

## Frontomedian activation depends on both feedback validity and valence: fMRI evidence for contextual feedback evaluation

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Activation within the posterior frontomedian cortex (pFMC) is suggested to be involved in decision conflict, which typically emerges whenever one does not know which action to choose in order to receive a positive outcome. Decision conflict attenuates due to learning which is often indicated by and therefore confounded with the receipt of increasingly frequent positive and decreasingly frequent negative feedback. The present functional Magnetic Resonance study aimed to disentangle the influence of the factors processing of negative feedback and contextual feedback evaluation on pFMC activation. Participants performed a forced choice paradigm in which they had to decide which one out of two competing stimuli would win in a virtual competition game. In one condition (rule learning, RL), participants were provided with valid feedback so that contextual feedback evaluation had a guiding function for action and thus enabled learning. In contrast, participants received no valid information from feedback in another condition (putative learning, PL) and hence could not learn on the basis of contextual feedback evaluation. However, a learning effect in the latter condition was simulated by gradually increasing the frequency of positive feedback and decreasing the frequency of negative feedback according to a learning model which was derived from pilot data. Importantly, participants were naive with respect to feedback manipulations. Beyond confirming pFMC activation for decision conflicts, a significant interaction between validity and valence of feedback in pFMC revealed the specific contribution of contextual feedback evaluation processes on activation of this area. Not the processing of negative feedback per se, which was found to elicit activation within anterior cingulate cortex, but the evaluation of feedback against the background of the current mental model is suggested to be reflected by pFMC activation.

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### Introduction

In everyday life, we often have to decide under uncertainty due to incomplete knowledge, and by gathering and evaluating external

information, we try to resolve this uncertainty. Feedback operationalizes this information in real life situations as well as in experimental learning paradigms. Generally speaking, feedback is information about how far one has progressed toward a goal. Feedback is hence a *relational concept*: it can only be interpreted with reference to a goal and with reference to previous feedback information. Behavioral consequences following this contextual feedback evaluation depend on the feedback valence: negative feedback signals for a behavioral or strategic change, whereas positive feedback serves as a “keep-at-it” signal and thus leads to the development of a preference for one option over time.

However, since any learning or performance improvement depends on contextual feedback evaluation against the background of previous (feedback) experiences, the receipt of decreasingly frequent negative feedback and the decreasing demand on contextual feedback evaluation are necessarily confounded in our everyday life as well as in the experimental situation. Hence, it is not clear whether activation in a region suggested to reflect uncertainty in decision making, the posterior frontomedian cortex (pFMC), is elicited because of the processing of negative feedback per se or because of ineffective (and therefore constantly high) contextual feedback evaluation as how to adapt behavior. The present functional Magnetic Resonance Imaging (fMRI) study set out to disentangle these two factors. Using the same rule learning paradigm as in a previous fMRI experiment (Volz et al., 2004) and by modeling the feedback phase, we particularly aimed to investigate if activation within pFMC reflects the processes of contextual feedback evaluation against the background of previous experiences or whether uncertainty related activation derives from the processing of negative feedback per se. By manipulating feedback validity but not the frequency of negative feedback in a learning situation, we designed a condition in which contextual feedback evaluation had no guiding function for action and hence could not lead to a coherent knowledge base. The feedback distribution of invalid feedback in this condition was predetermined and modeled according to a learning curve drawn from a preceding learning study (on the same material). We termed this condition putative learning (PL) as participants were provided with decreasingly frequent negative feedback thus leading to the impression to learn despite invalid feedback. In contrast, in another

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condition, which we termed rule learning (RL) condition, participants could learn valid decision rules by means of valid feedback.

A replication of previous results (Volz et al., 2004) was expected for the RL condition as well as for the PL condition, i.e., we predicted that uncertain decisions relative to a neutral control condition would elicit increased activity within the pFMC, dorso-lateral prefrontal and posterior parietal areas. However, specific contributions as to the question whether pFMC activation reflects the processing of negative feedback per se or rather contextual feedback evaluation processes could exclusively be revealed by the interaction of feedback validity by feedback valence indicating differential feedback processing subject to feedbacks' contextual utility. This effect was tested by an interaction contrast with the factors' feedback VALIDITY and feedback VALENCE. Feedback valence was expected to affect the anterior cingulate cortex (ACC), an area which is suggested to reflect the detection of unfavorable outcomes or response errors (Garavan et al., 2003, 2004; Ridderinkhof et al., 2004; Ullsperger and von Cramon, 2001, 2004), rather than pFMC. Hence, for contrasting negative with positive feedback trials (main effect of the factor feedback VALENCE), activation was expected within ACC but not in pFMC.

