RESEARCH ARTICLE

When global rule reversal meets local task switching: The neural mechanisms of coordinated behavioral adaptation to instructed multi-level demand changes

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Abstract

Cognitive flexibility is essential to cope with changing task demands and often it is necessary to adapt to combined changes in a coordinated manner. The present fMRI study examined how the brain implements such multi-level adaptation processes. Specifically, on a “local,” hierarchically lower level, switching between two tasks was required across trials while the rules of each task remained unchanged for blocks of trials. On a “global” level regarding blocks of twelve trials, the task rules could reverse or remain the same. The current task was cued at the start of each trial while the current task rules were instructed before the start of a new block. We found that partly overlapping and partly segregated neural networks play different roles when coping with the combination of global rule reversal and local task switching. The fronto-parietal control network (FPN) supported the encoding of reversed rules at the time of explicit rule instruction. The same regions subsequently supported local task switching processes during actual implementation trials, irrespective of rule reversal condition. By contrast, a cortico-striatal network (CSN) including supplementary motor area and putamen was increasingly engaged across implementation trials and more so for rule reversal than for nonreversal blocks, irrespective of task switching condition. Together, these findings suggest that the brain accomplishes the coordinated adaptation to multi-level demand changes by distributing processing resources either across time (FPN for reversed rule encoding and later for task switching) or across regions (CSN for reversed rule implementation and FPN for concurrent task switching).

KEYWORDS

cognitive flexibility, cognitive control, cortico-striatal loops, fronto-parietal network, instructionbased learning, rapid instructed task learning, rule reversal, task set reconfiguration, task switching

1 | INTRODUCTION

We perform tasks according to a certain set of rules. A task becomes difficult to perform when its rules are complex, completely unknown, or not well practiced. But even if the rules of individual tasks are simple, explicitly instructed, and well-practiced, performing the tasks can still be challenging if one has to switch between different tasks (e.g., typing an email vs. answering a phone call) or if one has to obey changed or even reversed task rules (e.g., typing an email on an English keyboard vs. a German keyboard where the keys for letter “y” and “z” are reversed). In many real-life situations task switching and rule change occur in combination and often they are structured according

to a temporal hierarchy. On the one hand, task rules are typically stable within a certain environment and only need to be changed when entering a new environment (e.g., typing rules on different keyboards; driving rules in different countries). On the other hand, within the same environment, the priority of tasks is changing all the time even though the rules of the individual tasks remain unchanged. For instance, when commuting between the UK and France, on a local level, a car driver needs to switch between tasks in a second (e.g., switching between answering a phone call and monitoring the traffic ahead), whereas the global rules are changing at a much slower pace (e.g., concerning right- and left-hand traffic, the rules are stable within the country and altered only after crossing the border).

Importantly, in the examples above, the challenge was *not* to learn from feedback whether tasks or rules might have changed. Rather, the challenge was to coordinate multi-level adaptation processes based on explicitly available prospective information or instruction. This raises the question how local adaptation processes (i.e., within environment) and global adaptation processes (i.e., across environments) are coordinated based on explicit instruction and whether and in which particular manner they might interact. Are people capable of handling task switches and rule changes independently of each other especially with the aid of explicit instruction? Moreover, how do people cope with these challenges throughout practice after the rules have changed?

Accordingly, we devised an experimental design in which frequent and unpredictable, yet explicitly instructed, trial-by-trial task switching requirements were embedded within blocks of trials with stable overall task rules, which, in turn, could change between blocks at a considerably slower pace. The task rules were explicitly instructed at the beginning of each block. For this reason, participants did not need to rely on trial-and-error feedback but instead could start encoding and using the current rules right after the instruction (Ruge & Wolfensteller, 2016b; Ruge, Karcz, Mark, Martin, Zwosta, & Wolfensteller, 2017). The present study asked whether instructed rule changes, instructed task switches, and possible interactions might be associated with dissociable neural processes possibly as a function of practice following rule changes.

While the cognitive and neural processes involved in task switching and rule change alone have been studied extensively, the flexible adaptation to the combination of task switching and rule change has rarely been investigated. As an exception, a recent neuroimaging study orthogonally crossed task switching and rule reversal on a trial-by-trial basis (De Baene, Albers, & Brass, 2012). However, this study lacked the temporal hierarchy between task switches and rule reversals the present study is particularly interested in.

It is well known, that task-switching alone in the absence of rule changes impairs behavioral performance. Participants respond more slowly and make more errors when switching between tasks rather than repeating the same task (Kiesel et al., 2010; Vandierendonck, Liefooghe, & Verbruggen, 2010). This holds true even if the impending task can be prepared in advance (e.g., Meiran, 1996; Rogers & Monsell, 1995). In line with the behavioral costs of task switching neuroimaging studies have revealed task switching to be supported by increased recruitment of areas within a generic fronto-parietal cognitive control network (cf., Cole & Schneider, 2007) including lateral prefrontal cortex (LPFC) regions, medial prefrontal cortex regions (MPFC), and parietal cortex regions (Brass & von Cramon, 2002, 2004; Braver, Reynolds, & Donaldson, 2003; De Baene et al., 2012; De Baene & Brass, 2014; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Ruge, Muller, & Braver, 2010; Shi, Meindl, Szameitat, Müller, & Schubert, 2014; Shi, Zhou, Muller, & Schubert, 2010; Sohn, Ursu, Anderson, Stenger, & Carter, 2000; Yeung, Nystrom, Aronson, & Cohen, 2006; for reviews see De Baene & Brass, 2014; Ruge, Jamadar, Zimmermann, & Karayanidis, 2013).

