

Aus dem Institut
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der Medizinischen Fakultät Charité – Universitätsmedizin Berlin

DISSERTATION

Switch-Independent Task Representations in Frontal and
Parietal Cortex

zur Erlangung des akademischen Grades
Doctor medicinae (Dr. med.)

vorgelegt der Medizinischen Fakultät
Charité – Universitätsmedizin Berlin

von

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Datum der Promotion: 18.12.2020

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Abstrakt Englisch

In order to adapt to the surrounding dynamic environment humans must be able to frequently switch between tasks. This switching requires cognitive control. It is effortful and impairs task performance which is reflected in behavioral switch costs. Task switching research has investigated the contributions of top-down and bottom-up processes on switch costs and there is an ongoing debate about the composition of the behavioral performance decrease present in switch trials. fMRI studies that investigated the underlying neural processes of task switching have mostly focused on regional activation differences. Frontal and parietal regions show increased activity for task switches and task repetitions, but investigation of activation differences yielded heterogeneous results. Recent multivoxel pattern analysis enables the investigation of neural task representations which are located in frontal and parietal brain regions. The question arises how these task representations might be subject to task switching processes: they might be strengthened by increased control demands during switching or be degraded by interference of the previous task set. Alternatively, task representations might not be affected by task switching processes and task representation might generalize across switched-to and repeated tasks. The present study cued participants to perform one of two tasks (with equally frequent task repetitions and switches). It compares the accuracy with which a linear classifier is able to decode the currently performed task from patterns of participants' brain activity. This reflects the strength of a task representation. As expected, tasks were represented in frontal and parietal cortex. However, there was no difference of decoding accuracy between switch and repeat trials. Moreover, tasks are represented in a switching independent spatial pattern in these regions. There was no evidence for the decodable strength of task representations to account for the performance cost associated with task switching.

Abstrakt Deutsch

Um sich an die umgebene dynamische Umwelt anzupassen müssen Menschen in der Lage sein häufig zwischen Aufgaben zu wechseln. Diese Wechsel erfordern kognitive Kontrolle. Sie sind aufwendig und beeinträchtigen die Ausführung der Aufgaben, was sich in behavioralen Wechselkosten widerspiegelt. Bisherige Forschung zu Aufgabenwechseln hat die Mitwirkung von *Top-down* und *Bottom-up* Prozessen an Wechselkosten untersucht und es besteht eine fortwährende Debatte um die Zusammensetzung der behavioralen Leistungsminderung in Wechselaufgaben. fMRT Studien, welche die zugrundeliegenden neuronalen Prozesse untersuchten, haben sich überwiegend auf die regionalen Aktivierungsunterschiede konzentriert. Frontale und parietale Regionen zeigen verglichen mit Aufgabenwiederholungen eine erhöhte Aktivität während Aufgabenwechseln. Die Untersuchungen dieser Aktivitätsunterschiede ergeben jedoch heterogene Ergebnisse. Jüngste Multivoxel-Muster-Analysen ermöglichen die Untersuchung von neuronalen Aufgabenrepräsentationen, welche in frontalen und parietalen Hirnregionen lokalisiert sind. Es stellt sich die Frage in welcher Form diese Aufgabenrepräsentationen von Aufgabenwechselprozessen beansprucht werden: sie könnten von durch Aufgabenwechsel erhöhte Kontrollanforderungen verstärkt oder von interferierenden vorangehenden Aufgabensets geschwächt werden. Die vorliegende Studie wies Versuchsteilnehmer an eine von zwei Aufgaben auszuführen (mit insgesamt gleichfrequenten Aufgabenwechseln und Aufgabenwiederholungen). Sie vergleicht dabei die Genauigkeit mit welcher ein linearer Klassifikator in der Lage ist die aktuell ausgeführte Aufgabe auf Grundlage der Hirnaktivität des Teilnehmers zu dekodieren. Dies reflektiert die Stärke der Aufgabenrepräsentation. Wie zu erwarten waren die Aufgaben im frontalen und parietalen Kortex repräsentiert. Allerdings gab es keinen Unterschied der Dekodierungsgenauigkeit zwischen Wechsel- und Wiederholungsaufgaben. Darüber hinaus sind die Aufgaben in diesen Regionen durch ein vom Wechsel unabhängiges räumliches Muster repräsentiert. Es gibt keine Hinweise dafür, dass die dekodierbare Stärke der Aufgabenrepräsentationen zu den Leistungseinbußen beiträgt, welche mit Aufgabenwechsel assoziiert sind.

Manteltext

Task switching

Humans live in a dynamically changing multitask environment, requiring frequent changes between cognitive tasks. The numerous perceivable stimuli at each moment in time provide an even greater amount of possible actions to be performed (Meiran, 2000). When sitting in front of the computer to work on an important manuscript the telephone starts to ring. Luckily, we are able to ignore some stimuli (the ringing telephone), yet still have to choose between other possible actions (checking the news on the internet or actually start writing). The question arises as to how humans are able to perform tasks in a goal-directed manner - how do we select and organize the required cognitive processes to ensure successful performance? Some form of top-down control is needed to select and execute the goal-relevant task despite competing stimuli and action possibilities (Corbetta & Shulman, 2002; Kok, Ridderinkhof, & Ullsperger 2006; Cole & Schneider, 2007; Sakai, 2008).

The *task switching paradigm* has been used to study this form of cognitive control (Meiran, 2010; Kiesel et al., 2010). A typical version, the cued task switching paradigm, presents participants a stimulus (e.g. a geometrical object) and a cue that indicates which of two (or more) possible actions is to be performed (e.g. assessment of the object's shape or judgement of its color).