These hypotheses were developed based on the assumption that participants trust in feedback validity. If feedback in PL would not be taken seriously and thus leading to a disregard of feedback information, activation differences between PL and RL (which were presumed within pFMC) could not be unambiguously attributed to effects of differential feedback validity. In order to control for this possible effect, we employed a perceptual putative learning (PPL) condition with a distribution of invalid feedback parallel to PL. By manipulation and instruction, we ensured that feedback in PPL was taken seriously. Participants' decisions in the PPL condition were based on very briefly flashed cues (20 ms) and participants were instructed that they would learn and improve their performance on a purely perceptual basis even if they could not consciously identify the briefly flashed cues. In a first step, the conditions PPL and PL were compared. Only if this contrast would not yield significant activation within pFMC could we exclude trust in feedback to be influential on this area. Hence, potential activation differences between PL and RL could then be interpreted without potential confounds due to the effects of disregarding the feedback. Subsequently, we could calculate the contrast between the conditions RL and PL.

## Materials and methods

### Participants

Fifteen (10 female, mean age 25.9, range 23–33 years) right-handed, healthy volunteers participated in the fMRI experiment. Informed consent was obtained from each participant according to the declaration of Helsinki. Experimental standards were approved by the local ethics committee of the University of Leipzig. Data were handled anonymously.

### Stimuli, task, and experimental session

Stimuli consisted of comic pictures showing UFOs differing either in color or figure (see Fig. 1). Four different colors and

figures were employed. Within each trial, two UFOs were concurrently presented, one on the right and one on the left side of the screen (degrees of visual angle: 2.0). Participants had their index fingers on a left and a right response button, spatially corresponding to the stimulus locations on the screen. One pair of UFOs was presented for 2 s during which participants' response was recorded. Subsequently, a feedback was presented for 1.5 s. The experimental session was designed such that participants were presented with blocks of five trials of the same experimental condition, which was announced by a verbal task cue of 5 s. The inter-block-intervals were 5 s and these also constituted the non-events. In all experimental conditions, participants' task was to indicate which of the two concurrently presented UFOs would win in a virtual competition game. When the stimulus pair came up, participants were instructed to press the response button spatially corresponding to the UFO they expected to win. The response phase was restricted to the presentation time of the stimuli, i.e., 2 s. Feedback showing a masking beyond recognition of both UFOs indicated that the subject had decided in favor of the loser (negative feedback) whereas the presentation of the entire chosen UFO and the masking beyond recognition of the non-chosen UFO indicated that the subject had decided in favor of the winner (positive feedback). The feedback following late responses (time outs) was identical to the negative feedback, i.e., both stimuli were masked.

In the *rule learning condition* (RL), participants were asked to detect valid decision rules as depended on stimulus attribute. In order to choose the winning UFO participants had to learn pairings where one attribute trumped another attribute (see Table 1). For example, if a red and a green UFO were concurrently presented, participants learned that the red UFO trumps the green one in this particular pairing. As four different attribute values were used, six different pairings could be generated which were valid throughout the entire experimental session, e.g., red always trumped green if presented concurrently. Feedback in RL depended on participants' response and was therewith valid. Thus, participants could learn the pairings by contextual feedback evaluation. For half of the participants, the pairings of the colored UFOs were decisive in order to learn the rules; for the other half, the pairings of the figures were the determining factor.

Parallel to RL, in the *putative learning condition* (PL), participants were asked to detect valid decision rules as depended on stimulus attribute. However, participants could not learn the pairings by contextual feedback evaluation as feedback was independent from their response but modeled according to a pre-determined feedback schedule relating trial number to feedback valence. This schedule modeling a realistic learning curve was derived from a pilot study in which a different group of participants learned the different UFO pairings by valid feedback. That way, the presentation of feedback  $x$  at timepoint  $t_x$  was entirely pre-determined so that participants' response had no influence on the specific feedback presentation. Accordingly, PL and RL differed only in feedback validity and therewith in feedbacks' guiding function. Important to note, feedback validity was manipulated unbeknownst to participants.