Besides the investigation of local trial-by-trial task switching processes, the slower-paced modification of global rule set has also been widely studied with neuroimaging methods in particular

employing reversal learning procedures. Typically, reversal learning studies examined trial-and-error learning of either deterministic or probabilistic relationships between stimuli and responses and typically used a single pair of stimuli which reversed its mapping onto two alternative responses on a regular but unpredictable basis (Budhani, Marsh, Pine, & Blair, 2007; Cools, Clark, Owen, & Robbins, 2002; Ghahremani, Monterosso, Jentsch, Bilder, & Poldrack, 2010; Kringelbach & Rolls, 2003; Mitchell et al., 2009; O'Doherty, Critchley, Deichmann, & Dolan, 2003; Remijne, Nielen, Uylings, & Veltman, 2005; Xue, Ghahremani, & Poldrack, 2008). These studies consistently emphasized the role of the lateral part of the orbitofrontal cortex (OFC)/ventrolateral prefrontal cortex (VLPFC) and the caudate nucleus in reversal learning processes. In addition, an involvement of the more extended fronto-parietal cognitive control network which is typically reported in task switching studies also seems to play a role in handling interference due to reversed response requirements (Mitchell et al., 2009; Xue et al., 2008). Interestingly, instead of feedback-driven reversal learning, a recent study examined instruction-based reversal learning using a rule instruction procedure similar to the one employed in the present study (Ruge & Wolfensteller, 2016a). That study found similar results as previous feedback-driven reversal learning studies with lateral OFC and anterior caudate supporting successful encoding of the rule reversal instruction whereas the fronto-parietal control network supported reversal-related control processes during subsequent memory-based reversed rule implementation. However, all these previous reversal learning studies examined the brain dynamics associated with the reversal of simple multiple-choice S-R rules that were *not* further organized according to different task sets. Therefore, possible interactions between rule reversal learning and task switching could not be assessed.

The crucial question to be addressed by the present study was whether the combination of local trial-wise task switching processes embedded within global block-wise instructed rule reversal processes would alter the previously reported brain activation effects observed when both processes were studied in isolation. Furthermore, by realizing a sequence of multiple rule implementation trials after each new rule instruction we were additionally able to elucidate the influence of repeated practice on these adaptation mechanisms (see Ruge & Wolfensteller, 2010, 2016b). Several previous studies have suggested an anterior-posterior gradient within the lateral prefrontal cortex reflecting different hierarchical levels of action control associated with rule complexity or temporal integration demands (Badre & D'Esposito, 2007; Koechlin, Ody, & Kouneiher, 2003; Koechlin & Summerfield, 2007, see Reynolds, O'Reilly, Cohen, & Braver, 2012 for an alternative account). However, it is far from clear whether the coordinated implementation of global rule reversal demands and local task switching demands (which has not been studied yet) constitutes an additional hierarchical layer and how this might be organized neurally. It is hence an open question whether the interaction between global rule reversal and local task switching will activate different (hierarchically higher) brain areas compared to each of the two main effects of global rule reversal and local task switching.

An alternative possibility is that global rule reversal might simply increase task switching demands, which in turn, should be reflected by

an amplification of switching-related activation in the same fronto-parietal control areas that are also active under nonreversal conditions. Moreover, in line with previous reports of a long lasting fronto-parietal activation increase after reversal instructions (Ruge & Wolfensteller, 2016a) we might expect a long lasting increased engagement of these generally switching-related fronto-parietal areas across several trials following a reversal instruction.

Another possibility is that task switching and rule reversal processes could be implemented independently of each other, a scenario that implies main effects for task switching and rule reversal either in overlapping brain regions (e.g., fronto-parietal) or in different brain regions (e.g., fronto-parietal vs. lateral OFC), but no interactions.

2 | MATERIALS AND METHODS

2.1 | Participants

Thirty-four healthy participants' data were collected. All the participants were right-handed volunteers with normal or corrected-to-normal vision. They took part in the experiment after obtaining informed consent according to the Declaration of Helsinki. The study was approved by the local ethics committee. Each participant was paid 8€/hour. The data of two participants were excluded from further analysis owing to head movement (>4 mm). Thus, ultimately, the data sets of 32 participants were available for analysis (sixteen females; mean age 25.5 years; range 20–36 years; SD 3.9 years).

2.2 | Procedure

The present paradigm was modified from the cued task switching paradigm (see Meiran, 1996; Shi et al., 2010). Different from previous experimental procedures, the task rules were not constant across the entire experimental session but instead could change after a sequence of 12 trials. The currently valid task rules were explicitly instructed at the beginning of a new block of 12 trials and could either be identical or reversed relative to the rules of the preceding block. Within a block, the situation was the same as in the typical task switching design where the current trial could either require a task switch or a task repetition. Subjects were required to work through a sequence of 64 blocks, each starting with an explicit *instruction phase* followed by an *implementation phase* of 12 practice trials (6 practice trials for each of two tasks). The instructions were displayed for 4.5 s and informed about the currently valid “rule set” comprising the rules for a face gender categorization task and for a number parity categorization task (see Figure 1). In addition to the actual rule instructions a centrally displayed symbol indicated whether the rules stayed the same or changed with respect to the preceding block (“=” for a nonreversal block or “X” for a reversal block). This additional symbol was redundant but intended to reduce the risk that subjects might overlook a rule change. The currently required responses (left index finger or right index finger) were indicated by the location of the written words (in German) for the respective stimulus categories of each task. For each subject only two (out of four possible) combinations of face and number rules were

