial BA 8 and pre-SMA are difficult to disentangle due to missing macroscopical landmarks between these areas, and the same applies to the distinction between these regions and ACC. However, since it is widely accepted that laminar differentiations reflect functional differentiations of the cortex, it can be suggested that the considered areas underly different aspects in behavior under uncertainty. For instance, mesial BA 8 is a granular prefrontal isocortex, whereas ACC can be subdivided into agranular (BA $24'$) and dysgranular (BA $32'$) cortex.

In view of existing data, however, it appears that mesial BA 8 on the one hand and BA $32'/24'$ on the other appear to be preferentially engaged in different experimental paradigms on uncertainty. This view, which was already sketched in chapter 3.4.2, will be outlined in more detail in in the following.

Studies on conflict that report BA $32'/24'$ (often in company with pre-SMA) typically use paradigms such as e.g. the Eriksen flankers task or go/no go tasks (e.g., Bunge, Hazeltine, Scanlon, Rosen, & Gabrieli, 2002; Garavan, Ross, Murphy, Roche, & Stein, 2002; Luks, Simpson, Feiwell, & Miller, 2002; Ruff, Woodward, Laurens, & Liddle, 2001; Ullsperger & von Cramon, 2001, 2003). Common features of these paradigms are (a) SR-rules are simple (one-to-one mappings), often spatially compatible, and usually known and instructed beforehand, (b) two response tendencies are activated concurrently, so that conflict arises on the response level, (c) errors are usually induced by time pressure and perceptual difficulty, (d) conflict can be diminished by a close stimulus inspection, and (e) feedback evaluation allows to improve performance in perceptual and motor skills. In these paradigms, either ACC or pre-SMA are differently engaged in two sub-processes of conflict, as can be stressed by contrast building. The ACC is predominantly reported in error monitoring (Bunge et al., 2002; Garavan et al., 2002; Kiehl, Liddle, & Hopfinger, 2000; Ullsperger & von Cramon, 2001), whereas BA 6/pre-SMA (sometimes extending into mesial BA 8) is rather reflecting conflict detection (Kiehl et al., 2000; Ruff et al., 2001; Ullsperger & von Cramon, 2001). Based on these findings, the functional dissociation between pre-SMA and ACC has become a focus of research (Ullsperger & von Cramon, 2001, 2003) and was confirmed in recent meta-analysis by Fassbender, Hester, and Garavan (2003).

In contrast, ACC activation is typically absent in a different type of paradigm regarding conflict reporting mesial BA 8 activation. These studies investigated hypothesis testing with low restrictions (Elliott & Dolan, 1998), the application of arbitrary SR-rules (Goel & Dolan, 2000), and the detection of arbitrary SR-rules (Knutson et al., 2003). Common features of these are (a) SR-rules are complex (many-to-many mappings), arbitrary and usually unknown beforehand, (b) decisions tendencies depend on previously evaluated feedbacks, so that conflict arises on the knowledge level, (c) errors are not induced by time pressure, but by cognitive difficulty, (d) conflict can be diminished by mnemonic search, and (e) feedback evaluation allows to improve performance in cognitive skills and knowledge. From all these features, however, feedback evaluation appears to be the most relevant for BA 8 activation. Accordingly, BA 8 is not found in a number of paradigms that at first glance seem to match several of the features listed above, but do not allow for a feedback-based learning of SR-rules (Bush et al., 2002; Casey et al., 2000; Paulus et al., 2002, 2001).

In sum, it is suggested that both Exp.1 and Exp.2 draw rather on BA 8 than on ACC (BA $32'/24'$) because the employed tasks induced a sustained feedback-dependence of task performance, i.e., deliberate choices based on mnemonic searches, as in contrast to forced responses based on perceptual cues. To put it shortly, BA 8 and ACC may distinguish “decision conflicts” from “response conflicts”. Considering a distinction proposed by Reason (1990), these could be suggested to precede “mistakes” in the latter and “action slips” in the former case.

4.4.3 Attribution-dependent activation of uncertainty

In addition to mesial BA 8 significant activations within the MFG, IFJ, and IPS were found to be activated significantly in internally attributed uncertainty versus control condition. The same sample of areas was found to increase with increasing internally attributed uncertainty (parametric effect) and in direct task contrast between internally attributed and externally attributed uncertainty (Exp.1 vs. Exp.2). These findings confirm the hypothesis that uncertainty due to insufficient knowledge will engage brain areas sub-serving WM functions.

The MFG (BA 46/9) is also referred to as mid-dorsolateral prefrontal area (Petrides, 2000). Activations within this region have been reported when monitoring and manipulation of information within WM is required (D'Esposito et al., 1998). The monitoring of mnemonic information across trials is taken to be the key feature of tasks activating mid-dorsolateral prefrontal areas (Kostopoulos & Petrides, 2003; Petrides, 2002) as in contrast to memory retrieval per se which has been shown to specifically activate the mid-ventrolateral prefrontal cortex.

In the present experiment, mnemonic information referred to SR-rules that were defined by different non-spatial object properties. The mid-dorsolateral prefrontal coordinates in the present study fit to those reported for non-spatial WM in a recent meta-analysis by Owen (2000) (Talairach coordinates right: $35, 32, 19$; left: $-42, 23, 19$).

The manipulation of actively maintained information within WM is suggested to rely on mid-dorsolateral prefrontal cortex (Hartley & Speer, 2000; Petrides, 2002). Accordingly, the increasing activity within these areas is taken to reflect increasing demands in computations on stored information, specifically the reduction of all possible SR-rules to a smaller set of valid SR-rules. In the case of trained rules, the cue referred to five valid SR-rules concerning property X (e.g. comic figure). In the case of learned rules, participants knew that the cue referred to five valid SR-rules concerning property Y (e.g. color), but not to which exactly. In the case of explored rules, participants knew that the cue referred to five valid SR-rules, but not to which property they applied. Finally, whenever participants had to test whether either the trained or the learned rule-group were valid, the range of to-be-checked SR-rules was twice as large as in the trained or learned rules condition. Hence, parametric variations of the mid-dorsolateral prefrontal activation is taken to reflect different requirements on reducing the range of potential SR-rules.

In addition to MFG, posterior parietal areas (IPS) were found to be co-activated, as typical for WM functions (Owen, 2000). In contrast to the prefrontal components of this network, the posterior parietal areas are taken to maintain all SR-rules that are valid in an experiment (Bunge et al., 2002). From this set currently valid SR-rules are selected by corresponding prefrontal sites (Miller & Cohen, 2001; Smith & Jonides, 1999). By manipulating the number of SR-rules (sample sizes) with which participants started the present study, experimental conditions differed in their requirement to maintain SR-rules, and therefore draw differently on posterior parietal areas.

Regarding IFJ activation, it has been shown that the implementation of learned SR-rules elicits activation within the this area (Brass & von Cramon, 2002; Nagahama et al., 2001). This interpretation can be applied to IFJ activation in the present experiment, where the selection and implementation of appropriate SR-rules is required throughout the experiment and co-varies as a function of SR-knowledge. Activation was found to decrease within the same or closely adjacent areas during the course of the experimental session (see Figure 4.4). This effect replicated findings from Exp.1, though coordinates differed slightly. As discussed in the previous study, a decrease in IFJ activation was interpreted to reflect a decrease in effort in implementing valid SR-rules. The same explanation applies to the parametric modulations of IFJ area: as the range of potentially valid SR-rules is reduced, IFJ activation decreases. Note that activation modulation in IFJ cannot be attributed to retrieval success, because increasing success would be reflected in a negative co-variation with decreasing IFJ response.

4.4.4 Conclusion

Together with Exp.1, present data demonstrate that both externally attributed uncertainty and internally attributed uncertainty modulated the posterior frontomedian cortex, specifically in mesial BA 8. However, while the former attribution of uncertainty elicited activations within a dopaminergic sub-cortical network, the latter induced additional activations within a fronto-parietal network. Findings thereby confirm that memory search is an appropriate coping strategy in this type of uncertainty. Concluding, mesial BA 8 reflects *that* we are uncertain, additional networks *what we do to achieve future rewards*.