In the *perceptual putative learning condition* (PPL), pairings showed two identical UFOs (presented for 2 s) and additionally five arrows in the middle of the screen which were presented for only 20 ms. Three of the five arrows pointed in the direction of the winning UFO, the other two arrows pointed in the opposite direction. Participants were asked to choose the UFO which was

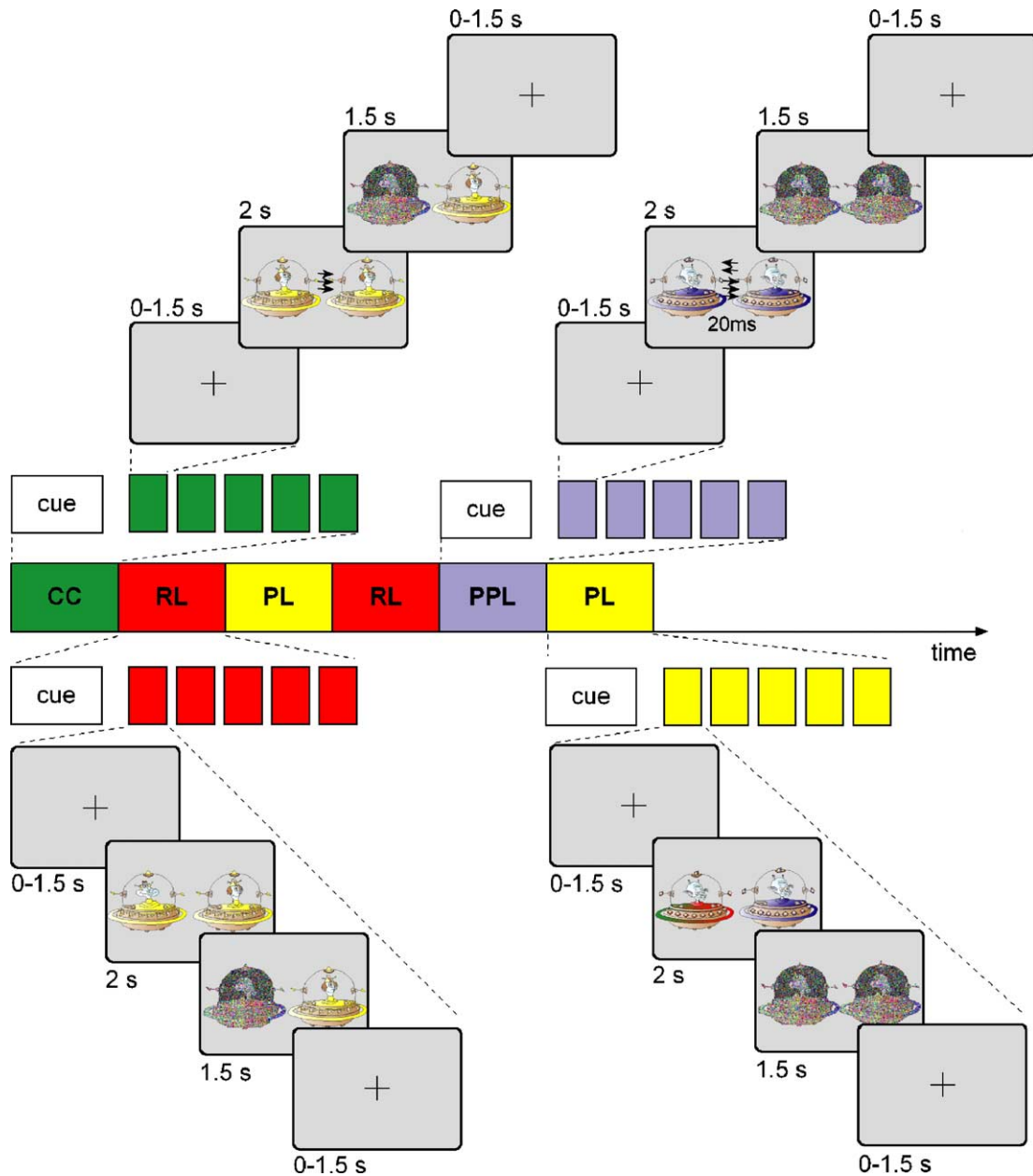


Fig. 1. Example of the stimulation: blocks with different experimental conditions (color-coded) were presented in randomized order (RL: rule learning, PL: putative learning, PPL: perceptual putative learning, CC: control condition). One block consisted of a verbal task cue (5 s) and 5 trials of the same experimental condition. Each trial started with a variable jitter time of 0, 500, 1000, or 1500 ms which was followed by a fixed stimulus presentation of 2 s, during which participants' response was recorded, and a fixed feedback presentation of 1.5 s. The five arrows in condition PPL were presented for 20 ms only. On the left hand panels, positive feedback is shown; on the right hand panels, negative feedback is shown.

indicated by the three arrows. Parallel to PL, feedback in PPL was independent from participants' response but modeled according to a learning curve which was derived from pilot data. Participants were naive in this respect but instructed that their performance would improve on a purely perceptual basis even if they could not consciously identify the briefly flashed arrows.

In the *control condition* (CC), pairings showed two identical UFOs and additionally three arrows in the middle of the screen for 2 s. All three arrows definitely indicated in the direction of the winning UFO. Participants were simply asked to choose the indicated stimulus.