A well replicated finding in task switching research shows higher accuracy and faster responses to tasks that have been repeated in contrast to tasks that have just been switched to (Jersild, 1927). Such a performance decrease from sequences of repetition trials to sequences of switch trials (e.g. AAAA vs ABAB; Allport, Styles, & Hsieh, 1994) can be observed. These *mixing costs* are considered to reflect "global" costs of task switches compared with single task blocks (Los, 1996; Hübner, Futterer, & Steinhauser, 2001; Rubin & Meiran, 2005).

Because these mixing costs do not necessarily reflect switching processes but may also arise due to confounds, such as higher working memory load in mixed tasks (Rogers & Monsell, 1995; cf. Rubin & Meiran 2005), most task switching research has focused on the also observed “local” performance decrease for switch trials compared with repetition trials in mixed task sequences (e.g. AABABB; Rogers & Monsell, 1995). This effect has been termed *switch cost*, and led to a broad discussion on the underlying mental processes (see Kiesel et al., 2010 for a review). While the decreased accuracy is held to be an indicator for less reliable task performance during switch trials the bulk of task switching research focusses on the switch cost of reaction time, thus slower responses on switch trials when compared to repetition trials, so that it further mentioning of switch costs will refer to such.

Theoretical background of switch costs

It has been postulated that the switch cost reflects the time needed for the reconfiguration of the relevant task set, removing the parameters of the previous task set to replace with the task set at hand (Rogers & Monsell, 1995). The *task set reconfiguration* theory has been backed by the finding that increased preparation time for a task leads to decreased switch costs (Monsell, Sumner, & Waters, 2003), although even with increased preparation time a residual switch cost remains present (Rubinstein, Meyer, & Evans, 2001).

Another popular theory about the underlying processes is that of *task-set inertia*. In this theory, task-set parameters of the previous, irrelevant task are still present and cause interference that needs to be overcome to perform the now relevant task. This assumption is supported by asymmetric switch costs: switching from a difficult task to an easy task creates greater switch cost than vice versa (Allport et al., 1994; Wylie & Allport, 2000). The time to resolve the older, more difficult task-set interference is greater than overcoming the interference of the easier task – this is reflected in the unequal switch cost.

By utilizing explicit cues for each task, further research was able to show that both of the above stated concepts appear to be reflected in the switch cost: the influence of time between cue (what task is to be performed) and stimulus (actual performance) on switch cost reflects task specific reconfiguration processes: longer preparation intervals leaving more time for reconfiguration which in turn result in smaller switch costs (Meiran, 1996). The effect of time between stimulus and the following task cue on switch costs is an indicator that task set inertia also contributes to them: longer intervals leaving more time for the previous, now irrelevant task set activation to decay result in less switch costs (Meiran, Chorev, & Sapir, 2000). Cued task switching also has its caveats, e.g. confounds of cue switching in task switching (Logan & Bundesen, 2003; Mayr & Kliegl, 2003). However, in line with these findings many theorists argue that the above outlined concepts appear to be both reflected in switch costs: the cognitive control required to switch to performing a different task (e.g., loading a new task-set into working memory and reconfiguring stimulus-response rules) *and* the involuntary processes such as proactive interference from a previous task-set, between-task crosstalk, and stimulus-driven retrieval of currently irrelevant task-sets (for reviews see Monsell, 2003; Kiesel et al., 2010; Vandierendonck Liefoghe, Verbruggen, 2010).

Task switching in neuroimaging

Neuroimaging studies have used functional magnetic resonance imaging (fMRI), to study the neural basis of cognitive control (Miller & Cohen 2001; Bunge, 2004; Poldrack, 2006; Aron, 2007). In line with the theoretical background from behavioral studies outlined above neuroimaging has been used to find evidence for and against top-down and bottom-up related neural processes involved with task switching (Wager, Jonides, & Reading, 2004; Shallice, Stuss, Picton, Alexander, & Gillingham, 2008; Richter & Yeung, 2014). However, one has to keep in mind that while having a relatively high spatial resolution fMRI suffers from low

temporal resolution. The localization of activity is in most cases based on blood oxygenation level dependent (BOLD) response signals which unfolds over several seconds, as the blood oxygenation level increases in active neural tissue (Logothetis & Wandell, 2004). This limitation appears crucial when adapting the task switching paradigm for fMRI research. Its main effect, the switch cost, is mostly based on relatively small reaction time differences when compared to the pacing of fMRI scan acquisition. Timing considerations are also important when designing a task switching fMRI experiment. For example: with inter-trial intervals that are too long subjects might treat each trial as an individual event or restart trial (Allport & Wylie, 2000), with little incentive for the establishment of a stable task set (Richter & Yeung, 2014). Thus, observed effects in data based on BOLD signal of fMRI studies might always be accounted to an ill chosen design compromise between slow trial pacing to acquire separable BOLD responses and faster pacing that is required in order to allow the creation of stable task sets. Bearing this in mind fMRI can be used to understand and integrate the concepts of the presumed top-down and bottom-up processes involved in task switching (Richter & Yeung, 2014). It should be noted that other techniques, such as electroencephalography (EEG, Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Nicholson, Karayanidis, Bumak, Poboka, & Michie, 2006; Jost, Mayr, & Rösler, 2008) or lesion studies (Aron, Monsell, Sahakian, & Robbins, 2004; Mayr, Diedrichsen, Ivry, & Keele, 2006; Shallice, Stuss, Picton, Alexander, & Gillingham, 2008a, 2008b) have also been used to investigate neural mechanisms under task switching, but are not discussed here.

In general, most previous research found task switching related activity in frontal and parietal regions (Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Sohn, Ursu, Anderson, Stenger, & Carter, 2000; Braver, Reynolds & Donaldson, 2003; Sakai & Passingham, 2003; Crone, Donohue, Honomichl, Wendelken, & Bunge, 2006; Gruber, Karch, Schlueter, Falkai &

Goschke, 2006; Yeung, Nystrom, Aronson, & Cohen, 2006; Jamadar, Hughes, Fulham, Michie, & Karayanidis, 2010; see Wager et al., 2004; Karayanidis et al., 2010 for meta analyses).