Chapter 5

Experiment 3

5.1 Introduction

The physician who diagnoses a patient, the broker who has to decide whether or not to sell (the shares), or the student who needs to answer questions in an examination, all face uncertainty due to incomplete or unreliable knowledge. In all examples the actor is concerned with the existence of several options rather than with just one and thus uncertainty depicts the persons' belief about the variability of possible outcomes (Teigen, 1994). But how can this uncertainty be resolved in order to prescribe drugs, sell shares, or answer examination questions? A reduction of knowledge uncertainty, which constitutes in the reduction of the range of all possibilities to the relevant alternatives, is typically achieved by gathering and evaluating external information which is feedback in experimental situations. By comparing what has been achieved to what was initially wished to achieve, feedback contains information about how far someone has progressed towards his/her specific goal. Generally, negative feedback (usually an error) constitutes the converse of an efficient action. By indicating that something has gone astray, negative feedback signals for an attitude change. In contrast, positive feedback serves as a "keep-at-it" signal. Thus, without knowledge of results there is no progress such as learning or performance improvement. The preference for one option develops over time as it is supported by an increasing amount of positive feedback. By the same time an increase in relevant knowledge occurs. These two factors, the increasing amount of positive feedback and the increasing amount of relevant knowledge are thus confounded by nature.

Exp.1 and 2 suggested that the neural correlate of uncertain decisions, regardless of the attribution of uncertainty, is mesial BA 8. Based on these findings and results from other imaging studies (Elliott & Dolan, 1998; Goel & Dolan, 2000), it is assumed that this cortical substrate is particularly engaged in feedback-based hypothesis testing on valid SR-associations that leads to behavioral modifications. Furthermore, parametric effects in Exp.1 and 2 revealed that activation within mesial BA 8 decreased with increasing certainty. Certainty in experimental paradigms is supposed to be mediated via an increase of positive feedback which, in this context, indicates an increase in knowledge. For example, in hypothesis testing tasks an increase in positive feedback indicates the successful set-up of valid SR-rules according to which the task at hand can effectually be accomplished. Therefore, a real learning process is supposed to reduce activation within mesial BA 8.

In contrast, solely receiving an increasing amount of positive feedback independent from the actual response should not increase knowledge. This is because feedback in a so-called *pseudo learning process* does not allow to set-up a reliable knowledge base since it has no informative content.

Accordingly, if activation within mesial BA 8 actually depends on relevant knowledge, then exclusively an increase of relevant knowledge, indicated by positive feedback, should reduce activation within mesial BA 8. In contrast, an increase of solely positive feedback, simulating a learning process (pseudo learning), should not lead to an activation reduction within mesial BA 8.

Using the same experimental paradigm as in the preceding experiments, the third one set out to investigate whether an independent manipulation of knowledge and feedback would lead to different cerebral effects within mesial BA 8. A dissociation on the brain level was hypothesized such that activation within mesial BA 8 would solely be reduced by a real learning process but not by a pseudo learning process. For the real learning process a replication of the results of Exp.2 was expected such that real learning would induce activation both within mesial BA 8 and within WM networks. By using a subtractive design the different contributions of an increasing amount of knowledge and that of an increasing amount of positive feedback on activation within mesial BA 8 were investigated.

5.2 Method

5.2.1 Stimuli and task

In order to allow for a comparison between Exp.3 and Exp.2, only some features of the experimental paradigm were modified. As before, participants had to predict which of two concurrently presented stimuli would win in a virtual competition game. The same stimulus material was used as in Exp.1 and 2 but with two modifications. First, the shape of the UFO's was not relevant in the present paradigm and therefore it stayed the same throughout the entire experimental session. Second, within both remaining stimulus dimensions (i.e., color and figure dimension), all six possible pairings were generated by combining their four different levels (e.g., within the color dimension, the pairings red-yellow, red-blue, yellow-blue, yellow-green, blue-green, and red-green were presented).

In order to induce a *real learning* condition and a *pseudo learning* condition, participants were provided with differently valid feedbacks. The distinct feedback validity was unbeknown to the participants. In the real learning condition, one stimulus dimension represented a rule group consisting of six different sub-rules specifying the correct feedback. The six rules were valid throughout the experiment. Feedback depended on participants' response and was therefore informative in order to set-up valid SR-rules. In the pseudo learning condition participants were instructed that one stimulus dimension represented a rule group consisting of six different sub-rules. However, feedback was not specified by the rules but modeled according to a pre-determined reinforcement schedule relating trial number to feedback quality. Hence, feedback was uninformative in order to set-up valid SR-rules. The assignment of stimulus dimensions to either real learning or pseudo learning was balanced between participants.

In order to model a realistic time course of successful learning, i.e., the distribution of increasing positive respectively decreasing negative feedback over time, a learning model was extracted from pilot data. In the pilot study one group of participants learned the color rules, another group learned the figure rules. Since the learning curves did not differ significantly between the two groups $(F(3,16) = .58; p = .63)$, the two learning curves were averaged. The resulting distribution relating trial number to the value of the feedback was subsequently employed to simulate a learning process in the pseudo learning condition in the fMRI session.

In the real as well as in the pseudo learning condition participants were instructed to press the response button spatially corresponding to the stimulus they excepted to win (e.g., after the task cue “color rules are valid”, if the red stimulus will win against the blue, or conversely). In the control condition, pairings showed two identical stimuli (same color, shape, and figure). Three arrows in the middle of the screen indicated which of these two stimuli would win. Participants were asked to simply indicate the stimulus that was indicated by the arrows.

Modifications due to pilot data

As before, the implementation of the manipulation was tested in a pilot study. This was done to investigate whether the presence of the pseudo learning condition would deteriorate or even prevent successful learning in the real learning condition. Participants were instructed that the two conditions did not differ in any respect.

Ten volunteers (5 female, mean age 22.2, range 19-25 years) participated in the pilot study. A repeated measures ANOVA with the 2-level factor condition yielded a significant main effect for RT ($F(1,9) = 64.8; p < .0001$) such that participants were slower (in choosing their response) in the pseudo learning condition (mean $RT = 1217.3ms$, $SD = 151.8$) than in the real learning condition (mean $RT = 785.1ms$, $SD = 71.3$) The assumption that the presence of a pseudo learning effect would impair successful learning was proven to be incorrect. Participants learned the correct SR-rules in the course of the experimental session as indicated by a significant difference in the rate of correct responses against chance level in the fourth quartile ($t(9) = 19.4; p < .0001$). As well a repeated measures ANOVA with the 4-level factor quartile yielded a significant main effect for the rate of correct responses indicating a significant learning progress ($F(3,7) = 41.2; p < .0001$) (see Table 5.1).

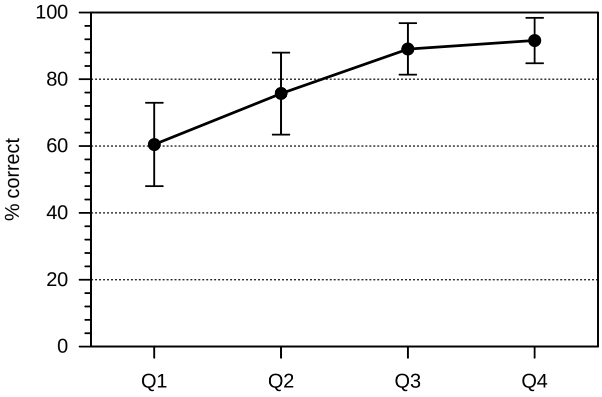

Figure 5.1: *The rate of correct responses for the real learning condition in the pilot study are plotted per quartile (20 blocks).*

However, after completion participants reported that *something was odd* with the pseudo learning condition. This feeling of oddness was not only supported by a significant difference in reaction times (as reported above) but also by a significant difference in uncertainty judgments with regard to response selection in the two conditions as revealed by a post-experimental survey (Wilcoxon signed-rank test: $Z = -2.7; p(1tailed) < .001$). After the experiment participants had to indicate their (un-) certainty in response selection with regard to the two rule groups on a fivefold graded ordinal scale of measurement. Generally, participants indicated a higher uncertainty in response selection in their respective pseudo learning condition. In order to determine whether the degree of the observed difference reflects a substantial one a non-parametric Wilcoxon signed-rank test was calculated. [1] Furthermore, as revealed by the post-experimental survey, nobody suspected the feedback to be invalid in the pseudo learning condition but anybody reported that it was very difficult and demanding to figure out the valid SR-rules in this condition.