For conditions RL, PL, and PPL, 23 blocks were presented each and 10 blocks for the control condition. Each block consisted of a cue presented for 5 s and 5 consecutively presented trials each of which lasting 5 s (see Fig. 1). Blocks were presented in randomized order, and the order was balanced between participants. Trials were balanced with regard to the probability of transition. In order to increase the temporal resolution of the BOLD-response, trials were presented with variable onset delays, i.e., each trial started with a variable jitter time of 0, 500, 1000, or 1500 ms (average 750 ms). This variable jitter time was followed by a fixed stimulus presentation of 2 s and a fixed feedback presentation of 1.5 s. Accordingly, the

Table 1  
Pairings of valid decision rules as dependent on stimulus attribute

Color as the decisive attribute	Figure as the decisive attribute
Red trumps yellow	A trumps B
Yellow trumps blue	B trumps C
Green trumps blue	A trumps C
Yellow trumps green	D trumps A
Red trumps green	C trumps D
Blue trumps red	D trumps B

A, B, C, and D indicate different figures.

average stimulus-onset-asynchrony (SOA) was 5 s, and the average inter-stimulus-interval (ISI) 1.5 s.

### Imaging

Imaging was performed at 3T on a Bruker Medspec 30/100 system equipped with the standard bird cage head coil. Slices were positioned parallel to the bi-commissural plane (AC-PC) with 16 slices (thickness 5 mm, spacing 2 mm) covering the whole brain. A set of 2D anatomical images was acquired for each participant immediately prior to the functional experiment, using an MDEFT sequence (256 × 256 pixel matrix). Functional images in plane with the anatomical images were acquired using a single-shot gradient EPI sequence (TE = 30 ms, 64 × 64 pixel matrix, flip angle 90°, field of view 19.2 cm) sensitive to BOLD contrast. During each trial, 2 images were obtained from 16 axial slices at the rate of 2.5 s. 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.

### Data analysis

The MRI data were processed using the software package LIPSIA (Lohmann et al., 2001). Functional data were corrected for motion artifacts using a matching metric based on linear correlation. To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation was applied. A temporal highpass filter with a cut-off frequency with 1/170 Hz was used for baseline correction of the signal and a spatial Gaussian filter with 5.65 mm FWHM was applied. The anatomical slices were co-registered with the full brain scan that resided in the stereotactic coordinate system and then transformed by linear scaling to a standard size. The transformation parameters obtained from this step were subsequently applied to the functional slices so that the functional slices were also registered into the stereotactic space. This linear normalization process was improved by a subsequent processing step that performed an additional nonlinear normalization (Thirion, 1998). Slice-gaps were scaled using a trilinear interpolation, generating output data with a spatial resolution of 3 × 3 × 3 mm (27 mm<sup>3</sup>).

The statistical evaluation was based on a least-squares estimation using the general linear model (GLM) for serially autocorrelated observations (random effects model; Friston, 1994; Friston et al., 1995; Worsley and Friston, 1995). An event-related design was implemented, i.e., the hemodynamic response function was modeled by means of the experimental conditions for each stimulus (event = onset of feedback presentation). 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 6 s. The model equation including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley and Friston, 1995). Contrast images, i.e., estimates of the raw-score differences between specified conditions were generated for each subject. The single subject contrast images entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample *t* test across the contrast images of all subjects that indicated whether observed differences between conditions were significantly different from zero. Subsequently, *t* values were transformed into *Z* scores. To protect against false positive activations, only regions with *Z* score greater than 3.1 ( $P < 0.001$ ; uncorrected) and with a volume greater than 225 mm<sup>3</sup> (5 voxels) were considered.

As the main goal of the present study was to investigate brain activity related to feedback processing subject to its contextual utility, we differentiated between positive and negative feedback trials in conditions RL and PL and modeled them as different events. Trials in condition PPL and CC were not dissociated but modeled as single events. These six conditions and one condition modeling the null events entered the GLM.

## Results

### Behavioral results

For condition RL, we found a learning effect as indicated by both a significant increase of correct responses over the experimental session ( $F(4,56) = 7.1$ ;  $P < 0.0001$ ) as well as by a significant difference of the rate of correct responses against chance level in the last quintile ( $t(14) = 5.4$ ;  $P < 0.0001$ ; see also Table 2). A learning effect in the condition RL also revealed when reaction times (RT) were taken as a measure of performance (RT of correct responses:  $F(4,56) = 3.88$ ,  $P = 0.008$ ; overall RT:  $F(4,56) = 3.14$ ,  $P = 0.02$ ). This effect was not paralleled in the condition PL: overall RT did not decrease as a function of learning across quintiles ( $F(4,56) = 2.23$ ,  $P = 0.08$ ). As the classification of correct and incorrect responses in the condition PL was pre-determined, it is neither possible nor reasonable to take correct responses as an