An obvious question to neuroimaging would be whether there is a difference in neural activity between switch and repeat trials. This could reflect the reconfiguration processes and/or increased task interference during task switching. However, results are heterogeneous and do not provide unambiguous support towards switch specific neural activation differences: while many studies do find the increased neural activity during task switching in frontal and parietal regions to differ between switch and repeat trials (see Richter & Yeung, 2010 for a meta analysis), some studies do not find this difference (Brass & von Cramon, 2002, 2004; Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Luks, Simpson, Feiwell, & Miller, 2002; Ruge et al., 2005, Cavina-Pratesi et al., 2006; Gruber et al. 2006). Some null results can be explained by design decisions - some of which are fMRI related, as explained above. Others are not fMRI specific, such as the use of high switch probabilities, which leads to lower switch costs (Monsell & Mizon, 2006) and possibly weaker activation difference (e.g. Brass & von Cramon, 2004; Crone et al. 2006). Therefore, it can be stated that task switching might generally be associated with frontal and parietal neural activation, but there are many exceptions (also see Ruge, Jamadar, Zimmermann, & Karayanidis, 2013 for a review). The fronto-parietal network is typically linked to executive function and attention (Aron, 2007; Petersen & Posner, 2012) and shows activation increase in situations of high cognitive demand (Duncan, 2010). The quantitative difference in these regions under task switching demands does provide support for the reconfiguration theory, because it assumes that task switching relies on top-down processes. However, such activation differences can also be explained by task set inertia, as the increased activity might reflect the neural reaction to the raised between-task competition in task switches (Ruge et al., 2013). Additionally, such differences might be the product of adaptation

processes, which have also been observed to gradually take place during consecutive repetitions (De Baene & Brass, 2011).

A more unique indicator in favor of the task reconfiguration theory would be a switch specific activation as opposed to the mere relative activation difference described above. In case of a qualitative reconfiguration process to take place during switching one would expect activation of regions only under switch conditions. However, such explicit switch related activation has not been confirmed (Ruge et al., 2013) and the areas observed to be active under switching are also activated in repetition trials. Such quantitative difference of neural activity is found both in task preparation (Brass & von Cramon, 2004) and task execution (Dove, 2000). This has led to the conclusion that similar processes occur under switch and repeat conditions, only varying quantitatively in the amount of processing required (Kiesel et al., 2010; Ruge et al., 2013).

Theories of task set inertia have been tested in neuroimaging studies using a different approach: subjects perform tasks that evoke activity in different brain regions, thus being dissociable in univariate analysis. A persistent activity of the previous task during the new (switched to and now relevant) task would be an indicator for the previous (now irrelevant) task set to remain active. Such persistent activity has been observed (Wylie, Javitt, & Foxe, 2006). It has also been shown that its strength predicts the size of behavioral switch costs (Yeung, Nystrom, Aronson, & Cohen, 2006), lending further support to the idea of between task competition as a bottom-up source of performance costs in task switching. It is important to note, that in this theoretical context of bottom-up influence on the switch cost some form of higher cognitive control is still required to select the relevant and suppress the irrelevant task set (Monsell, 2003), so that it doesn't rule out such processes to also contribute to switch costs.

MVPA and task sets

Most previous fMRI research on the topic of task switching has investigated neural substrates of the underlying processes by contrasting overall BOLD signal differences of the various switch conditions. This univariate approach applies spatial smoothing and normalization to the acquired data. Statistical analyses is then performed with a general linear model for each individual voxel (Friston et al., 1995). Mass-univariate studies consider differences between great quantities of voxels but consider each individual voxel separately, focusing on regional differences (Haynes & Rees, 2006). Applied to task switching, univariate approaches allow assumptions about the brain regions that mediate possible conflicts or reconfigure parameters of tasks during task switching. However, the question on how task switching related processes affect the encoding and transformation of tasks in the brain cannot sufficiently be answered by univariate studies.

Recent multivoxel pattern analysis (MVPA; Kriegeskorte, Goebel, & Bandettini, 2006; Haynes & Rees 2006; Haynes, 2015) has been used to investigate neural task representations. MVPA considers information that might be present in patterns of multiple voxels. The concept provides a link between mental task representation and the corresponding fMRI activity patterns. This method of content-selective spatial patterning derives concepts from neural representation theories that involve population codes, where each content involves the distributed activation of more than one representational unit (Pouget, Dayan, & Zemel, 2000). It is important bear in mind that voxel population is different from the neural population: each voxel reflects a population receptive field, thus the summed activity of large quantities of neurons. The relationship between the acquired BOLD signal and the underlying activity are complex and can be indirect (Logothetis & Pfeuffer, 2004).

Using MVPA, brain activity is analyzed at the level of patterns consisting of a set of spatially conjoined voxels (e.g. selected in form of a sphere). These samples of brain activity are then

assigned labels indicating the experimental condition under which they were acquired. A classification algorithm is then trained on part of the samples. The remaining samples, that constitute the test dataset, are then used to assess whether the classifier is able to correctly assign the labels with the information learned in the training dataset. The proportion of correctly assigned labels is then compared against the proportion of samples that would have been labeled correctly based on guessing alone. If the classifier is able to do classify the new test set into the correct labels with statistically significant above-chance accuracy, it is presumed to have extracted and generalized information from the training data set (for more information see Haynes, 2015).

Regarding task representations, classifiers are able to extract information about tasks in sets of voxels (Haynes, Sakai, Rees, Gilbert, Frith & Passingham, 2007) located in parietal (Bode and Haynes, 2009; Woolgar, Hampshire, Thompson, & Duncan, 2011; Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014; Wisniewski, Reverberi, Momennejad, Kahnt, & Haynes, 2015; Etzel, Cole, Zacks, Kay, & Braver, 2015), medial (Gilbert, 2011; Momennejad & Haynes, 2013), and lateral prefrontal cortex (Cole, Etzel, Zacks, Schneider, & Braver, 2011; Reverberi, Görge, & Haynes, 2012). Note, that these regions are also associated with task switching and the increased cognitive demands, as described above. The present study was able to replicate these findings of parietal and prefrontal locations to encode tasks.