Decelerated reaction times and the presence of “odd” feelings might be an indicator for higher uncertainty in decision making in the pseudo learning condition. However, it is also correct to assume, that odd feelings could eventually result in suspiciousness about feedback validity such that it might not be conceived of as self-induced. Subsequently, the attribution of success which is assumed to lead to a reduction in uncertainty would not occur. If this holds true, the contrast between real learning and pseudo learning would be confounded by the factor *attribution of success*.

In order to control for this possible confound, an additional control condition was prepared for the fMRI experiment. This condition resembled the pseudo learning condition but assured that feedback was conceived of as self-induced. Since this second control condition was designed as a hybrid between the pseudo learning and the control condition it was termed *pseuco* condition. Contrasting the pseuco condition with the pseudo learning condition should give information about a possible confounding effect of attribution of success with regard to activation within the region of interest, i.e., mesial BA 8. Accordingly, in the additional control condition participants were not required to learn something but to accomplish a perceptually very demanding task. By supplying an increasing amount of positive feedback, delivered according to a pre-determined reinforcement schedule, an improved perceptual performance was simulated. The feedback distribution in the pseuco condition correlated significantly with the feedback distribution employed in the pseudo learning condition ($r(pseuco/pseudo) = .89; p < .0001$). It was assumed that participants would experience an apparent learning progress because of an improvement of perceptual discrimination but without the need to set up a knowledge base of valid SR-rules. Due to the lack of decision rules, par-

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[1] This was done since the scale cannot be assumed to have the properties of an equal-interval-scale.

ticipants had no chance to control for the correctness of the supplied feedback. Therewith a suspiciousness about the feedback validity was prevented.

In the additional control condition, pairings showed two identical stimuli (same color, shape, and figure). Three of five arrows in the middle of the screen indicated which of these two stimuli would win. Participants were asked to simply indicate the stimulus that was indicated by the three arrows. Perceptual difficulty was induced by the presentation time of the arrows, i.e., all five arrows were presented for only 20ms. Participants were told that their performance would increase due to a significantly better perception by time, i.e., simply as a function of time. Note that participants were again completely ignorant about feedback validity.

As before, the additional control condition was tested in a pilot study. Six volunteers (3 female, mean age 24, range 23-25 years) participated in the pilot study. A query past the experiment revealed that all participants believed that their perception got better in the course of the experiment. This is supported by a significant decrease in reaction times over the course of the experimental session ($F(3,3) = 3.4; p = .044$). Therefore, it was inferred that participants attributed successful accomplishment to themselves.

For an overview over the interrelations of the experimental conditions and associated manipulated factors, see Table 5.1.

Table 5.1: *Interrelations between the employed conditions and the manipulated factors.*

		increase of ...	
Condition	...knowledge	...positive feedback	...success
real learning	yes	yes	yes
pseudo learning	no	yes	?
pseuco condition	no	yes	yes
control condition	no	no	no

5.2.2 Experimental design

The experimental design was identical to that used in Exp.1 and 2 with regard to presentation, time course, randomization, and jittering. Parallel to Exp.2 (but different to Exp.1) a verbal cue at the beginning of each block was presented to announce the respective experimental condition. Overall, 23 blocks were presented for the real learning, pseudo learning and pseuco condition, respectively, and 10 for the control condition, resulting in 79 blocks or 395 trials altogether.

5.2.3 Participants

Fifteen (10 female, mean age 25.9, range 23-33 years) right-handed, healthy volunteers participated in the fMRI experiment. After being informed about potential risks and screened by a physician of the institution, subjects gave informed consent before participating. The experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.

5.2.4 Procedure

The procedure was conducted as described in chapter 2.6.

5.2.5 Data analysis

In order to investigate whether activation within mesial BA 8 is reduced only by increasing the amount of knowledge or also by increasing the amount of positive feedback a subtractive design was realized. The conditions real learning, pseudo learning, pseuco, and control were all modeled as separate onset vectors within the same model. Contrast maps were generated that extracted the four effects of interest independently from each other. Accordingly, the following comparisons were carried out: First, it was tested for the main task effect for either real learning and pseudo learning. That is, testing the hypothesis that there is no activation within mesial BA 8 (the parameters for both conditions are the same) against the hypothesis that there is activation (the parameter for the respective learning condition is greater than that for the control condition). Only the contrast *real* *learning versus control condition* was expected to show a significant decrease of activation within mesial BA 8 over the course of the experiment. Second, in order to control for the factor attribution of success with regard to activation within mesial BA 8, a direct contrast between pseudo learning and the pseuco condition was calculated. In the case of no difference within mesial BA 8 between pseudo learning and the pseuco condition, the fourth comparison was calculated: In order to look at voxels where the difference between real learning and pseudo learning accounts for a significant amount of variance a direct contrast between the two conditions was calculated.

5.2.6 MRI data acquisition

The acquisition of the MRI data was conducted as described in chapter 2.6. One functional scan consisted of 1108 images and each image of 16 slices.

5.2.7 MRI analysis

All preprocessing and evaluation steps were calculated by using the software package LIPSIA (Lohmann et al., 2001) as described in chapter 2.4.

5.3 Results

5.3.1 Behavioral data

In Table 5.2 error rates for the real learning condition and RT for each condition are shown per quartile. In Figure 5.2 RT are plotted for each condition per quartile. One quartile consisted of 20 blocks, i.e., 100 trials. A repeated measures ANOVA with the 4-level factor condition yielded a significant main effect for RT ($F(3, 33) = 80.6; p < .0001$). Also the single contrast between real learning and pseudo learning yielded a significant main effect for RT, such that participants were slower in the pseudo learning condition than in the real learning condition ($(F1, 11) = 112.9; p < .0001$). RT in the pseuco condition as well as in the control condition decreased significantly over the course of the experiment (pseuco: $F(3,42) = 3.5; p = .024$; control: $F(3,42) = 4.7; p = .007$). This does not apply to the distribution of the RT in the real learning and pseudo learning condition, respectively (real learning: $F(3,42) = 2.6; p = .067$; pseudo learning: $F(3,42) = 1.8; p = .158$). Reaction times in the pseuco condition were faster in general since stimuli were presented for only 20ms and participants could respond as soon as the stimuli appeared. A learning effect was indicated by both a significant decrease of error rates over the course of the experiment ($F(3,42) = 5.1; p = .004$) (see Table 5.2) and a significant difference of the rate of correct responses against chance level in the fourth quartile ($t(14) = 5.0; p < .0001$). The distribution of decreasing negative feedback in the real learning condition correlated significantly with both employed learning models ($r(real/pseudo) = .72; p < .0001; r(real/pseuco) = .65; p < .0001$). Also, the two models simulating learning effects correlated significantly with each other ($r(pseudo/pseuco) = .89; p < .0001$) (see Figure 5.3).

Table 5.2: *Error rates (mean and SD in percent) for the real learning (RL) and reaction times (RT) (mean and SD in ms) per quartile (Q1-4) for real learning (RL), pseudo learning (PL), pseuco condition (PC), and the control condition (CC) in the fMRI experiment (*n*=15).*

	RL *Errors*	RL *RT*	PL *RT*	PC *RT*	CC *RT*
Q 1	38.6 (10.9)	1275.1 (119.4)	1237.3 (135.5)	959.1 (197.0)	776.9 (136.4)
Q 2	30.5 (16.6)	1199.0 (168.0)	1202.8 (159.3)	970.5 (143.8)	701.6 (123.4)
Q 3	32.4 (15.0)	1222.8 (183.8)	1193.9 (162.8)	947.1 (167.3)	717.8 (114.9)
Q 4	24.0 (18.1)	1194.0 (180.0)	1170.2 (206.7)	854.6 (167.1)	670.3 (122.0)