Table 2  
Mean reaction times (RT, in ms) of correct responses in condition rule learning (RL), mean RT of all responses in condition RL and putative learning (PL), and percentage of correct responses in RL

	RT RL correct	RT RL all	RT PL all	RL correct
Quintile 1	1306.043 (33.893)	1276.531 (31.212)	1255.519 (39.498)	56.841 (2.691)
Quintile 2	1262.226 (42.864)	1235.647 (39.008)	1208.743 (41.532)	69.778 (4.175)
Quintile 3	1188.495 (9.813)	1171.554 (54.224)	1218.508 (44.049)	65.556 (4.876)
Quintile 4	1249.101 (49.476)	1239.325 (47.563)	1169.341 (41.910)	70.000 (3.442)
Quintile 5	1211.518 (42.805)	1193.963 (46.481)	1174.369 (55.649)	75.000 (4.663)

indicator for learning. A perceptual learning effect in the condition PPL was not present as the rate of objectively correct responses in the condition PPL did not increase across quintiles ( $F(4,56) = 2.0$ ;  $P = 0.11$ ); furthermore, the rate of objectively correct responses in the last quintile did not differ significantly from performance at chance level ( $t(14) = 0.93$ ,  $P = 0.37$ ). RT data paralleled this result: no significant decrease of RT of objectively correct responses across quintiles revealed ( $F(4,52) = 1.16$ ,  $P = 0.34$ ). In the conditions PL and PPL, pre-determined feedback schedules were implemented in order to simulate regular learning effects. Both dummy learning models correlated significantly with each other ( $r(\text{PL}/\text{PPL}) = 0.89$ ;  $P < 0.0001$  (1-sided)) as well as with the actual learning curve in RL as measured by the rate of correct responses over time ( $r(\text{RL}/\text{PL}) = 0.72$ ;  $P < 0.0001$  (1-sided);  $r(\text{RL}/\text{PPL}) = 0.64$ ;  $P < 0.0001$  (1-sided)).

In a post-session survey, participants were asked for their confidence ratings in decision making in condition RL and PL, for their impressions with regard to learning effects, and for their suspiciousness in feedback validity. Confidence ratings in PL and RL revealed to be significantly different such that a higher decision uncertainty was experienced in PL than in RL (Wilcoxon signed-rank test:  $z = -2.2$ ;  $P = 0.027$ ). Twelve of the fifteen participants reported that their performance in PPL with regard to their perception of the briefly presented arrows increased over time. None of the participants reported not having been able to identify the arrows. Despite participants' inability to name the valid decision rules in condition PL and their uncertainty in decision making in this condition, they nevertheless had the impression having learned something. Participants inferred this because of the increasingly frequent positive feedback they received. Finally, none of the participants reported suspiciousness in feedback validity, neither in PL nor in PPL.

#### MRI data

Firstly, the two learning conditions with invalid feedback were compared by directly contrasting PL- and PPL-trials. Only if this contrast would not yield significant activation within pFMC could we interpret potential differences in pFMC activation between PL and RL without confounds due to effects of disregarding the feedback. The contrast PL > PPL did not yield significant activation within pFMC.

As hypothesized, contrasting RL-trials with control trials as well as PL-trials with control trials, significant activation revealed within pFMC and posterior parietal cortex along the banks of the intraparietal sulcus. Further activations were found within the insula, precuneus, cuneus, and cerebellum. The contrast RL > CC elicited additional activation in the midbrain area; whereas the contrast PL > CC elicited additional activation within dorsolateral prefrontal areas (see Table 3 and Fig. 2).

As hypothesized, the interaction contrast feedback VALIDITY by feedback VALENCE revealed significant activation within the pFMC. Additionally, significant activation was found within the pre-supplementary motor area (preSMA), the left insula, and parietal operculum (see Table 3 and Fig. 3, lower panel). In order to specify this interaction, the corresponding percentage signal change in the BOLD contrast was extracted (see Fig. 3). It revealed that signal intensity of negative feedback trials in RL and both feedback types in PL were comparably high, whereas the signal intensity for positive feedback trials in RL was low. Hence, data implied that both positive and negative feedback trials in

Table 3

Anatomical specification, hemisphere, Talairach coordinates ( $x$ ,  $y$ ,  $z$ ), and maximal  $Z$  scores ( $Z$ ) of significantly activated voxels for the control contrasts of rule learning and putative learning, the interaction contrast feedback VALIDITY by feedback VALENCE, and for the contrast negative versus positive feedback trials in rule learning