realized throughout the experiment (rule set A: female-left, male-right for the face task; odd-left, even-right for the number task; rule set B: the reversed A mappings). The nonreversal blocks and the reversal blocks appeared alternately (the order of rule set was AABB). The *implementation phase* followed the *instruction phase* after a 1,500 ms interval (including 500 ms empty screen, 700 ms central fixation, and 300 ms empty screen after the fixation). The *implementation phase* contained 12 trials including six face task trials (male or female) and six number task trials (odd or even) in pseudo-randomized order such that there were three task switch trials and three task repetition trials for each task type. Note that the first trial of each block was defined as a switch trial but was excluded from all analyses due to its special status (see below). In other words, each task type was practiced six times and each task transition (switch or repetition) occurred 6 times. Hereafter, the very first trial of a block is labeled “p_1st” (“p” stands for practice). All the other eleven trials were labeled according to the number of times each of the two tasks was implemented in the current block (practice level p1 to p6). For instance, if the first trial was a face task, the other five face tasks were p2 to p6 and the six number tasks were p1 to p6. Both, the behavioral data and the imaging data were analyzed in terms of these 6 practice levels (p1–p6). To assess behavioral and brain activation dynamics across practice trials within blocks, practice trials p1 to p6 trials were divided into early trials (mean of p1 to p3) and late trials (mean of p4 to p6). Because p_1st followed the block instructions by a fixed 500 ms interval (short and no jitter) its activation may not be discriminable from activation related to the block instruction. Furthermore, it might include a restart process which makes it different from all the other trials (Poljac, Koch, & Bekkering, 2009). Therefore, this p_1st trial was always excluded from further analyses.

Each trial started with a pre-cue presented for 600 ms which indicated the currently relevant task. There were two types of pre-cues. In half of the blocks, the pre-cue was the written German word for currently relevant task type (i.e., “face” or “number”). In the remaining blocks, the pre-cue explicitly repeated the currently instructed rule of the currently relevant task (e.g., female-left, male-right or odd-left, even-right). The order of blocks was pseudo-randomized with respect to pre-cue type so that each pre-cue type equally often. We expected a rule-cue benefit especially in rule reversal blocks as compared to non-reversal blocks. However, cue type turned out to have no significant interaction with rule reversal both in behavior and brain activation. Thus the data were collapsed across both cue types to keep the report concise.

In each trial, 200 ms after the offset of the pre-cue, a target was presented for 800 ms. The target was a picture of a face with a number word superimposed (approximately centered on nose of the displayed face). Two different male and two different female face pictures were used (Collection of Facial Images: Faces94; <http://cswwww.essex.ac.uk/mv/allfaces/faces94.html>); the superimposed number could be 1, 2, 8 or 9. As a result, 16 distinct face/number overlays were employed as target stimuli (see also Stelzel, Brandt, & Schubert, 2009).

Participants made a forced two-choice response based on the rules instructed for the current block of trials. They were asked to respond as fast and as accurate as possible using either their left or their right

FIGURE 1 Schematic depiction of the experimental procedure. (a) Exemplary sequence of two consecutive blocks initiated by instruction displays of the currently valid task rules (English translation). Block $N - 1$ is a nonreversal block (indicated by the “=” sign) whereas block N is a rule reversal block (indicated by the “X” sign). (b) Exemplary sequence of 12 implementation trials where “p” stands for practice level with respect to each task (num = number task; face = face task), (s) stands for task switching, and (r) stands for task repetition. (c) Exemplary single implementation trial

index finger. Before the start of next trial, there was a variable interval of 1,200, 4,100 or 7,000 ms (with the ratio of 74.0%, 20.8% and 5.2%). At the end of each block, feedback was presented for 800 ms indicating the rate of correct responses in this block. After an inter-block interval (of 1, 2, 3, or 4 s), the next block started with the instruction display. All stimuli were presented on a black background in the center of the screen and subtended within 5° of visual angle.

In total, this experiment contained an equal number of 32 nonreversal and 32 reversal blocks, respectively. The 64 blocks were assigned to 4 scanning runs. Each run lasted 14 min 50 s. Participants took a short break of approximately 1–2 minutes between runs.

2.3 | Functional MRI recording

Imaging was performed on a 3 T scanner (TRIO; Siemens, Erlangen, Germany) equipped with a standard head coil at the Dresden Neuroimaging Center. T2*-weighted echo-planar images (EPI) with blood oxygenation level-dependent contrast were acquired (TR = 2,000 ms, TE = 30 ms, flip angle = 80°). Thirty-two axial slices (matrix size = 64×64 voxels, field of view = 256×256 mm², thickness = 4 mm, spacing = 0.8 mm) were acquired parallel to the AC-PC plane, covering the whole brain. The order of acquisition of the slices was from bottom to top. The first four volumes (dummy volumes) were discarded because of possible instabilities in the magnetic field at the beginning of a run. In total 1,780 functional images were acquired in four runs. Stimuli were displayed on a back-projection screen mounted in the bore of the magnet behind the participant's head, by using an LCD projector. Participants viewed the screen by a mirror mounted on the head coil.

2.4 | Functional MRI data analysis

Preprocessing of all functional images was carried out using SPM8 (Wellcome Department of Cognitive Neurology, London, UK). Images were interpolated in time to account for the differences in acquisition time between slices (slice timing). All images were spatially realigned to the first volume for head movement correction, and then normalized into Montreal Neurological Institute (MNI) space by registering the mean functional image to the standard EPI template image provided by SPM8 (images were re-sampled to $3 \times 3 \times 3$ mm³ isotropic resolution). The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to accommodate inter-participant anatomical variability.