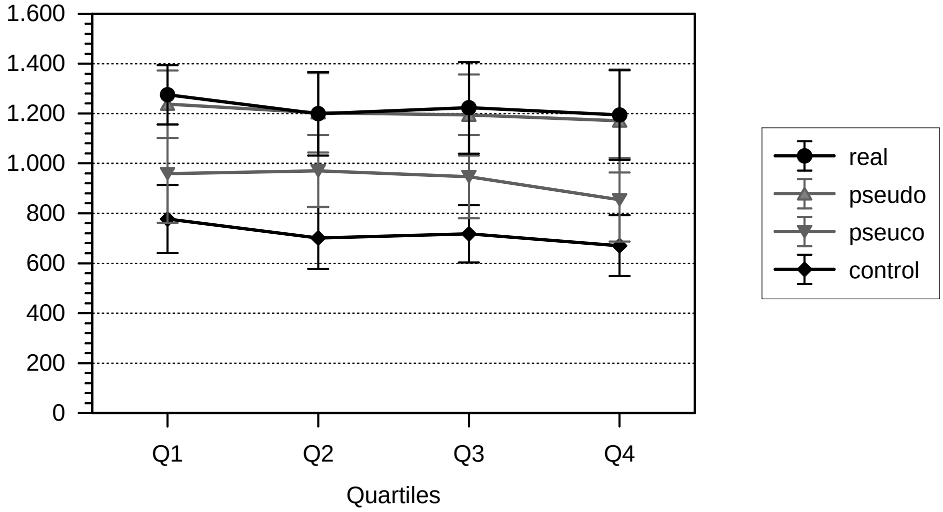

Figure 5.2: *Reaction times (RT) are plotted per quartile (20 blocks) for all conditions.*

5.3.2 Post-session survey

After completion of the functional session, confidence judgments were collected, i.e., participants were interviewed about their confidence in decision making over the course of the experiment with regard to each condition. Furthermore, they were asked to report in more detail what they thought and how they felt during the experimental session.

In general, all participants reported that the two conditions in which they were asked to figure out valid rules (real learning and pseudo learning) differed with respect to the experienced confidence in decisions. Participants indicated a higher uncertainty in response selection in pseudo learning as in real learning as indicated by a significant difference in (un-)certainty judgments (Wilcoxon signed-rank test: $Z = -2.2; p = .027$). All participants reported difficulties in identifying the valid rules in the pseudo learning condition. However, nobody suspected the feedback to be incorrect or invalid, rather they distrusted their memory of event occurrences and ability in drawing inferences. In unison, participants noticed that they acquired the rules in some way due to the increasing positive feedback. How-

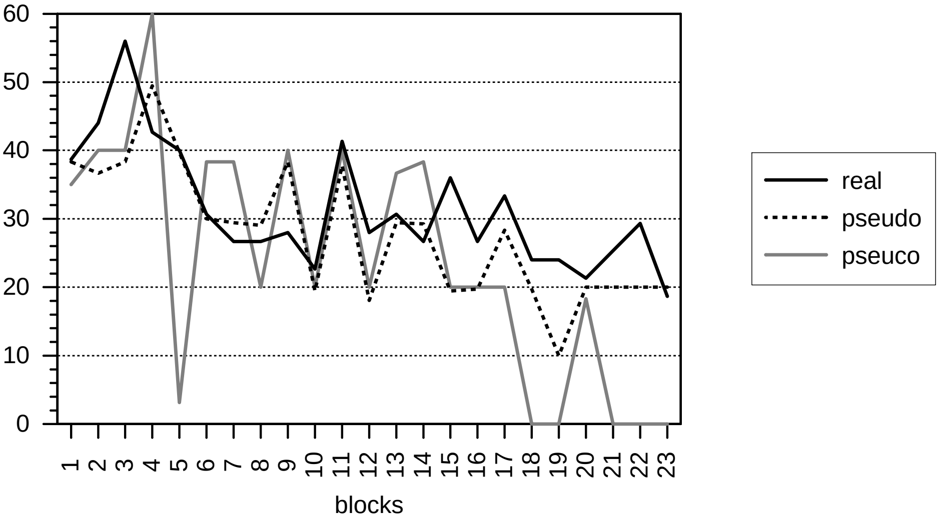

Figure 5.3: *The decreasing distribution of erroneous responses in the real learning condition and the modeled distributions of decreasing negative feedback for the pseudo learning condition and the pseuco condition are shown over the course of the experiment (1 block consisted of 5 trials).*

ever, they were astonished by the fact that they still made mistakes in the end and that they could not repeat the rules as fluently as in the real learning condition past the experimental session. Hence, introspective judgments did not indicate suspiciousness about the feedback validity in the pseudo learning condition. Also turned out by the survey was participants' ignorance about the nature of the feedback in the pseuco condition, i.e., participants really believed that their perception got better by time. Together, the survey revealed that the simulation of a pseudo learning process respectively the simulation of improved perception was highly effective.

5.3.3 MRI data

Effects of real learning

The main effect of task was tested by contrasting the real learning condition against the control condition. As shown in Table 5.3 and Figure 5.4, significant activations were found within the left posterior frontomedian cortex (mesial BA 8), the right pre-SMA, the left inferior prefrontal area (inferior frontal junction area (IFJ), i.e., at the cross-section of the inferior frontal sulcus and the inferior pre-central sulcus), bilaterally within the antero-superior insula, within the left posterior parietal cortex (along the banks of the intraparietal sulcus (IPS)), bilaterally within the precuneus, the left cuneus, dorsal premotor cortex, aqueduct, and the right cerebellum.

Table 5.3: *Anatomical specification, hemisphere, Talairach coordinates* (x, y, z)*, and maximal z-scores (Z) of significantly activated voxels in real learning versus control condition.*

Area	Hemisphere	x	y	z	Z
Frontomedian Cortex (mesial BA 8)	L	-5	19	44	**4.6**
Pre-supplementary motor area (pre-SMA)	R	1	6	53	**4.7**
Inferior frontal junction area (IFJ)	L	-41	7	38	**4.1**
Antero-superior Insula	L	-29	22	6	**4.0**
	R	34	18	12	**4.1**
Intraparietal sulcus (IPS)	L	-35	-51	44	**5.0**
Precuneus	L	-5	-68	53	**4.6**
	R	10	-71	23	**3.8**
Cuneus	L	-17	-74	15	**4.9**
Cerebellum	R	4	-68	-15	**3.8**
Aqueduct	L	-2	-35	-15	**4.0**
Dorsal premotor cortex	L	-26	-2	65	**4.1**

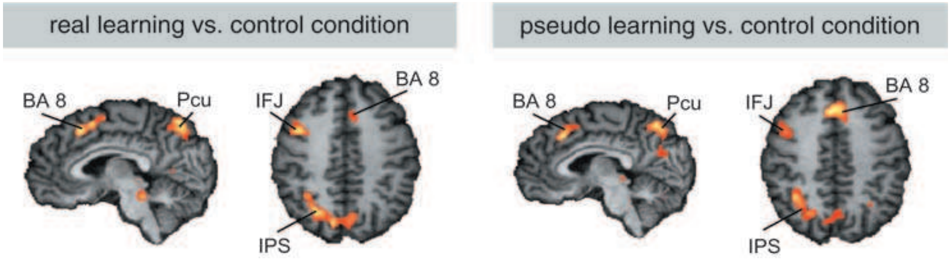

Figure 5.4: *The left panel shows the main task effect (Z* $>$ 3.09*) for real learning versus control condition; the right panel the main task effect for pseudo learning versus control condition. Group-averaged activations are shown on sagittal (x=-5) and axial (z=32;50) slices of an individual brain normalized and aligned to the Talairach stereotactic space. For activation coordinates see Table 5.3 and 5.4. Abbreviations: BA 8, mesial BA 8; Pcu, Precuneus; IFJ, inferior frontal junction area; IPS, intraparietal sulcus.*

Effects of pseudo learning

The main task effect of pseudo learning was tested by contrasting the pseudo learning condition against the control condition. As shown in Table 5.4 and Figure 5.4, significant activations were found within left mesial BA 8, the left IFJ, the left mid-portion of the middle frontal gyrus (MFG), bilaterally within the antero-superior insula, within the left posterior parietal cortex (along the banks of the IPS), the right precuneus, the left extra-striate visual area, the left parietoccipital sulcus, and dorsal premotor cortex.

Control for the attribution of success

In order to control for the factor attribution of success with regard to activation within mesial BA 8, a direct contrast between pseudo learning and the pseuco condition was calculated. As a result, no significant activation was found within the region of interest, i.e., mesial BA 8. Accordingly, since the factor attribution of success did not lead to different cerebral effects within mesial BA 8, the pseuco condition will be neglected in the following.