Area	Hemisphere	$x$	$y$	$z$	$Z$
<i>Rule Learning vs. Control Condition</i>					
Posterior frontomedian cortex (pFMC)	L	-4	18	44	3.5
Anterior insula	L	-37	17	8	4.3
	R	37	17	11	3.5
Precuneus	L	-4	-66	41	3.7
Intraparietal sulcus (IPS)	L	-28	-63	41	4.1
	L	-34	-47	41	4.5
Cuneus	R	1	-80	23	3.7
Midbrain area (MA)	L	-4	-35	-14	3.9
Cerebellum	R	31	-62	-23	4.5
	R	13	-68	-29	3.9
<i>Putative Learning vs. Control Condition</i>					
Posterior frontomedian cortex (pFMC)	R	4	26	35	4.3
Dorsolateral prefrontal cortex	L	-40	20	29	4.0
Dorsolateral prefrontal cortex	R	49	11	35	3.5
Anterior insula	L	-34	17	8	3.9
	R	34	20	0	3.9
Precuneus	L	-4	-68	41	4.0
Intraparietal sulcus (IPS)	L	-28	-62	41	4.6
	L	-37	-45	41	4.3
Cuneus	L	-7	-71	20	4.0
Cerebellum	L	-28	-57	-23	4.4
	L	-7	-75	-23	4.3
	R	34	-71	-17	4.4
<i>Interaction Feedback Validity x Feedback Valence</i>					
Posterior frontomedian cortex (pFMC)	L	-7	32	36	4.1
	L	-4	24	35	4.1
Presupplementary motor area (pre-SMA)	L	-4	11	44	3.6
Anterior insula	L	-31	20	5	3.5
Parietal operculum	L	-43	-24	20	4.1
<i>Negative vs. Positive Feedback Trials in Rule Learning</i>					
Posterior frontomedian cortex (pFMC)	L	-4	26	32	4.0
Presupplementary motor area (pre-SMA)	L	-4	12	44	4.0
Anterior insula	L	-40	14	-6	4.2
	R	37	23	-6	3.7
Thalamus	L	-13	-12	5	3.6

condition PL were processed like negative feedback trials in condition RL. To test for this interaction effect, a repeated measures ANOVA on the percentage signal changes was calculated. Results revealed a significant interaction effect ( $F(2,12) = 6.0$ ;  $P = 0.007$ ). Furthermore, the same analysis revealed a significant main effect of the factor feedback VALENCE ( $F(1,13) = 6.6$ ;  $P = 0.02$ ) but none for the factor feedback VALIDITY ( $F(2,12) = 2.1$ ;  $P = 0.16$ ).

The MRI data of the main effect of the factor feedback VALIDITY which was calculated by contrasting PL- and RL-trials

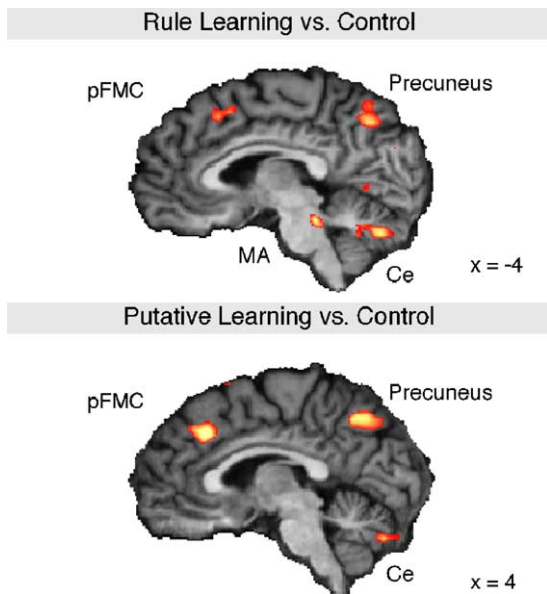


Fig. 2. Results of the control contrasts: upper panel: rule learning > control condition; lower panel: putative learning > control condition ( $Z > 3.09$ ). Group-averaged activations are shown on sagittal slices of an individual brain normalized and aligned to the Talairach stereotactic space. For activation coordinates see Table 3. Abbreviations: pFMC: posterior frontomedian cortex; Ce: cerebellum; MA: midbrain area.

revealed significant activation within pFMC (Talairach coordinates:  $x = 4, y = 35, z = 44, Z = 3.5$ ; Talairach and Tournoux, 1988) and the cerebellum (Talairach coordinates:  $x = -35, y = -73, z = -27, Z = 3.7$ ; see Fig. 3, top panel). The main effect of the factor feedback VALENCE which was calculated by contrasting negative with positive feedback trials did not reveal any frontomedian area despite activation within the anterior cingulate cortex (ACC; Talairach coordinates:  $x = 4, y = 30, z = 17, Z = 3.5$ ) and pre-SMA (Talairach coordinates:  $x = -4, y = 12, z = 41, Z = 3.3$ , see Fig. 3). Yet, effects of the factor feedback VALENCE on pFMC and pre-SMA were found when contrasting negative feedback trials with positive feedback trials in condition RL (see Table 3).