Task representations have been subject to further research. The neural task code can be compositional (Reverberi et al., 2012) and its representational strength, measured by the decoding accuracy of the classifier, is altered by rule complexity (Woolgar, Afshar, Williams, & Rich, 2015) and skill acquisition (Jimura, Cazalis, Stover, & Poldrack, 2014). On the other hand, their coding can also be robust and the task representation remains unaffected by whether

tasks were novel or were performed routinely (Cole et al., 2011) or whether tasks were externally cued or chosen freely (Wisniewski, Goschke, & Haynes, 2016).

Essential new findings: Task sets in task switching

In face of the previously outlined discussion about task switching theories and the reconfiguration or cross-talk of task-sets the question appears immanent as to how task representations are affected by task switching. With the capability of MVPA to investigate task representations two questions regarding this topic are answered in the present study:

(1) How do different control demands on task switch versus repeat trials affect the strength of neural task representations?

(2) Is the neural code of task representations independent of task switching?

The first question can be more accurately phrased for the MVPA method used: does the decoding accuracy with which the classifier can decode tasks from neural activation patterns differ between task-switch and task-repeat trials? The present study's results indicate that task decoding does not differ between task switching and task repetition (see below). One might have expected that the decoding accuracy does differ with the assumption of proactive interference due to task set inertia (Allport et al., 1994) or inhibition by previously established task sets (Goschke, 2000; Mayr & Keele, 2000). These processes are plausible candidates to modulate task representations because they presumably result in task representations that are less distinct on switch trials compared with repeat trials due to a transient increase in the recently performed task activation (Yeung & Monsell, 2003). In contrast to less discriminable switch-trial task representations as a result of such bottom-up processes it has also been postulated that higher cognitive control demands in switch trials might sharpen the representations of relevant variables needed for current task performance. A greater discriminability would lead to enhanced lower-level processing of the relevant information

enabling selective gating of information that is processed in decision making and action selection (Waskom et al., 2014). As a consequence of these considerations a difference in task set distinctness could show in a difference of task decoding accuracy. The absence of such an effect does not rule out the effect of task inertia, inhibition or top-down control processes. The present results did not find evidence for a significant difference in task decoding. This suggests that the aforementioned well supported theoretical processes take place at a different stage of task processing but not on the level of task representations. Moreover, the implication of cognitive control needed to select the relevant task set does not require that the neural representation of the different tasks is altered. It is sufficient that the system is capable of rapidly deactivating an old and retrieving or implementing a new task set. For instance, a connectionist network that relies on task representations as sustained activation patterns is flexible to the degree that it is able to easily switch from one to another attractor state representing different tasks without interference of other tasks. This would not require activation patterns representing tasks to change. This idea is similar to the interpretation of findings of context-independent rule representations that are considered to allow robust selective attention to the information relevant to the current task (Zhang, Kriegeskorte, Carlin, & Rowe, 2013).

Along this idea the present study also answered a second question: Is the neural code of task representations independent of task switching? More specifically, is the classifier able to extract spatial activation patterns from switch trials and generalize them to correctly classify patterns of repeat trials of the same task?

The present study's findings of switch independent task representations have, to our knowledge, not been demonstrated before. It adds to the findings of previous research that demonstrate generalization of task sets across varying experimental conditions such as

novelty (Cole et al., 2011), difficulty (Wisniewski et al., 2015) or being freely chosen/externally cued (Wisniewski et al., 2016). Such robust encoding of tasks under different contexts appears beneficial as it allows fast retrieval and access to task sets and thus permits efficient flexibility in a dynamic environment (Zhang et al., 2013).

It should be noted, that further research on this topic appears to yield diverging results. While Waskom et al., 2014 did observe different decoding accuracies of rules regarding perceptual discriminations for switch and repeat trials, they did not observe behavioral switch costs. This complicates assumptions made about task switching related processes, as switch costs are the basic principle task switching research is based upon. Qiao et al. 2017 observed behavioral switch costs and higher task decoding accuracies in repeat compared to switch trials. This is complemented with the finding of increased neural representational pattern dissimilarity across consecutive trials for switch trials compared with repeat trials (Qiao, Zhang, Chen, & Egner, 2017). However, another study has failed to observe task decoding accuracies to differ between switch and repeat trials (Long & Kuhl, 2018). These divergent findings on the influence of switching on task representations suggest that further research is needed to clarify the role of task domain specific effects and attentional processes regarding task representations (Liu & Hou, 2013).

Further questions for future research

Because decoding accuracies in the present study did not turn out to be a function of the behavioral switch cost further neuroimaging research is needed to understand the composition of neural processes responsible for the performance cost. The present study's paradigm was not designed to decide between suggested top-down or bottom-up theories, but indicates that these processes might take place at a different level of task processing and

not at the level of task representation. Future task switching MVPA designs might target the temporal dynamics of task set retrieval in switch and repeat trials.

Furthermore, the present study decoded task sets from an execution phase and did not dissociate task preparation and actual task performance due to the temporal limitations of the highly optimized MVPA design for fMRI. The preparation phase of tasks has received a great deal of attention by univariate fMRI studies (see Ruge et al., 2013 for a review) because longer task preparation phases lower the behavioral switch costs and are thus thought to contain a large portion of the task related processes responsible for the performance cost. It is thus feasible to further investigate this phase and the modifiable factors (e.g. cue-stimulus interval; stimulus-cue-interval) by observing its effects on task representations.