To estimate condition-specific event-related BOLD activation the general linear model (GLM) was applied (Friston et al., 1995). First, we computed GLMs for each participant including model regressors for the instruction phase as well as for the implementation phase. Regressors were created by convolving stick functions associated with the repeated occurrence of condition-specific events with the hemodynamic response function (HRF). Modeling incorporated a temporal high-pass filter with a cutoff frequency of 1/256 Hz accommodating the fact that the design included slow signal components associated with the different rule types (nonreversal/reversal) due to approximately 2 times 60 s between the onsets of rule blocks of the same type.

Activation elicited by the block-wise instructions were modeled by four separate regressors resulting from the factorial combination of the two rule transitions (reversal vs. nonreversal) and the content of the rules (rule set A vs. rule set B, B = reversed A). Instructions were modeled as events of 4.5 s duration. Activation elicited by the first trials of each block (p_1st) was separately modeled by two regressors for nonreversal blocks and reversal blocks. Another 22 regressors resulted

from the factorial combination of the two rule transitions (reversal vs. nonreversal), the six practice levels (p1-p6), and two task transition types (task switch vs. task repetition). Note that by definition, the first repetition trial was always preceded by at least one other trial of the same task. Therefore, there was no p1_repeat trial (accordingly no regressors for reversal_p1_repeat and nonreversal_p1_repeat). All error trials were modeled by an additional regressor of no interest. These 25 ($2 + 22 + 1$) conditions were modeled as events of zero duration time-locked to the onset of the task cue at the beginning of a trial. Finally, performance feedback at the end of blocks was modeled by one additional regressor as events of zero duration. Beta values of these regressors were estimated according to the standard ordinary least-squares (OLS) method. Contrast images based on single subject beta estimates were then tested for statistical significance on the group level.

In the *instruction phase*, the effect of rule transition (nonreversal versus reversal) was analyzed. In the *implementation phase*, the main effects of rule transition (nonreversal versus reversal), practice level (early (p1-p3) versus late (p4-p6) practice trials within a block), and task transition (task repetition versus task switch), as well as the interactions among them were analyzed. To identify activations common to different contrasts we applied a conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005).

Contrasts were assessed by one-sample t-tests and were statistically evaluated based on a cluster-size threshold to control for family-wise-error (FWE) rate based on the Gaussian random field theory as implemented in SPM8. The cluster-forming voxel-level threshold was set to $p < .001$ (Woo, Krishnan, & Wager, 2014). All reported clusters reached a cluster-corrected significance level of $p < .05$. Cluster-size correction was applied on the whole brain level and for circumscribed anatomically defined regions of interest (ROIs) according to a-priori hypotheses regarding the OFC and the basal ganglia regions. Masks for these anatomical structures were extracted with the toolbox wfu pickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003) based on AAL labels. The OFC mask included the bilateral inferior, middle, and superior orbitofrontal gyri and the basal ganglia mask included the bilateral caudate, putamen, and pallidum.

Significant clusters identified in these primary analyses were submitted to additional post-hoc analyses on contrasts that were independent of the cluster-defining contrasts. These clusters were defined as 9 mm spheres centered on each cluster's peak voxel and statistical testing was performed using small volume correction. In cases where these post hoc tests revealed no significant results using the general cluster-level thresholding procedure we also applied FWE-correction on the voxel level (within the 9 mm spheres) and we even lowered the threshold to $p < .05$ uncorrected to ensure that we would not miss any weak effects. Note that in all cases even these uncorrected tests failed to produce significant results suggesting that, if anything, we might have missed very small effects that were not detectable with the given statistical power of the present study.

3 | RESULTS

3.1 | Behavioral results

Mean reaction time (RTs) and error rates were submitted to separate $2 \times 2 \times 2$ repeated-measures ANOVA, with the factors rule transition

(nonreversal versus reversal), task transition (task repetition versus task switch), and practice level (early versus late practice trials within a block).

RTs were significantly slower in rule reversal blocks than in nonreversal blocks (main effect of rule transition; $F(1,31) = 7.43$, $p < .01$, 6 ms rule reversal cost). The main effect of task transition was significant ($F(1,31) = 61.24$, $p < .0001$, 56 ms task switch cost). The interaction between task transition and practice was significant ($F(1,31) = 5.54$, $p < .05$) reflecting that the switch costs were smaller in late trials than in early trials (49 vs. 63 ms). Additionally, two tendencies towards statistical significance were observed. The interaction between rule transition and task transition: switch cost tended to be larger in the reversal block than in the nonreversal block (60 vs. 52 ms; $F(1,31) = 3.35$, $p = .077$). The main effect of practice: early trials tended to be faster than late trials (656 vs. 661 ms; $F(1,31) = 3.58$, $p = .068$). All other ANOVA effects were not significant ($F_s < 0.95$, $p_s > 0.33$). Note, in particular, that rule reversal effect was not significantly modulated by practice.

Error rates were significantly higher in reversal blocks than in nonreversal blocks (main effect of rule transition; $F(1,31) = 5.73$, $p < .05$, 4.49% vs. 3.63%). Error rates were significantly higher in task switch trials than task repetition trials (main effect of task transition; $F(1,31) = 26.37$, $p < .0001$, 4.84% vs. 3.28%). Furthermore, the interaction between rule transition and task transition was significant ($F(1,31) = 4.67$, $p < .05$) reflecting that switch costs were smaller in reversal blocks compared to nonreversal blocks (1.10% vs. 2.03%). This effect was restricted to late trials as indicated by the significant three-way interaction ($F(1,31) = 5.84$, $p < .05$ (switch cost reversal_late = 0.35% vs. switch cost nonreversal_late = 2.39%, $t(31) = 3.10$, $p < .005$; switch cost reversal_early = 1.84% vs. switch cost nonreversal_early = 1.67%, $t(31) = 0.30$, $p > .76$). All other ANOVA effects were not significant ($F_s < 2.59$, $p_s > .12$).