## Discussion

The present fMRI study aimed to disentangle the influence of two factors in learning situations, the processing of negative feedback and contextual feedback evaluation processes, on activation in brain areas suggested to reflect decision conflict, particularly the posterior frontomedian cortex (pFMC). In a first step, pFMC was confirmed to be activated by decision conflicts, i.e., decisions under uncertainty. Notably, findings from the interaction contrast feedback VALIDITY by feedback VALENCE revealed the specific contribution of contextual feedback evaluation on pFMC activation suggesting that not the mere processing of negative feedback elicits frontomedian activation but rather the processing of feedback against the background of previous experiences.

The activation found for the effects of decision uncertainty replicated the findings of pFMC to be involved during decision conflict (Volz et al., 2003, 2004). This sort of conflict was present both in RL and PL as the decision for a rewarding option was not clear-cut as compared to decisions in the control condition. In

general, pFMC activation is suggested to be involved in situations when one does not know which action to choose in order to receive a positive outcome, as confirmed by studies on hypothesis testing, rule application, and probabilistic or classification learning (Aron et al., 2004; Elliott and Dolan, 1998; Goel and Dolan, 2000;

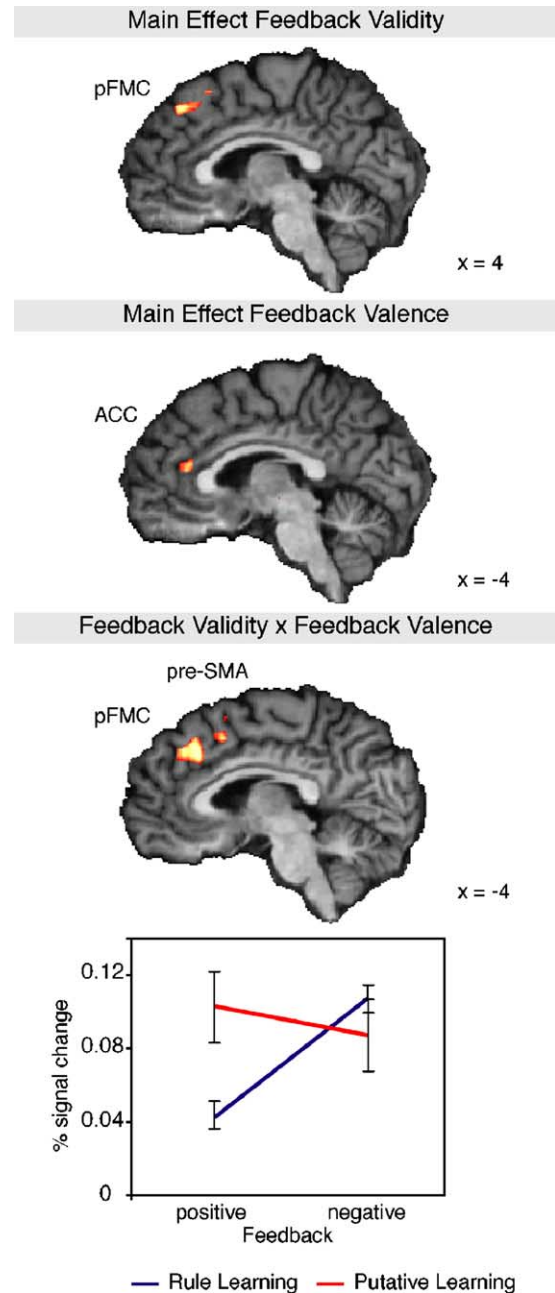


Fig. 3. Results of the main effect feedback VALIDITY (upper panel), feedback VALENCE (middle panel), and of the interaction feedback VALIDITY by feedback VALENCE (lower panel) that revealed the specific contribution of contextual feedback evaluation on pFMC activation. For the interaction effect, the mean percentage signal changes with standard error are depicted for rule learning (RL) and putative learning (PL), split by feedback valence. Note that pre-SMA activation in the main effect feedback VALENCE is not visible as the activation was located in the left hemisphere (Talairach coordinates:  $x = -4, y = 12, z = 41$ ). Abbreviations: pFMC: posterior frontomedian cortex; ACC: anterior cingulate cortex; pre-SMA: pre-supplementary motor area.