As mentioned above, recent research (Qiao et al., 2017) has already used representational similarity analysis (RSA; Kriegeskorte et al., 2008) in order to assess the similarity of task sets between switching conditions. This approach appears promising for further investigation of task sets in the different phases of preparation and execution.

The divergent results of switch dependent (Waskom et al. 2014; Qiao et al., 2017) and switch independent (Long & Kuhl, 2018) task representations also call for further research in order to identify the factors that influence the modulation of task decoding. It appears that future studies regarding these factors should target the actual content of tasks (Qiao et al, 2017) and attentional features thereof (Liu & Hou, 2013).

The concepts of MVPA task decoding might also be seminal when used on designs with three or more tasks. This setting of task switching should allow further disentanglement of the interference of previous task sets (Mayr and Keele, 2000).

In conclusion the present study provides novel insights into the effects of task switching on neural task representations. The decoding of task revealed no reliable differences between switch and repeat trials. Task is encoded independent of the switch and repeat condition in frontal and parietal regions. These findings suggest that the underlying neural processes of task switching take place at a different stage of task processing – not on the level of task representations.

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„Ich, Lasse Steffen Loose, versichere an Eides statt durch meine eigenhändige Unterschrift, dass ich die vorgelegte Dissertation mit dem Thema: „Switch-Independent Task Representations in Frontal and Parietal Cortex“ selbstständig und ohne nicht offengelegte Hilfe Dritter verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel genutzt habe.

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„Switch-Independent Task Representations in Frontal and Parietal Cortex“

Journal of Neuroscience, 2017

Beitrag im Einzelnen:

Literaturrecherche; Entwicklung des experimentellen Paradigmas; Verfassen und Stellen des Ethikantrags;

Pilotierung: Entwicklung der Präsentations- und Datenerhebungsskripte sowie technische Realisierung im Behavioralen Labor; Probandenakquise; Datenerhebung und Evaluierung der erhobenen Pilotierungsdaten; Insgesamt vier Veränderungen des experimentellen Designs mit Zielsetzung der Fehler- und Störfaktoranalyse, Vergrößerung des zentralen behavioralen (*switch cost*) Effekts sowie der Optimierung für spätere multivariate Datenanalyse; Durchführung von fünf Pilotexperimenten; Stimulusentwicklung; Entwicklung der Präsentation des finalen Experiments.

Experimentelle Durchführung: Erstellen des experimentellen Designs und Optimierung für die spätere Datenanalyse; Festlegen und Planen der später durchzuführenden Analysen; technische Realisierung der Trainingsphase im behavioralen Labor; Probandenakquise; Auswertung der Trainingsphase; technische Realisierung des Experiments (Tests und Durchführung der Präsentation im Scanner; Behaviorale Datenerhebung im Scanner; Synchronisation der Präsentationsskripte mit dem MRT-Scanner); Datenerhebung durch MRT Scanner.

Datenanalyse: Datenvorbehandlung; Verknüpfen der behavioralen und der MRT Daten; Kontrolle der Datenvorbehandlung; Identifizieren von Ausschlusskriterien; Erstellung der Skripte zur Errechnung der Generalisierten Linearen Modelle unter Berücksichtigung der relevanten Regressoren sowie Durchführung und Kontrolle von deren Berechnung; Erstellung und Auswertung der Plausibilitätsprüfung der erhobenen MRT-Daten; Univariate Datenanalysen. Multivariate Datenanalyse: Implementierung der Decoding Toolbox und Durchführung der Searchlight Analyse; Gruppenanalyse der Decoding Analysen; Entwicklung

und Durchführung der Region-of-Interest Analyse Skripte (Individuelle und Gruppenanalyse).
Durchführung und Auswertung der behavioralen Datenanalysen (ANOVA; t-Tests).
Publikation: Erstfassung des Manuskriptes; Erstellung der Darstellungen, Tabellen und
Abbildungen; Editieren des Manuskriptes und Einarbeitung der Vorschläge der Co-Autoren;
Einreichen des Manuskripts beim Journal of Neuroscience. Revision des Manuskriptes:
Editieren des Manuskripts und Einarbeitung der Vorschläge der Gutachter. Erstellen und
Durchführen weiterer Analysen auf Grundlage der Gutachtervorschläge: Ergänzung der
Ergebnisse mit entsprechenden *BayesFactor*-Berechnungen; Vergleich von *Cross-*
classification Decodings mit einfachen (gerichteten) Decodings; Erstellung und Vergleich der
Ergebnisse des verwendeten *Linear Classifier* mit einem *Representational Similarity*
Classifier. Einarbeiten der zusätzlichen Ergebnisse in das Manuskript; Erstellung des
Gutachter-Antwortschreibens; Abschließende Korrespondenz nach Akzeptanz mit dem
Journal of Neuroscience bis zur Publikation.

Unterschrift, Datum und Stempel des betreuenden Hochschullehrers

John-Dylan Haynes

Lasse Steffen Loose

Auszug aus der Journal Summary List (ISI Web of Knowledge)