In summary, significant task switching costs and rule reversal costs were found in both RT and error rates. In addition, the RT switch cost was reduced by practice. The results also indicate that, compared to task-repetition trials, participants may have performed the task-switch trials with more caution in the reversal blocks than in the nonreversal blocks. This is suggested by the observation that error rate switch cost was reduced in the reversal blocks in late trials whereas RT switch costs tended to be larger in the reversal blocks.

3.2 | Imaging results

We analyzed modulations of brain activation across the implementation phase as well as in the preceding instruction phase. We first wanted to assess the neural correlates of local task switching by analyzing the main effect of task transition in the implementation phase. Secondly, we wanted to assess the neural correlates of global rule reversal processes by analyzing the main effects of rule reversal both during the *instruction phase* and during the *implementation phase*. Specifically, for the implementation phase, we also assessed the interaction effects between task switching and rule reversal and how these effects might be modulated across practice (i.e., early vs. late during the implementation phase).

TABLE 1 Significantly higher activation in task switch trials than in task repetition trials (left panel) and significantly higher activation for reversal than nonreversal conditions during the rule instruction phase (right panel)

Brain region	MNI coordinates			Peak t	Brain region	MNI coordinates			Peak t
	x	y	z			x	y	z	
Instruction (reversal vs. nonreversal)					Task switching vs. Task repetition				
L lateral PFC	−42	44	16	3.87	L lateral PFC	−36	47	22	5.64
	−42	32	34	4.17		−45	32	31	5.46
	−42	14	22	3.91		−48	8	34	7.13
R lateral PFC	45	11	22	4.33	R lateral PFC	42	26	28	4.65
L OFC	−27	23	−20	4.87					
L Precentral Gyrus	−39	−10	61	6.06	L Precentral Gyrus	−27	−4	58	7.89
R Precentral Gyrus	27	−4	55	6.15	R Precentral Gyrus	36	−4	55	6.2
R Pre-SMA/ACC	12	26	31	4.79	R Pre-SMA/ACC	−6	20	46	8.4
L IPL	−48	−37	43	5.51	L IPL	−36	−52	46	9.63
R IPL	42	−43	34	5.51	R IPL	36	−58	37	5.39
Precuneus	9	−64	52	5.44	Precuneus	−3	−70	52	10.28
L anterior Striatum (Putamen/Pallidum)	−18	5	−11	5.16	L anterior Striatum (Pallidum/Putamen)	−18	−4	−5	5.16
R anterior Striatum (Putamen/Pallidum)	18	17	−8	5.20	R anterior Striatum (Pallidum/Putamen)	15	2	1	4.81
L anterior Insula	−33	20	7	4.29	L anterior Insula	−30	20	1	8.18
R anterior Insula	36	14	−5	4.94	R anterior Insula	33	20	7	6.65
L Thalamus	−12	−16	4	4.60	L Thalamus	−12	−16	10	7.46
R Thalamus	6	−19	7	4.21	R Thalamus	18	−13	10	7.18
L Calcarine Sulcus	−15	−76	10	6.25	L Calcarine Sulcus	−9	−79	7	7.52
L Lingual Gyrus	−24	−88	−17	6.12	L Inferior Occipital Lobe	−21	−94	−11	4.83
R Calcarine Sulcus	3	−97	−2	6.57	R Calcarine Sulcus	0	−91	4	6.73
					L Cerebellum	−30	−61	−32	7.26
					R Cerebellum	33	−67	−32	7.57

In short, an overlapping set of fronto-parietal regions was engaged in local task switching processes during the implementation phase and in global rule reversal processes – the latter exclusively during the instruction phase but not during the implementation phase. Moreover, we did *not* find significant interaction effects between local and global adaptation processes in the implementation phase. Furthermore, we identified two distinct cortico-striatal networks, one showing a stronger activation increase for reversal vs. nonreversal across practice and another one exhibiting generally increasing activation across practice. The results are described in detail in the following sub-sections.

3.2.1 | Local adaptation processes related to task transition

We found wide-spread activation in frontal and parietal regions characterized by higher activation in task switch trials than in task repetition trials (Table 1. right section; Figure 2a, marked by yellow). This included

activation in large parts of the left lateral PFC, more focally in the right lateral PFC (MFG/IFS), the anterior striatum (at the anterior junction of putamen and pallidum with an emphasis on the pallidum), the anterior cingulate cortex (ACC), the pre-supplementary motor area (pre-SMA), the SMA, the pre- and post- central gyri and dorsal MFG, the bilateral anterior insula, superior and inferior parietal lobules (SPL and IPL), precuneus, but also the thalamus, the posterior cingulate cortex, and the visual cortex.