Table 5.4: *Anatomical specification, hemisphere, Talairach coordinates* (x,y,z)*, and maximal z-scores (Z) of significantly activated voxels in pseudo learning versus control condition.*

Area	Hemisphere	*x*	*y*	*z*	***Z***
Frontomedian Cortex (mesial BA 8)	L	-5	24	38	**5.0**
Inferior frontal junction area (IFJ)	L	-44	6	38	**3.9**
Middle frontal gyrus (MFG)	L	-41	22	29	**4.2**
Antero-superior Insula	L	-32	22	6	**4.3**
	R	34	18	9	**4.7**
Intraparietal sulcus (IPS)	L	-35	-51	44	**5.4**
Precuneus	R	4	-60	50	**4.4**
Extra-striate visual area	L	-17	-96	3	**4.3**
Parietoccipital sulcus	L	-20	-66	15	**3.7**
Dorsal premotor cortex	L	-26	0	53	**3.4**

Direct contrast between real learning and pseudo learning

The question if activation within mesial BA 8 is reduced only by increasing the amount of knowledge (real learning) or if activation is also reduced by increasing the amount of positive feedback (pseudo learning) was investigated by calculating a direct contrast between real learning and pseudo learning trials. The resulting contrast image contained contrast values describing the effective difference between these experimental conditions (i.e., the difference between the two means). As a result, the comparison between real learning and pseudo learning trials revealed no significant difference within any brain region.

In order to explore this finding of no difference with regard to the percent signal change in real learning and pseudo learning, the signal courses were analyzed. In order to attain this information, trial-averaged signal courses for each condition (and subject) were taken from a specified voxel within mesial BA 8, plus 8 adjacent neighbors within the same slice (2D). [2] Furthermore, differences between the minimum and maximum activation for real learning and pseudo learning were calculated. The minimum activation was sought in the time range of 0 to 5s and the maximum activation in the time range of 3 to 8s. These time ranges were chosen in accordance with reports about the usual time ranges of time-to-onset and time-to-peak (Neumann, Lohmann, Zysset, & von Cramon, 2003). It revealed that the signal courses of both conditions showed a significant, positive correlation ($r = .66; p = .01$) and that the differences between the minimum and maximum activation did not differ significantly ($t(14) = -.60; p = .56$).

5.4 Discussion

Exp.3 was designed to investigate whether activation in brain areas identified to be involved in higher and lower degrees of knowledge uncertainty is reduced exclusively by increasing the amount of knowledge or also by increasing the amount of positive feedback . Accordingly, it was investigated whether an alternative way to reduce activation within mesial BA 8 may be to increase the amount of solely positive feedback in the absence of knowledge acquisition.

5.4.1 Activation within mesial Brodmann Area 8

As a result, the activation patterns of real learning and pseudo learning did not differ in any respect. Accordingly, in contrast to the initial hypothesis it made no difference on the cerebral level whether activation within mesial BA 8 was reduced by increasing the amount of knowledge or by increasing the amount of positive feedback .

As revealed from Exp.1 and 2, mesial BA 8 can be taken to be particularly engaged in feedback-based hypothesis testing on valid SR-rules. Moreover, results from Exp.2 suggested that the more positive feedback is received indicating a successful set-up of SR-rules the less activation is elicited within mesial BA 8.

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[2] As a specified voxel the activation focus within mesial BA 8 from the main effect real learning was taken ($x = -5, y = 19, z = 44$).

As revealed from Exp.3, the increasing amount of positive feedback is sufficient to lessen activation within mesial BA 8 regardless of the objective possibility to set-up valid SR-rules. That is, an increased frequency of positive feedback is suggested to be powerful to lower uncertainty in decision making. This may be due to the fact that the supply of increasing positive feedback leads to an overconfidence in correctness, i.e., the overestimation of the likelihood of the favored hypothesis.

In general, the assessment of confidence or the degree of belief in a given hypothesis integrates different kinds of evidence, i.e., the strength of the evidence and its weight or predictive validity, respectively. The distinction between strength and weight of evidence is closely related to the distinction between the size of an effect (e.g., the difference between two means) and its reliability (e.g., the standard error of the difference) (Griffin & Tversky, 1992). One major finding of the literature on judgments under uncertainty indicated that subjects are often more confident in their judgments than it is warranted by the facts, i.e., being overconfident (Ayton, & McClelland, 1997; Griffin & Tversky, 1992; Sieck & Yates, 2001; Stone & Opel, 2000). Particularly, it has been shown that overconfidence results from the fact that subjects are more sensitive to the strength of evidence than to its weight (Griffin & Tversky, 1992). This means that subjects' confidence is determined by the balance of arguments for and against the competing hypotheses but with insufficient regard to the credence of the evidence. On the other hand, this mode of judgment leads to underconfidence when subjects undervalue the strength of evidence and overvalue the weight of evidence. For example, when evaluating a letter of recommendation for a student written by a former teacher two aspects of the evidence have to be considered: How positive is the letter and how credible is the writer? If it is focussed primarily on the positivity of the recommendation with insufficient regard to the credibility of the writer, overconfidence will occur. In contrast, if it is focussed mainly on the credibility of the writer with insufficient regard to the positivity of the recommendation, underconfidence will occur (Griffin & Tversky, 1992).

Accordingly, we suggest that in Exp.3 subjects' tendency to focus on the strength of evidence led to an undervaluation of the prior probability of the hypothesis in question. Consequently, the low or even nonexistent predictive validity of evidence could not be considered in the balance assessment of arguments. Subsequently, the degree of belief in a given hypothesis was not biased by information about the credence of evidence but strengthened by the increased frequency of positive outcomes.

Other explanations of overconfidence puts it down to unrealistic optimism (e.g., Weinstein, 1987, 1989) or wishful thinking (e.g., Babad, 1987; Harvey, 1992). According to this view, overconfidence is caused by the generalized tendency to overestimate the likelihood of positive outcomes and to underestimate the likelihood of negative outcomes. Yet, this assumption raises the question about the mechanisms responsible for producing this bias. Possibly, it could be due the recruitment process of arguments, i.e., the generation of arguments favoring the selected alternative in order to produce confidence judgments (Koriat, Lichtenstein, & Fischhoff, 1980). In Exp.3 participants experienced an increasing amount of positive feedback in all three experimental conditions except for the control condition in which the amount of positive outcomes stayed the same throughout the experiment (see Table 5.5). Therefore, it is highly probable that participants overestimated the likelihood of positive outcomes and underestimated the likelihood of negative ones. The recruitment process of arguments favoring the current working hypothesis is thus supported by an increasing amount of positive feedback. Subsequently, confidence in correctness is supposed to rise.

This assumption is supported by the finding that subjects' confidence in correctness increases with experience. Behavioral studies on motor skill tasks showed that the relationship between subjects' confidence in correctness and the length of practice seemed to depend more on subjects' expectation about the effects of practice than on the actual effects of practice (Harvey, 1994). A similar explanation may apply to our data too, such that the temporal duration of task performance influenced the confidence in correctness. In the pseudo learning condition both the expectation and the experience about the effects of practice (indicated by increasing positive outcomes) were validated. This may subsequently have produced an illusion of learning. The simulated improvement of skill and knowledge may thus

Table 5.5: *For the three conditions real learning, pseudo learning, and pseuco the ratios of* **correct** *to incorrect responses are listed per quartile (1 quartile consisted of 28 trials). Ratios of correct and incorrect responses in real learning and pseudo learning did not differ significantly (*$\chi^2(3,15) = .06; p = .99$*).*

	real learning			pseudo learning			pseuco condition		
quartile 1	**61**	:	39	**58**	:	42	**52**	:	48
quartile 2	**70**	:	30	**68**	:	32	**68**	:	32
quartile 3	**68**	:	32	**72**	:	28	**74**	:	26
quartile 4	**76**	:	24	**82**	:	18	**96**	:	4

have resulted in a reduction in decision conflict.