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12	TRENDS IN NEUROSCIENCES	20,061	11.439	0.026860
13	BRAIN	52,061	10.840	0.075170
14	SLEEP MEDICINE REVIEWS	6,080	10.602	0.010720
15	ANNALS OF NEUROLOGY	37,251	10.244	0.053390
16	Translational Stroke Research	2,202	8.266	0.005260
17	NEUROSCIENCE AND BIOBEHAVIORAL REVIEWS	24,279	8.037	0.048460
18	NEUROSCIENTIST	4,738	7.461	0.008730
19	NEURAL NETWORKS	10,086	7.197	0.015290
20	FRONTIERS IN NEUROENDOCRINOLOGY	3,924	6.875	0.006040
21	NEUROPSYCHOPHARMACOLOGY	24,537	6.544	0.042870
22	CURRENT OPINION IN NEUROBIOLOGY	14,190	6.541	0.034670
23	Molecular Neurodegeneration	3,489	6.426	0.009850
24	CEREBRAL CORTEX	29,570	6.308	0.058970
25	BRAIN BEHAVIOR AND IMMUNITY	12,583	6.306	0.026850
26	BRAIN PATHOLOGY	4,952	6.187	0.007750
27	Brain Stimulation	4,263	6.120	0.014510
28	NEUROPATHOLOGY AND APPLIED NEUROBIOLOGY	3,654	6.059	0.006350
29	JOURNAL OF CEREBRAL BLOOD FLOW AND METABOLISM	19,450	6.045	0.028280
30	JOURNAL OF NEUROSCIENCE	176,157	5.970	0.265950
31	Molecular Autism	1,679	5.872	0.006320
31	Translational Neurodegeneration	589	5.872	0.002280
33	GLIA	13,417	5.846	0.020530
34	Neurotherapeutics	3,973	5.719	0.008980
35	PAIN	36,132	5.559	0.038000
36	NEUROIMAGE	92,719	5.426	0.152610
37	Acta Neuropathologica Communications	2,326	5.414	0.011550
38	Multiple Sclerosis Journal	10,675	5.280	0.021890

Switch-Independent Task Representations in Frontal and Parietal Cortex

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Alternating between two tasks is effortful and impairs performance. Previous fMRI studies have found increased activity in frontoparietal cortex when task switching is required. One possibility is that the additional control demands for switch trials are met by strengthening task representations in the human brain. Alternatively, on switch trials, the residual representation of the previous task might impede the buildup of a neural task representation. This would predict weaker task representations on switch trials, thus also explaining the performance costs. To test this, male and female participants were cued to perform one of two similar tasks, with the task being repeated or switched between successive trials. Multivoxel pattern analysis was used to test which regions encode the tasks and whether this encoding differs between switch and repeat trials. As expected, we found information about task representations in frontal and parietal cortex, but there was no difference in the decoding accuracy of task-related information between switch and repeat trials. Using cross-classification, we found that the frontoparietal cortex encodes tasks using a generalizable spatial pattern in switch and repeat trials. Therefore, task representations in frontal and parietal cortex are largely switch independent. We found no evidence that neural information about task representations in these regions can explain behavioral costs usually associated with task switching.

Key words: cognitive control; fMRI; MVPA; parietal cortex; task switching; task set

Significance Statement

Alternating between two tasks is effortful and slows down performance. One possible explanation is that the representations in the human brain need time to build up and are thus weaker on switch trials, explaining performance costs. Alternatively, task representations might even be enhanced to overcome the previous task. Here, we used a combination of fMRI and a brain classifier to test whether the additional control demands under switching conditions lead to an increased or decreased strength of task representations in frontoparietal brain regions. We found that task representations are not modulated significantly by switching processes and generalize across switching conditions. Therefore, task representations in the human brain cannot account for the performance costs associated with alternating between tasks.

Introduction

To reach desired goals, humans are often required to switch between different tasks. This important aspect of cognitive control

allows flexible adjustment of behavior to changing circumstances (Kok et al., 2006). Such adjustments are often investigated using the task-switching paradigm, requiring subjects to switch frequently between two or more tasks (Meiran, 2010). Typically, participants react more slowly and perform less accurately on tasks that they just switched to compared with tasks that were repeated multiple times (Jersild, 1927; Spector and Biederman, 1976). These switch costs (Rogers and Monsell, 1995) reflect cognitive control processes (Goschke, 2000) that affect task processing and the implementation of tasks (Monsell, 2003), as well as

Received Nov. 23, 2016; revised May 15, 2017; accepted June 21, 2017.

Author contributions: L.S.L., D.W., M.R., T.G., and J.-D.H. designed research; L.S.L. and D.W. performed research; L.S.L. and D.W. analyzed data; L.S.L., D.W., T.G., and J.-D.H. wrote the paper.

This work was supported by the Bernstein Computational Neuroscience Program of the German Federal Ministry of Education and Research (Grant 01GQ1001Q); the German Research Foundation within the Collaborative Research Center Volition and Cognitive Control: Mechanisms, Modulations, Dysfunctions (DFG Grants SFB 940/1 and SFB 940/2); German Research Foundation Grants Exc 257, NeuroCure, and KF0247. This research was also supported by the Research Foundation Flanders (FWO) and the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 665501, and FWO grant FWO.OPR.2013.0136.01. We thank Kai Gørgen, Achim Meier, Fernando Ramirez, Jelle Demanet, and Marcel Brass for helpful comments on this project.

The authors declare no competing financial interests.

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DOI:10.1523/JNEUROSCI.3656-16.2017

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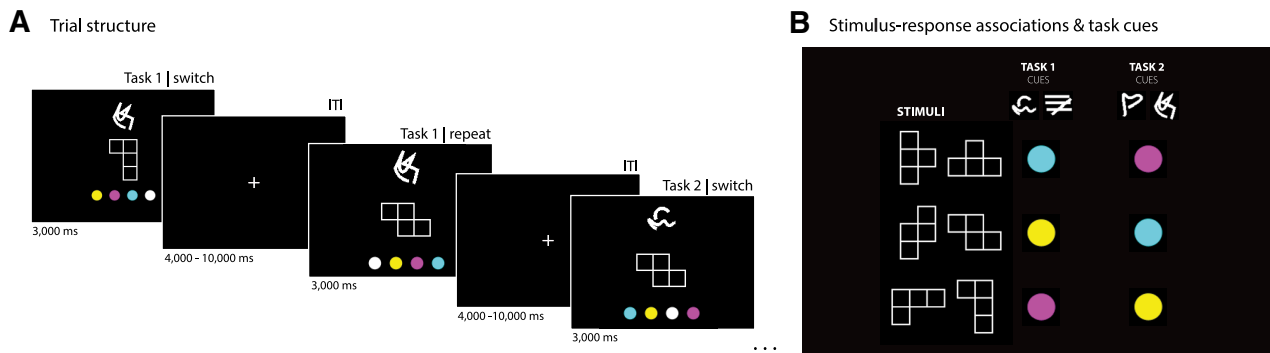