The two-way interactions between task transition and rule reversal and between task transition and practice level as well as the three-way interaction between all three factors were neither significant on the whole brain level nor at the most lenient threshold (i.e., $p < .05$ uncorrected) in post hoc analyses confined to spherical ROIs centered on peak coordinates identified for the task transition main effect. Thus, the fronto-parietal control network was more strongly engaged for task

FIGURE 2 Summary of the key imaging results. (a) The fronto-parietal cognitive control network supports local task switching processes during the implementation phase and global rule reversal processes during the instruction phase. In yellow: significantly higher activation in task switch trials than in task repetition trials. In red: significantly higher activation for reversal than nonreversal conditions during the rule instruction phase. The overlap of red and yellow voxels is displayed in orange and corresponds to the conjunction analysis results depicted also in orange in Figure 2b. (b) In addition to the fronto-parietal control network, two distinct cortico-striatal networks were differently involved in learning processes across implementation trials after rule instruction. In light blue: The cortico-striatal network including right putamen, SMA, pre- and post-central gyri, and posterior insula/operculum showed a stronger practice-related activation increase in reversal blocks compared to nonreversal blocks. In deep blue: The cortico-striatal network including caudate head, lateral OFC, ventral medial PFC, and temporal cortex showed similar practice-related increase in both reversal blocks and nonreversal blocks as revealed by a conjunction analysis. (c) Mean beta estimates (plus standard error) for the peak voxels of exemplary regions in the three distinct networks playing different functional roles under combined local-global adaptation demands. LPFC: lateral prefrontal cortex; MFG: middle frontal gyrus; IFS: inferior frontal sulcus; ACC: anterior cingulate cortex; IPL: inferior parietal lobe; SPL: superior parietal lobe; aStriatum: anterior striatum; aInsular: anterior insula; VMPFC: ventral medial PFC; OFC: orbitofrontal cortex; SMA: supplementary motor area; ST: superior temporal cortex; plnsular: posterior insula [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Two distinct cortico-striatal networks showed different practice-related increase pattern in reversal blocks and nonreversal blocks

Brain region	MNI coordinates X	Peak y	z	t
<i>Reversal (late - early) vs. Nonreversal (late - early)</i>				
R Precentral Gyrus/SMA	15	-19	67	4.72
L Postcentral Gyrus	-24	-34	58	4.83
L Paracentral Lobule/SMA	-6	-19	55	4.82
R Putamen	33	8	4	4.22
L posterior Insula/Operculum	-36	-16	13	5.45
R posterior Insula/Operculum	48	-19	19	4.63
<i>Conjunction (reversal (late-early), nonreversal (late-early))</i>				
L ventro-medial PFC ^a	-3	53	-2	4.13
L Superior Temporal Gyrus ^a	-39	11	-23	4.74
R Caudate Head ^b	9	14	-2	3.90
L Caudate Head ^b	-9	11	1	3.85
R lateral OFC ^b	36	23	-14	3.84

^aSignificant activations on the whole-brain level.

^bSignificant activations on the level of anatomically defined ROIs (basal ganglia or OFC, respectively). OFC: orbitofrontal cortex; PFC: prefrontal cortex; SMA: supplementary motor area.

switching than for task repeating and this effect was statistically independent of rule reversal and practice level. The detailed activation patterns of representative clusters in the left lateral MFG and in the left IPL are plotted in Figure 2c, upper two panels with orange borders.

3.2.2 | Global adaptation processes related to rule reversal during the instruction phase

We observed stronger activation for reversed rules than for nonreversed rules *during the instruction phase* in a large set of regions (see Table 1, left section; Figure 2a, activation marked in red). Similar to the task switching-related activations, this included the lateral PFC, the ACC, the pre-SMA, the SMA, the pre- and post-central gyri and dorsal MFG, the anterior insula, the SPL, and the IPL. Additionally, we found activations in the left OFC and in the anterior striatum (at the anterior junction of putamen, caudate, and pallidum with an emphasis on the putamen). The LPFC activation was more extended in the left than right hemisphere stretching from anterior to posterior along the MFG/IFS. By contrast, in the right hemisphere we observed significant activation only in the posterior part of the IFS.

Notably, these areas seem to largely overlap with the areas identified for local task transition effects during the *implementation phase* (see Figure 2a; Table 1 left and right sections). To confirm this statistically, we performed a conjunction analysis to test the common activation of these two contrasts. The result confirmed statistically that overlapping regions of the fronto-parietal control network were commonly involved in both, reversal-related processes during the instruction phase and switching-related processes during implementation (Figure 2b, marked by orange). Notable exception was the left OFC

which was exclusively activated for rule reversal vs. nonreversal during the instruction phase.

3.2.3 | Global adaptation processes related to rule reversal during the implementation phase

While we did not observe significant activations for the main effect of rule reversal (reversal vs. nonreversal) during the *implementation phase*, we did find several areas in which a practice-related activation increase was significantly stronger in reversal blocks than in nonreversal blocks (interaction contrast reversal(late-early) vs. nonreversal(late-early)). This interaction effect was observed in the right putamen, a cluster including SMA, bilateral pre- and post-central gyri, and the posterior portion of the paracentral lobule, as well as the two clusters in the posterior insula/operculum extending into the superior temporal cortex (Table 2 upper section; Figure 2b, marked by light blue). The three-way interaction additionally involving the factor task transition was neither significant on the whole brain level nor at the most lenient threshold (i.e., $p < .05$ uncorrected) in post hoc analyses confined to spherical ROIs centered on peak coordinates identified for the two-way interaction contrast. Hence, the reversal-related effects were statistically independent of task transition effects. The activation patterns of representative clusters in the right putamen and in the SMA/pre-central gyrus are plotted in Figure 2c, two panels with light blue borders.

To further characterize the interaction between rule transition and practice level in more detail, we assessed practice-related activation change separately for reversal blocks and for nonreversal blocks in the whole brain. We found for all the previously identified regions that significant practice-related *increase* could only be confirmed statistically

for reversal blocks but not for nonreversal blocks. None of the identified regions exhibited significant practice-related *decrease*, neither for reversal blocks nor for nonreversal blocks.