Further support comes from the clinical domain. Very early work by Jenkins and Ward (1965) on response-outcome contingency demonstrated that not the objective degree of control but the *proportion of positive outcomes* is the primary determinant of perception of control (see also Tennen, Drum, Gillen, & Stanton, 1982). That way, the subjective judgment of control is related to the probability of receiving the desired outcome rather than to the difference in outcome probabilities of all possible outcomes. The authors concluded that the perception of control should therefore be manipulable by systematically varying the frequency of non-contingent positive outcomes. This is exactly, what was done in Exp.3. Hence, it is assumed that the (manipulated) increased probability of desired, positive outcomes in the pseudo learning condition produced an illusion of control or an illusion of learning, respectively.

The presumption that the duration of task execution can influence (over-) confidence in performance is in conflict with the literature on judgments of learning (e.g., Koriat, 1997; Koriat, Sheffer, & Ma'ayan, 2002). According to the literature, the duration of task execution results in an *underconfidence-with-practice* (UWP) effect, i.e., an increased underconfidence in performance judgments despite a performance improvement (Koriat et al., 2002). Yet, the UWP effect is shown to occur with *repeated* practice. This means, still on the first presentation a tendency towards overconfidence was observed and only from the second presentation on a UWP effect (Koriat et al., 2002). Since these findings were mainly observed with the estimation of one's future recall performance of word lists, there is no clue for a temporal estimation from when on the UWP effect should be expected with hypothesis testing.

Together the monitoring of one's own performance via feedback could have led to an overconfidence and the illusion of knowing in real learning and pseudo learning. Consequently, knowledge uncertainty decreased. This is supported by the fact that the two conditions did not differ in their activation pattern within mesial BA 8. However, whether subjects' tendency to focus on the strength of evidence with simultaneous undervaluation of the weight of evidence is responsible for an (unduly) increase in certainty or rather the duration of performing a task remains to be elucidated in future studies.

5.4.2 Activation within dorsolateral and posterior parietal areas

As in Exp.2, significant activations, in addition to mesial BA 8, were found within the MFG, IFJ, and IPS.

Activations within the MFG and IFJ are in accordance with our prior hypotheses and results from previous imaging studies. The sustained monitoring and manipulation of feedback information across the experimental session was required in the present experiment in order to accomplish the task successfully. This demand, which is taken to be the key feature of tasks activating mid-dorsolateral prefrontal areas (MFG) (D'Esposito et al., 1998; Petrides, 2002), was instructed to apply to both real learning and pseudo learning. In the former as well as in the latter condition participants were required to implement appropriate task rules. This demand could be accomplished by updating task representations which has been shown to be reflected within the IFJ area (Brass & von Cramon, 2002; Nagahama et al., 2001).

Activations within posterior parietal areas are taken to maintain all SR-rules that are valid in an experimental session (Bunge et al., 2002) (see also 4.4.3). In Exp.2 it has been shown that different amounts of to be maintained SR-rules co-varied systematically with posterior parietal areas. Therefore, more activation within posterior parietal areas could have been expected for pseudo learning as compared to real learning (direct contrast) as the number of possible SR-rules, consistently reinforced by feedback, differed between the two conditions. In such a manner, that in pseudo learning the reduction of all possible SR-rules to a smaller set of the valid SR-rules was not as clear-cut and by expeditious means as in real learning. Therefore, pseudo learning could have been expected to draw more on posterior parietal areas than real learning. This assumption was indicated by an activation difference within the IPS for pseudo learning in the direct contrast (Talairach coordinates: $x = 22, y = -56, z = 38; Z = 3.7$; volume: $119 mm^3$). However, since the volume was less than 225 mm^3 (equivalent to 5 voxels), this activation was not considered as activated.

The involvement of WM networks in real learning as well as in pseudo learning are supposed to confirm that a typical coping strategy employed with perceived knowledge uncertainty constitutes in an intensive memory search, most likely in combination with the utilization of external information (Kahneman & Tversky, 1982).

Chapter 6

General discussion and future perspectives

The main findings of the experiments can be summarized as follows: First, uncertainty in decision making is reflected within mesial BA 8. Second, different variants of uncertainty entailing different coping strategies can be dissociated on the basis of additionally activated networks. And third, the evaluation of increasing positive feedback, not exclusively the acquisition of knowledge, reduces activation within mesial BA 8. Together, activation within mesial BA 8 appears to be engaged in setting up an environmental model that is tested and helps us to adapt our behavior stepwise and in a cumulative manner to the varying situational requirements. That way, mesial BA 8 can be conceived of as an area that tracks more or less uncertain outcomes with regard to an internal model and acts like a steering wheel that directs how uncertainty is dealt with.

In view of the existing literature and the employed paradigms, it is suggested that activation within mesial BA 8 on the one hand and activation within BA $32'/24'$ (often in company with pre-SMA) on the other are preferentially engaged in different decisions under uncertainty such that the former is elicited by well-defined problems whereas the latter is elicited by well-defined tasks. The present chapter will outline three major issues considering (1) the proposed fundamental difference between BA 8 activation as in contrast to BA $32'/24'$ activation, (2) in as much activation within mesial BA 8 can be differentiated from activation within anteriorly located BA 10, and (3) the final section comprises an outlook on worthwhile investiagtions in the near future.

BA 8 activation was found within a number of studies investigating uncertainty-related paradigms like detection and application of arbitrary SR-rules (Fletcher et al., 1999; Goel & Dolan, 2000; Goel et al., 1997; Knutson et al., 2003) or hypothesis testing (Elliott & Dolan, 1998). Uncertainty in these tasks as well as in the presently employed one is induced by cognitive difficulty. Although the initial state, the goal state and the operators (rules) which are used to transform one state into the other are clearly defined in the considered paradigms, the specific combination or sequence of the operators is not given or pre-determined. Rather, subjects have to logically reason how the difference between the initial state and the goal state is reduced in beeline. Aggravating is the fact when the operators are unknown and subjects have to figure out the operators in addition to the specific combination of those. A reduction of uncertainty can be achieved by a careful feedback evaluation. The returning information - presumed it is valid - signals whether or not the goal state is successfully achieved. By comparing different combinations of initial states and actions, common features of successful situation-responses-associations can be obtained resulting in the learning of a general strategy. Thus, this incremental solution approach is managed by an examination of drawn conclusions via feedback evaluation. According to the problem solving approach, all considered features meet the definition criteria for well-defined problems and at the same time for reflective decisions since the problem solving approach comprises the sub-process of decision making (compare 1.1.4).

In contrast, activation within BA $32'/24'$ (often plus BA 6) is found in a number of studies investigating uncertainty related paradigms like response conflict or error detection and error processing (e.g. Bunge et al., 2002; Garavan et al., 2002; Luks et al., 2002; Ruff et al., 2001; Ullsperger & von Cramon, 2001). These studies used paradigms like the Eriksen flankers task, speeded modified flankers tasks, or go/no go tasks. Uncertainty in these tasks is induced by time pressure or perceptual difficulty resulting in a co-activation of two response tendencies such that conflicts arise on the response level. Usually, the operators are known and instructed beforehand. That way, feedback does neither have to be sampled across trials nor does it provide new information but simply serves as an affirmative answer on a trial by trial basis. According to the problem solving approach, all considered features meet the definition criteria for well-defined tasks and at the same time for routinized or stereotype decisions.

Concluding, it appears that activation within mesial BA 8 is centrally involved in well-defined problems or reflective decisions, respectively. It is suggested that tasks requiring a sustained feedback-dependence of task performance will elicit activation within the posterior frontomedian cortex. In contrast, activation within BA $32'/24'$ has been shown to be centrally involved in well-defined tasks or routinized decisions, respectively. It is suggested that tasks requiring forced responses based on perceptual cues will elicit activation within BA $32'/24'$.

Accordingly, it is not peculiar to find BA 8 activation for errors compared to correct responses within some paradigms (Cools et al., 2002; Nieuwenhuis et al., 2003) and activation within BA $32'/24'$ for the same contrast within other paradigms (Carter et al., 1998; Ullsperger & von Cramon, 2001, 2003). The former investigated errors with probabilistic tasks, which we defined as reflective decisions, whereas the latter investigated errors in response conflict, which we defined as routinized decisions. Thus, it is suggested that errors occurring with decision conflicts draw on different brain areas than errors occurring with response conflicts.