Figure 1. Experimental paradigm. **A**, Trial structure. Each trial consisted of a target stimulus at fixation, a cue stimulus above, and four possible response options below. Each task screen was presented for 3000 ms, during which time participants could indicate a response using the left and right index and middle fingers. Each trial was followed by a fixation cross with a variable ITI (4000–10,000 ms, mean = 5525 ms). Responses were indicated by pressing the button corresponding to the mapped color on screen on a 2×2 button box with their index and middle fingers of both hands. Subjects were cued to perform one of two tasks, switching between tasks or repeating a task up to three consecutive times. **B**, S–R associations and task cues. The two tasks consisted of similar stimulus response mappings, associating stimulus shapes (in two possible orientations) with colors. Each task was indicated by one of two possible abstract cues.

proactive interference and between-task crosstalk (Allport et al., 1994; Yeung et al., 2006). However, the exact sources of switch costs are still under debate (Kiesel et al., 2010).

Previous fMRI studies investigated the neural basis of preparatory processes in task switching using univariate methods (Ruge et al., 2013). Although many results implicate the prefrontal and parietal cortical regions in task switching (Dove et al., 2000; Gruber et al., 2006; Jamadar et al., 2010), this finding is not always consistent (Ruge et al., 2013). Previous task-switching research mostly focused on neural correlates of task-switching processes in terms of BOLD signal differences between switch and repeat trials. Recently, multivoxel pattern analysis (MVPA) (Haynes, 2015) has been used to investigate neural task representations. Such representations are encoded in local spatial activation patterns in the lateral prefrontal, dorsal anterior cingulate, and posterior parietal cortex (Bode and Haynes, 2009; Gilbert, 2011; Woolgar et al., 2011; Wisniewski et al., 2015).

Different cognitive processes such as rule complexity (Woolgar et al., 2015) or skill acquisition (Jimura et al., 2014) have been shown to alter representations of tasks. However, whether and how task switching (and its associated cognitive control demands) influences task representations is still largely unknown. Behavioral switch costs in task switching reflect both the cognitive control processes required to switch to performing a different task, as well as involuntary processes such as proactive interference from a previous task set (Kiesel et al., 2010; Vandierendonck et al., 2010). Possibly, this also affects the representation of these tasks (Waskom et al., 2014). In other cases, task representations remain unaffected by whether tasks were chosen freely or were externally cued (Wisniewski et al., 2016) or if tasks were novel or were performed routinely (Cole et al., 2011). This suggests that tasks can also be represented independently of current cognitive control demands (Zhang et al., 2013). However, it has remained open whether and how task-switch related control demands and between-task crosstalk in task-switching contexts affect the neural representation of tasks.

To investigate the influence of task switching on task representations, two main questions are addressed in this study. First, do different cognitive control demands on task-switch versus task-repeat trials affect the strength of neural task representations? More specifically, does the accuracy with which tasks can be decoded from neural activation patterns differ between task-switch and task-repeat trials? Second, is the neural code in which

tasks are represented independent of control demands? Therefore, are tasks encoded using generalizable spatial activation patterns in switch and repeat trials?

To address these questions, subjects were instructed to perform one of two simple stimulus–response (S–R) mapping tasks while brain activity was measured with fMRI. We identified brain networks involved in representing tasks and then assessed task information in these regions for switch versus repeat trials separately. Furthermore, we tested whether brain regions encode tasks invariant to switch and repeat condition. Results indicated that tasks are represented generalizably in a frontoparietal network, suggesting that switch-related cognitive control demands exert no strong effect on neural task representations.

Materials and Methods

Participants

Forty-two right-handed subjects (21 females, 21 males, mean age: 25.2 years, range 20–30 years) with normal or corrected-to-normal vision participated in the study. We obtained written informed consent from each subject and the local ethics committee approved the experiment. Subjects received 30€ for their participation. No subject had a self-reported history of neurological or psychiatric disorders. We only invited subjects to the fMRI session whose accuracy in performing the tasks after training was >90%. Therefore, we had to discard one subject after the training session because of poor behavioral performance (see experimental paradigm). We discarded two further subjects because of technical problems during scanning and one subject due to excessive head movement during scanning. To ensure reliable behavioral performance, all subjects took part in a training session 1–3 d before the scanning. Overall, the fMRI data of 38 subjects (20 females, mean age: 25, age range 20–29 years) were used for our analyses.

Task and experimental paradigm

Subjects were cued to apply one of two S–R mappings (tasks) to a visual stimulus in each trial of the experiment. In half of the trials, the task was identical to the previous trial (repeat trials); in the other half of the trials, the task differed from the previous trial (switch trials). We instructed subjects to respond as quickly and accurately as possible.

The experiment was programmed using MATLAB version 7.11.0 (The MathWorks, RRID: SCR_001622) and the Cogent Toolbox (<http://www.vislab.ucl.ac.uk/cogent.php>). On each trial, we first presented a task screen for 3000 ms that simultaneously displayed a task cue, a target stimulus, and four colored circles used for the response-mapping assignment (Fig. 1 and see below). Subjects were allowed to respond in the same 3000 ms time window. The task screen was followed by an intertrial

interval (ITI) during which a fixation cross was presented centrally on the screen. ITIs varied among 4000, 6000, 8000, and 10,000 ms and were distributed pseudologarithmically to decorrelate trials in time. The mean ITI was 5525 ms.