Holroyd et al., 2004). All these paradigms, including the presently employed one, share the critical feature of detecting successful strategies so as to solve the task. The effective acquisition of the adequate strategy is realized by means of contextual feedback evaluation and indicated by increasingly frequent positive and decreasingly frequent negative feedback. This very process leading to experienced-based changes in behavior is also characterized as learning (Lieberman, 1993).

There is no doubt that feedback and especially errors are necessary for learning to occur (Annett, 1969; Freese and Zapf, 1994). Negative feedback tells the subject what has not yet been learned, whereas positive feedback usually reveals what is known. However, feedback can only be evaluated as to an internal goal or an external task. Feedback per se would be of no use in the absence of a context of previous experiences. Accordingly, feedback is a relational concept and without a set point to compare the feedback with it cannot have a guiding function in behavioral adaptation and optimization. The set point can be given from outside as well as internally be generated, thus, feedback can be extrinsic or intrinsic. In rule learning paradigms like in the presently employed one, subjects have to rely on extrinsic feedback information, particularly on negative feedback, in order to acquire an adequate mental model. Mental models have been described as “small-scale models” of reality that are used to anticipate events and to reason (Johnson-Laird, 2001). Hence, each mental model can be conceived of as representing a situational context for a certain class of events, i.e., it captures what is common to all the different ways in which an event may occur. Transfused to the present study: in RL negative feedback signals that the current mental model has to be adapted, whereas positive feedback fosters the current representation. In contrast, in PL, both negative and positive feedback signal for an inadequate mental model calling for adjustments. Hence, all outcomes that are unexpected according to the current mental model indicate representational shortcomings.

What are the processes underlying this signal for behavioral changes? Anatomic data revealed dopaminergic projections from the ventral tegmental area through the ventral striatum into the frontomedian cortex (Williams and Goldman-Rakic, 1998), which are suggested to provide phasic teaching signals to modify and update stimulus-response mappings (Inase et al., 1999; Schultz, 1998, 2002). Based on empirical data and modeling work Cohen et al. (2002) more specifically suggest phasic dopamine effects to serve as gating signals indicating either that new inputs should be encoded and maintained, or that currently maintained representations have to be updated in response to salient, reward-predicting information. Accordingly, we assume that teaching signals elicited by unexpected outcomes result in modifications and updating of the current mental model by considering previous feedback information. The attribute of being unexpected is not a characteristic of the external feedback but of the feedback against the background of the current mental model. Unexpected outcomes hence describe the boundaries of the small-scale model of reality one has developed so far. As a result, the subject may realize that something is not known well enough, which may then lead to self-reflective thoughts and new phases of exploration. Although the frequency and amount of negative feedback were the same in both rule learning conditions, PL-trials engaged the pFMC more consistently than RL-trials. This finding is suggested to result from the fact that in PL both negative and positive feedback trials were unexpected. The percentage signal changes in pFMC support this view: negative feedback in RL and both feedback types in PL

did not differ significantly, thus, suggesting feedback in PL being processed similar to negative feedback in RL. Hence, we propose pFMC activation to arise from the further processing of teaching signals against the background of the current mental model.

Yet, this interpretation depends on participants' trust in feedback validity. If participants would not have taken the feedback seriously, they may not have paid attention to feedback information. Subsequently, participants might have engaged in other processes than contextual feedback evaluation. In order to control for this possible effect, the perceptual putative learning condition (PPL) was employed in which it was ensured that feedback was taken seriously. When contrasting the two putative learning conditions, PL and PPL, no significant activation within pFMC revealed so that we can exclude trust in feedback being influential on this area. A supporting datum for participants' trust in feedback both in PL and PPL derives from post-session survey results: none of the participants reported suspiciousness in feedback validity. Despite reported decision uncertainty in condition, PL participants specified the impression that they obviously must have acquired the valid decision rules as indicated by increasingly frequent positive feedback. Based on the latter instance, rule acquisition was inferred in PL rather than reported based on acquired knowledge. In contrast, participants reported to certainly know the valid decision rules in RL. This impression was accounted for by increasingly frequent positive feedback and verbalizable knowledge. The latter factor apparently differed between the two conditions, RL and PL.

Together, the present study revealed pFMC activation to reflect contextual feedback evaluation processes against the background of previous (feedback) experiences rather than the mere processing of negative feedback. The latter assumption was not only invalidated by the interaction contrast feedback VALENCE by feedback VALIDITY but also by the main effect of the factor feedback VALENCE: contrasting negative with positive feedback trials elicited frontomedian activation within ACC and pre-SMA but not within pFMC. Accordingly, based on these results, we suggest pFMC to reflect the processing of unexpected outcomes against the background of previous experiences, i.e., against the current small-scale model of reality that is used to anticipate events.

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