In error research the determination of cognitive effort of an action is used to distinguish different types of errors, i.e., mistakes from action slips. Also in decision research the factor “cognitive effort” is used to distinguish more or less uncertain decisions. Relating the taxonomy of errors to the one of decisions, it is suggested that different types of decisions are associated with different kinds of errors such that reflective decisions generate mistakes, routinized decisions action slips. Action slips are defined as errors resulting from some failure in the execution and/or storage stage of an action sequence and can therefore be observed as externalized *actions-not-as-planned* (Reason, 1990). In contrast, mistakes are defined as "failures in the judgmental and/or inferential processes involved in the selection of an objective or in the specification of the means to achieve it" (Reason, 1990, p.9). That way, mistakes refer to complex errors which could only be solved with a substantial amount of cognitive effort. In contrast, action slips refer to simple errors, mostly movement errors, which can easily be corrected without much of cognitive effort. Reconciling mistakes and action slips with errors in different types of decisions-problems, it appears that errors in routinized or stereotype decisions signal for a failure in the execution of known decision rules or for a failure in the storage of heurisitcs, whereas errors in reflective decisions signal for a failure in the inferential process involved in the specification of the decision rules. Therefore, it is suggested that qualitatively different errors engage different brain areas.

Considering the existing literature and the present results we conclude that the posterior frontomedian cortex is involved in cognitive processes like feedback evaluation and hypothesis testing, i.e., tasks which require a sustained feedback evaluation of task performance. However, at first glance, this conclusion is in conflict with the proposition that mesial BA 10 is centrally involved in these very cognitive processes (for a review see Christoff & Gabrieli, 2000). It appeared that the anterior-most parts of the middle and superior frontal gyri are involved in reasoning tasks like the Tower of London task (TOL) (Baker et al., 1996), inductive reasoning tasks (Goel et al., 1997; Osherson et al., 1998), and the Raven's Progressive Matrices Test (RPM) (Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997).

It could be hypothesized that the cause for this difference is founded within the type of tested problem such that studies reporting BA 10 activation employed ill-defined problems whereas studies reporting mesial BA 8 activation employed well-defined problems. Several imaging studies reporting activation within BA 10 used tasks with a closed problem, i.e, clearly defined operators, and an open solution situation, i.e., an ill-defined goal state. By definition these ill-defined problems are divergent-production problems which are characterized by an open-endedness of the solutions and by a knowledge base specifying how to solve the problem. The open-endedness of the problem is induced by a lack of feedback. That way, participants cannot test whether or not their answer was correct. For example, due to the lack of feedback in the RPM participants stayed ignorant whether or not their analytic reasoning was correct. The lack of feedback could also give rise to the possibility that there is more than one correct answer or that the correct answer varies inter-individually depending on one's one internal reference system. The latter is supported by studies investigating evaluative judgments (Zysset, Huber, Ferstl, & von Cramon; Zysset et al., 2003) and coherence judgments (Ferstl & von Cramon, 2001, 2002) which found activation within the aMPFC. Feedback was delivered in neither study. Subjects were asked to judge statements with regard to personal preference (Zysset et al., 2002, 2003) or coherence (Ferstl & von Cramon, 2001, 2002), respectively. As subjects were not supplied with an objective reference system (which would have been confirmed by feedback) they had to assess the external stimulus on an internal scale. Studies investigating pleasantness judgments in which obviously no feedback could be given, also found activation within the aMPFC and related the activation to introspectively oriented mental activities (Gusnard et al., 2001).

However, inconsistent with our hypothesis is evidence suggesting that mesial BA 10 may also be involved in feedback evaluation (Elliott et al., 1997). Feedback evaluation is also a central component of the Wisconsin Card Sorting Test (WCST) and some studies using the WCST reported activation within BA 10 (Nagahama et al., 1996; Ragland et al., 1998). Elliott and co-workers (1997) investigated the neural response to feedback versus no feedback by using a version of the TOL. They found BA 10 activation when participants received feedback versus not receiving feedback. However, feedback was entirely *independent* from participants' response. Positive feedback was supplied in 100% or 80% of the cases, respectively, regardless whether or not the response was correct. A past-session survey revealed that all participants realized the feedback to be invalid. That way, participants had to engage in the evaluation of self-generated sequences of moves independent from the supplied feedback. Due to the invalidity of the feedback this kind of TOL resembled the TOL employed without feedback as inferences had to be made without an external reference system.

While reasoning tasks like the TOL or the RPM are designed to be workable without feedback the WCST is not. For example, in the RPM test subjects could engage in formal operations applied to sets and subsets of element features on each trial. Feedback is not needed to engage in the next trial in which another set of different element features has to be processed. Thus, the stimulus material and the operators are designed in a way that challenging processing is possible without feedback. The same applies to the TOL. In contrast, the WCST is not designed in a way that the task would be demanding on each trial without feedback. The critical feature of the WCST is the temporary rule change. Not until feedback is delivered the task is solvable. By employing this performance-dependent rule change (i.e., after a fixed number of correct trials, the rule is changed) the goal state is varying over the experimental session whereas the operators are identical. Hence, the WCST could be conceived of as a hybrid between well-defined and ill-defined tasks: Although the WCST has a closed problem and a closed solution situation the latter changes temporally making the definition of the goal state less definite. On the one hand the WCST resembles rule learning tasks like the presently employed one but on the other hand differs with respect to the additional demand to flexibly change rules. The latter implies that the decision from when on a negative feedback signals for a rule change is introspectively generated. This may be the reason why studies applying the WCST found activation within BA 10.

The considered reasoning tasks share a common substrate, namely the evaluation of self-generated responses or plans for actions. For example, in the TOL task the evaluation of self-generated sequence of moves is required, in inductive reasoning tasks the evaluation of self-generated hypotheses, in the RPM the evaluation of the plausibility of an argument, and in coherence or evaluative judgments the assessment of an external stimulus on an internal scale. Together, in all cases subjects evaluate information they have generated by themselves or retrieved. This assumption is supported by Gusnard and co-workers (2001) who specified the cognitive processes in which the (dorsal) aMPFC is involved as self-referential or introspectively oriented mental activities. These processes are required when non-routine cognitive strategies have to be generated and selected in novel situations. Considering classifications of decisions, ill-defined problems can be conceived of as constructive decisions. Concluding, it is suggested that activation within BA 10 is involved in self-referential evaluations and introspective thoughts (Gusnard et al., 2001; Zysset et al., 2003).

However, it needs further studies investigating well-defined and ill-defined problems which should be administered with and without feedback in order to test the proposed preliminary model. Furthermore, studies are needed that directly compare neural correlates of well-defined problems and well-defined tasks, at best within the same experimental paradigm. Another issue which is to be addressed is the dissociation of uncertainty and difficulty. A task is required in which both uncertainty and difficulty can parametrically be varied so as to disentangle the contributions of these two factors to cerebral activation.

The present results help to broaden the state of knowledge concerning neural correlates of uncertain decisions. Particularly, that different types of problems entailing different coping strategies may be crucial for the required brain networks. However, there are still more open questions than settled ones. For example, it has been shown that affective states have a highly important, yet little understood influence on how people think about, remember, and respond to social situations (Forgas, 2001). Recent research and theories illustrate how affective states can play a subtle and often subconscious role in guiding peoples’ thoughts, memories, judgments, attitudes and behaviors in social situations (Forgas, 1992). Moods can influence decisions as well as the structuring of cognitive material. In contrast to emotions, moods can be described as general and diffuse feelings which need not to be conscious. Generally, moods do not correspond to a specific goal and need not to be released by an event (Abele, 1991, 1992). Hence, although not knowing where from a specific mood is originating the person feels sad, depressive, cheerful or glad. Moods have been shown to influence the content as well as the process of cognition. In problem solving situations, subjects in a positive mood tend to use simplifying strategies and are quicker in decision making than neutrally tempered subjects (Isen & Means, 1983) whereas subjects in a negative mood tend to use more analytic strategies (Schwarz, 1990). Dependent on the task and context both of these strategies could yield good decisions. In general, negative moods could foster an analytic, precise, and detail-oriented processing whereas positive moods could foster simplifying and flexible processing as well as the use of heuristics (Forgas, 1992). It would be interesting to investigate whether or not this behavioral dissociation is also reflected on the brain level. For example, well-defined problems that require analytic strategies should be be more successfully solved by negatively tempered subjects than by positively tempered subjects. According to our hypothesis, subjects in a negative mood should elicit lower activation within frontomedian areas than subjects in a positive mood since the use of appropriate (analytic) strategies should decrease uncertainty.