3.2.4 | Practice-related activation change common for both reversal blocks and nonreversal blocks

While the above analysis identified several regions that exhibited a stronger practice-related increase for reversal blocks than for nonreversal blocks we were also interested in testing whether other regions might be characterized by practice-related increase or decrease common to both reversal blocks and nonreversal blocks. To identify common practice-related activation *increase* we performed a conjunction analysis for the contrasts reversal (late-early) and nonreversal (late-early)), see Table 2 lower section, Figure 2b, marked by deep blue. This analysis showed that the ventral medial PFC (VMPFC) and the left superior temporal cortex showed practice-related activation increase in both rule reversal and nonreversal blocks. Furthermore, within the anatomically defined basal ganglia and OFC ROIs, bilateral caudate head and right OFC showed significant activation increase in both types of blocks. The detailed activation pattern of the right caudate head is plotted in Figure 2c (panel with dark blue border). To identify common practice-related activation *decrease* we performed a conjunction analysis for the contrasts reversal (early-late) and nonreversal (early-late)). This analysis did not reveal significant results.

4 | DISCUSSION

The present study investigated local task switching in combination with instructed global rule reversal learning. On a general level, the neuroimaging results suggest that different aspects of global and local adaptation processes are implemented by partly overlapping and partly segregated neural systems. Evidence for integration between global and local adaptation processes was observed in the fronto-parietal control network which exhibited stronger local switching-related activation during the *implementation phase* as well as stronger activation on the global block level for reversed rules vs. nonreversed rules exclusively during the *instruction phase*, but no longer during subsequent implementation. By contrast, the subsequent *implementation* of reversed rules vs. nonreversed rules was associated with stronger practice-related increase independently of local switching demands in an almost completely segregated cortico-striatal system including the right putamen, the SMA, and the posterior insula/operculum. Finally, we observed a third nonoverlapping set of areas including the caudate head, the lateral OFC, and the VMPFC which exhibited increasing activation across rule implementation trials independent of both, global rule reversal demands and local task switching demands.

4.1 | The role of the fronto-parietal control network when local and global adaptation demands are combined

Similar frontal and parietal regions were commonly activated both locally for task switching processes during the *implementation phase* as

well as globally for reversed rule encoding processes during the *instruction phase*. There is now converging evidence that this fronto-parietal network forms a generic neural system that supports cognitive control processes of many forms (Cole & Schneider, 2007; Cole et al., 2013; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Duncan, 2013). It is therefore unsurprising that task switching and rule reversal both involved areas belonging to this network, which might reflect the common need of task set and rule set re-configuration and the control of interference arising from competing tasks or rules.

The finding that the fronto-parietal involvement was dissociated in time regarding task switching processes (implementation) and rule reversal processes (instruction) stands in contrast to a previous study by De Baene et al. (2012). In that study, regions within the fronto-parietal control network were found to be involved in both, task switching and rule reversal and, importantly, both during the preparation of task/rule implementation. The reason for this different pattern of results is likely due to the fact the task switching and rule reversal were orthogonally crossed on a trial-by-trial basis thus lacking the local-global hierarchy as realized in the present study. Together, this suggests that rule reversals – when valid for a considerable number of consecutive trials as in the present study – require fronto-parietal engagement only briefly during the instruction phase to fully re-establish the reversed rules – at least as far as fronto-parietal control processes are concerned.

While this is consistent with the almost negligible (yet significant) RT reversal cost of only 6 ms and error rate reversal cost of below 1%, it is at first glance inconsistent with previous findings from the trial-and-error reversal learning literature where some studies did imply the fronto-parietal network in reversal learning processes during rule implementation (Mitchell et al., 2009; Xue et al., 2008). This discrepancy might be due to quite different ways of how a rule reversal is initiated. In the present study, the currently valid rules were explicitly instructed independently of actual behavioral performance. By contrast, in previous studies a rule reversal was instead initiated via an error feedback signal contingent upon behavioral performance. Hence, in trial-and-error learning, reversal processes are by nature tightly linked to behavioral rule implementation. Yet, the evaluation of performance feedback might in fact be more closely related to the *instruction phase* in the current study rather than to the implementation of these just encoded rules. Interestingly, however, another recent instruction-based reversal learning study (Ruge & Wolfensteller, 2016a) compared the initial learning of novel rules with the subsequent reversal of these just acquired (thus, only weakly practiced) rules. Under such circumstances, instructed rule reversal did activate the fronto-parietal network throughout the entire *implementation phase*. This suggests that the absence of reversal-related fronto-parietal activation during implementation in the present study might be due to the fact that both rule sets were well learned because they were repeatedly used across the course of the experiment. Hence, both rules might have been transformed into less fragile memory representations. Under these circumstances, explicit instructions might be sufficient to update working memory representations in a highly specific manner. Once updated, working memory representations might then guide rule implementation

during the subsequent *implementation phase* without interference from the competing rule which can be maintained outside the currently active working memory buffer. By contrast, if reversed and initially learned rules are both still relying on relatively fragile working memory representations as in Ruge and Wolfensteller (2016a) this might imply strong interference throughout practice.

4.2 | The role of OFC in instructed and feedback-driven rule reversal

In a recent study on *instruction-based* reversal learning (Ruge & Wolfensteller, 2016a), reversal-related activation in the lateral OFC during the instruction phase was negatively correlated with the behavioral reversal cost in the subsequent rule implementing phase. This finding points to the importance of lateral OFC in reversed rule encoding via instruction. As mentioned above, most previous imaging studies have investigated rule reversal learning by trial-and-error where no explicit instruction is given and participants instead need to utilize response feedback to infer the currently valid rule. Such studies have emphasized the role of the lateral OFC/VLPFC for reversal learning by trial-and-error. In particular, these regions typically showed higher activation in trials before or at successful rule reversal compared to trials after successful rule reversal (Cools et al., 2002; Kringelbach & Rolls, 2003; O'Doherty et al., 2003; Remijne et al., 2005). This general finding indicates that these regions might be specifically relevant for reversed rule extraction rather than for their subsequent implementation. This is consistent with the results of the present study which indicate an increase in reversal-related activation in the lateral OFC only during the *instruction phase* (equivalent to rule extraction trials in feedback-driven learning) but not during the implementation of instructed reversed rules.

4.3 | The role of cortico-striatal loops in instruction-based rule reversal learning

In the *implementation phase*, we assessed brain activation dynamics under instruction-based reversal learning in order to explore how the brain gradually adapts to the reversed rule instructions. As discussed above most regions typically involved in feedback-driven reversal learning (fronto-parietal network regions and lateral OFC) were relevant for instruction-based reversal learning exclusively during the *instruction phase*. However, we did find that a different set of areas, including the right putamen, the SMA, pre- and post-central gyri, and the posterior insula/operculum exhibited practice-related activation increase specifically in rule-reversal blocks. Notably, most of these areas are part of the cortico-striatal motor loop (Alexander, DeLong, & Strick, 1986; Schell & Strick, 1984) with the putamen being widely believed to be involved in establishing habit-like (i.e., directly stimulus-triggered and increasingly automatized) action (Ashby, Turner, & Horvitz, 2010; Bal-leine, Delgado, & Hikosaka, 2007; Dolan & Dayan, 2013; Seger & Spiering, 2011; Yin & Knowlton, 2006) even within short periods of practice (Brovelli, Laksiri, Nazarian, Meunier, & Boussaoud, 2008; Ruge & Wolfensteller, 2015; Seger & Spiering, 2011). According to the standard view, the putamen is thought to receive input from

somatosensory and motor cortices including pre- and post-central gyri, and the terminal output region is thought to be the SMA which is critical for movement programming and control (Alexander et al., 1986; Schell & Strick, 1984). Interestingly, recent evidence suggests a functional link between posterior insula/operculum and the SMA and somatosensory cortex (see Drouman, Read, & Bechara, 2015 for review) and an involvement of this network in instructed stimulus-response learning (Mohr et al., 2016). This is in line with our present observation that posterior insula/operculum shares a similar functional profile with the rest of the cortico-striatal motor loop.

In light of this general functionality, it seems reasonable to assume that the specific activation increase across the course of a reversal block indicates that the putamen (together with the associated cortical areas) supports the re-learning or re-binding of instructed S-R associations which is required in the reversal block but not in the nonreversal block.

Different from the reversal-specific activation increase in areas belonging to the fronto-striatal motor loop, another set of co-activated frontal and striatal regions, including caudate head, OFC, VMPFC, and temporal cortex showed a similar practice-related activation increase in *both* reversal blocks and nonreversal blocks. Interestingly, this is the same set of regions that exhibited practice-related increase during the practice of instructed *novel* rules which never reversed (Ruge & Wolfensteller, 2010, 2013) and in the studies of feedback-driven novel rule learning (e.g., Brovelli et al., 2008; Toni, Ramnani, Josephs, Ashburner, & Passingham, 2001). One tempting interpretation of this common pattern across different learning paradigms suggests that these regions learn from scratch each time an ongoing learning episode is interrupted by a new instruction screen. In other words, these regions interpret novel learning blocks, reversal learning blocks, and nonreversal learning blocks all alike as "novel learning" situations so as if they are reset to baseline between blocks.

5 | CONCLUSIONS

Based on the present findings we propose that different aspects of local and global adaptation processes were implemented by partly overlapping and partly segregated neural systems when coping with these two hierarchically related demand changes. The fronto-parietal cognitive control network supported the encoding of reversed rules on the global block level at the time of explicit rule instruction before the same regions were subsequently involved in local task switching processes on the trial level. Hence, it seems that the (re-)configuration of rule set and task set are accomplished sequentially without further interaction during task implementation. By contrast, two distinct cortico-striatal networks supported different learning-related processes in the context of instructed rule reversal. The cortico-striatal "motor loop" (putamen, SMA, pre- and post-central gyri) together with the posterior insula/operculum seemed to support the rapid re-binding of instructed S-R associations. By contrast, another cortico-striatal network including caudate head, OFC, medial PFC, and temporal cortex which showed a similar practice-related increase across trials

irrespective of reversal learning demands, might support the learning of S-R associations from scratch each time an ongoing learning episode is interrupted by a new instruction.

Importantly, the present study realized only a subset of all possible combinations of factor levels regarding the “timescale of change” (global/local demand changes) and the “content of change” (rule reversal/task alternation). We were particularly interested in the asymmetrical relation between *global* rule reversal and *local* task switching. Specifically, we reasoned that in natural environments it is typically the case that we have to deal with infrequent changes of rules (e.g., driving rules in different countries) combined with frequent changes of the priority of tasks even though the rules of the individual tasks remain unchanged. Nevertheless, it would be an interesting follow-up question for future research to realize other combinations of factor levels, for instance, by combining local rule reversal under globally different task switching probability expectations.

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