Another interesting issue would be the investigation of uncertain judgments as compared to uncertain decisions. In general, decisions are made with regard to the expected consequences. This implies an implicit or explicit assessment of the consequences. The resulting evaluative or preference judgments are usually not observable, but the choice for a specific option are (Jungermann et al., 1998). Consequently, it could be assumed that judgments determine the choice for a specific option. However, in the words of Einhorn and Hogarth, judgment “is neither necessary nor sufficient for choice” (1981, p.73). The traditional assumption that judgment and choice are equivalent was proven to be incorrect by the fact that many heuristics yield a choice among options without providing evaluations of each alternative (Payne et al., 1993). Furthermore, the finding of the so-called *preference reversals* called the equivalence of judgment and choice into question. In short, preference reversal describes the robust finding that expressed preferences can be reversed depending upon whether a choice or judgment response is used. Although there are several explanations for this phenomenon, its cause is placed at the fact that variations in response mode cause a fundamental change in the way people process information.

From this it follows that it would be worthwhile to investigate whether or not uncertain judgments would involve the same brain areas as uncertain decisions.

For example, one could compare brain correlates of judgments about uncertain gambles to choices of uncertain gambles. To use judgments and choices of gambles is advised since there are objective dimensions, such as the amount and the probability of winning, which can be used to determine more or less uncertainty in judgments and choices. It could be hypothesized that choices of uncertain gambles should draw on different brain areas than judgments of uncertain gambles since different information procedures are proposed for these two response modes (Payne et al., 1993). Information processing in the choice mode is assumed to be primarily dimensional whereas processing in the judgment mode is assumed to be primarily alternative. In a dimensional-based procedure each dimension of one option is compared with the same dimension of another option whereas in an alternative-based procedure one item of information about one alternative is used as an anchor and subsequently this anchor is adjusted to take additional information into account. Hence, it will be interesting to investigate whether the behavioral response mode effect will be reflected by differential brain activations. That is, whether or not a change in the strategy for processing information as a function of the response mode will be related to different cerebral effects.

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List of Figures

List of Tables

Index

Abbreviations

ANOVA	Analysis Of Variance
BA	Brodmann Area
BOLD	Blood-Oxygen-Level-Dependent
EPI	Echo-Planar-Imaging
EU	Externally attributed Uncertainty
fMRI	functional Magnetic Resonance Imaging
FWHM	Full Width at Half Maximum
GLM	General Linear Model
IU	Internally attributed Uncertainty
MDEFT	Modified Driven Equilibrium Fourier Transform
MRI	Magnetic Resonance Imaging
NMR	Nuclear Magnetic Resonance
PET	Positron Emission Tomography
pFMC	posterior Frontomedian Cortex
rCBF	regional Cerebral Blood Flow
rCBV	regional Cerebral Blood Volume
RF	Radio-Frequency
SPM	Statistical Parametric Map
T	Tesla

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BRAIN CORRELATES OF UNCERTAIN DECISIONS

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Paper Behavioral studies showed that in decision making both the attribution of uncertainty (to internal or external factors) and the degree of uncertainty (low or high) bias our coping strategies. Externally attributed uncertainty (EU) is mostly reduced by the attempt to rate the probability of event occurrence, whereas internally attributed uncertainty (IU) is mostly reduced by the attempt to increase the amount of relevant knowledge, which is, in an experimental situation, typically accompanied by an increasing amount of positive feedback. On the basis of these findings, three functional Magnetic Resonance Imaging studies were conducted to investigate brain correlates of EU and IU, the reduction of the latter, and in as much brain correlates of EU differ from those induced by IU. With regard to reduction of IU, it was aimed to dissociate effects of increasing knowledge and effects of increasing positive feedback.

As a result, parametric analyses revealed that activation within the posterior frontomedian cortex (pFMC) increased with increasing uncertainty, no matter for which reason uncertainty emerged. However, increasing EU yielded additional activation within a sub-cortical network which is known to sub-serve dopaminergic modulations of the frontomedian cortex. In contrast, increasing IU elicited additional activation within areas underlying working memory processes. Both the increase in knowledge and positive outcomes elicited activation within the pFMC. Thus, uncertainty reduction is not exclusively dependent on the increasing amount of relevant knowledge but on the increasing amount of positive feedback. Present findings show, that the brain reflects for which reason we are uncertain. Correlates of uncertainty appear to reflect the evaluation of feedback in view of a to-be-tested model of valid stimulus-response-rules.

Selbstständigkeitserklärung

Hiermit erkläre ich, daß die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und daß die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

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Measurement of the Self-Diffusion Tensor of Water in the Human Brain

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Detektion und Quantifizierung von Hirnaktivität mit der funktionellen Magnetresonanztomographie

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Lokalisierung an internen Kontrollprozessen beteiligter Hirngebiete mithilfe des Aufgabenwechselparadigmas und der ereigniskorrelierten funktionellen Magnetresonanztomographie

18 Karsten Steinhauer

Hirnphysiologische Korrelate prosodischer Satzverarbeitung bei gesprochener und geschriebener Sprache

19 Silke Urban

Verbinformationen im Satzverstehen

20 Katja Werheid

Implizites Sequenzlernen bei Morbus Parkinson

21 Doreen Nessler

Is it Memory or Illusion? Electrophysiological Characteristics of True and False Recognition

22 Christoph Herrmann

Die Bedeutung von 40-Hz-Oszillationen für kognitive Prozesse

23 Christian Fiebach

Working Memory and Syntax during Sentence Processing.
A neurocognitive investigation with event-related brain potentials and functional magnetic resonance imaging

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Lokalisation von Doppelaufgabendefiziten bei gesunden älteren Personen und neurologischen Patienten

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26 Ulrich Müller

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Kontrollfunktion des Arbeitsgedächtnisses über interferierende Information

28 Ina Bornkessel

The Argument Dependency Model: A Neurocognitive Approach to Incremental Interpretation

29 Sonja Lattner

Neurophysiologische Untersuchungen zur auditorischen Verarbeitung von Stimminformationen

30 Christin Grünewald

Die Rolle motorischer Schemata bei der Objektrepräsentation:
Untersuchungen mit funktioneller Magnetresonanztomographie

31 Annett Schirmer

Emotional Speech Perception: Electrophysiological Insights into the Processing of Emotional Prosody and Word Valence in Men and Women

32 André J. Szameitat

Die Funktionalität des lateral-präfrontalen Cortex für die Verarbeitung von Doppelaufgaben

33 Susanne Wagner

Verbales Arbeitsgedächtnis und die Verarbeitung ambiger Wörter in Wort- und Satzkontexten

34 Sophie Manthey

Hirn und Handlung: Untersuchung der Handlungsrepräsentation im ventralen prämotorischen Cortex mit Hilfe der funktionellen Magnet-Resonanz-Tomographie

35 Stefan Heim

Towards a Common Neural Network Model of Language Production and Comprehension: fMRI Evidence for the Processing of Phonological and Syntactic Information in Single Words

36 Claudia Friedrich

Prosody and spoken word recognition: Behavioral and ERP correlates

37 Ulrike Lex

Sprachlateralisierung bei Rechts- und Linkshändern mit funktioneller Magnetresonanztomographie

38 Thomas Arnold

Computergestützte Befundung klinischer Elektroenzephalogramme

39 Carsten H. Wolters

Influence of Tissue Conductivity Inhomogeneity and Anisotropy on EEG/MEG based Source Localization in the Human Brain

40 Ansgar Hantsch

Fisch oder Karpfen? Lexikale Aktivierung von Benennungsalternativen bei der Objektbenennung

41 Peggy Bungert

Zentralnervöse Verarbeitung akustischer Informationen
Signalidentifikation, Signallateralisation und zeitgebundene Informationsverarbeitung bei Patienten mit erworbenen Hirnschädigungen

42 Daniel Senkowski

Neuronal correlates of selective attention: An investigation of electrophysiological brain responses in the EEG and MEG

43 Gert Wollny

Analysis of Changes in Temporal Series of Medical Images

44 Angelika Wolf

Sprachverstehen mit Cochlea-Implantat: EKP-Studien mit postlingual ertaubten erwachsenen CI-Trägern