Tasks were cued using abstract visual symbols presented at the top of the screen. They were free of semantic meaning to avoid a priori semantic associations (Fig. 1; Reverberi et al., 2012a; Wisniewski et al., 2015). Over the experiment, two different cues were associated with each task to allow for cue-independent task decoding (see below for details; also see Reverberi et al., 2012a, b). The cue–task associations were counterbalanced across subjects. The target stimuli consisted of three geometric objects (Fig. 1, T-shape, L-shape, Z-shape), each appearing in two possible orientations (0 and 90 degrees) and presented in the middle of the screen. Stimuli and their orientations were pseudorandomized to control for the influence of low-level visual features. The two tasks consisted of different S–R mappings that associated stimulus shapes with colors that in turn specified which response key had to be pressed. In task one, the T-shaped stimulus was associated with magenta, the Z-shaped stimulus with cyan, and the L-shaped stimulus with yellow. In task two, the T-shaped stimulus was associated with cyan, the Z-shaped stimulus with yellow, and the L-shaped stimulus with magenta. The S–R mappings were chosen to be similar to control for possible confounds due to difficulty differences between tasks (Todd et al., 2013). Furthermore, switch costs can also be affected by task difficulty (Arbuthnott, 2008). Below the target stimulus, four colored circles were presented that mapped colors to response buttons. The position of the each colored circle was pseudorandomized across trials, avoiding motor preparation of responses as well as balancing left-hand and right-hand button presses throughout the experiment. Subjects used index and middle fingers of both hands to indicate their response by pressing the button corresponding to the color on screen on a 2 × 2 button box (Current Designs). Three of the circles were relevant for the task (cyan, magenta, and yellow) and one was a dummy (white) that was not relevant in any trial. This was done to balance left and right button presses.

Each run contained 80 trials, which were ordered so that 50% appeared in a sequence length of 1 (e.g., task 1), 37.5% in a sequence length of 2 (e.g., task 1 – task 1), and 12.5% in a sequence length of 3 (e.g., task 1 – task 1 – task 1). This resulted in 50% switch trials and 50% repeat trials overall. In 50% of the trials, subjects performed task 1 and, in the other 50%, they performed task 2. Tasks and switch conditions were orthogonalized. Within each brief sequence of identical tasks, we only used one of the two possible cues; that is, in each of the subsequent repetitions of a task, the same cue was used (cue repetition). Please note that such cue repetitions might confound the measured switch cost because it might be composed in parts of or simply reflect cue–switch cost only. Given that we focused our analyses on the representation of task, not on the switch processes directly, this does not affect the interpretation of our main results (Mayr and Kliegl, 2003; but see Altmann, 2006, 2007). Furthermore, cues were counterbalanced with stimuli and ITIs to avoid possible confounds.

Following each completed run, the percentage of correct answered trials was presented and subjects were offered a short resting break of self-determined length. Subjects performed five runs in total. The experiment lasted ~75 min in total. A sixth run, in which subjects performed the tasks in a different sequential order, was not analyzed and is not included here.

One to 3 d before the scanning session, subjects performed a 90 min training session, during which they learned the S–R mappings. At the end of the training session, they performed two runs of the task as they would be presented in the scanner. Only if the accuracy during these runs was >90% were subjects invited to the scanning session. This was done to avoid possible learning effects during the MRI session.

Image acquisition

Functional imaging was conducted on a 3 T Siemens Trio scanner equipped with a 12-channel head coil. For each of the five relevant scanning sessions, we acquired 347 T2*-weighted (TR = 2000 ms; TE, 30 ms; flip angle, 90°) gradient-echo echoplanar images (EPI). Imaging parameters were as follows: TR, 2000 ms; TE, 30 ms; and flip angle, 90°. Each

volume contained 33 slices (thickness: 3 mm) separated by gaps of 0.75 mm. Matrix size was 64 × 64, the field of view (FOV) was 192 mm, and the in-plane voxel resolution was set to 3 mm² with a voxel size of 3 × 3 × 3 mm. A T1-weighted structural dataset was also collected. The parameters were as follows: TR, 1900 ms; TE, 2.52 ms; matrix size, 256 × 256; FOV, 256 mm; 192 slices (1 mm thick); flip angle, 9°.

Statistical analysis

In all analyses, only trials with correct responses and preceded by correct trials (no misses/errors) were included to avoid post-error slowing effects (Dudschig and Jentzsch, 2009). We analyzed behavioral and fMRI data using MATLAB version 2013a (The MathWorks). For the multivariate analyses, we used The Decoding Toolbox (TDT; Hebart et al., 2016). Unthresholded group-level parametric maps of all analyses can be found at NeuroVault (Gorgolewski et al., 2016, RRID: SCR_003806; <http://neurovault.org/collections/2011/>).

Behavior

For each subject, we assessed task performance by calculating the mean reaction time (RT) and mean accuracy (i.e., the percentage of trials that were correctly answered in time) across all runs. It has been reported previously that switching between tasks leads to increased RT and decreased accuracy in switch trials compared with repeat trials (Monsell, 2003). We tested these so-called switch costs by comparing switch and repeat trials in terms of mean RT and accuracy using paired-sample, one-sided *t* tests. To control for possible influences of task difficulty, we also assessed the influence of the two tasks and the four cues on RTs and accuracies using paired *t* tests and one-way repeated-measures ANOVAs, respectively. We expected task switches to have an effect on both accuracy and RT (switch cost), but did not expect the other variables to affect them.

Neuroimaging

First-level GLM analysis

In a first step, we analyzed functional data using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm>, RRID: SCR_007037). The functional volumes were unwarped, realigned, and slice time corrected. No spatial smoothing and no spatial normalization was applied at this point to preserve fine-grained patterns of voxel activations (Haynes and Rees, 2006).

The preprocessed data were used to estimate a voxelwise general linear model (GLM; Friston et al., 1994). Twelve regressors of interest were used in the GLM. First, regressors for the eight conditions of the experimental design: two (tasks) × two (cue-sets) × two (switch/repeat) were added. Second, four separate regressors of no interest were added, modeling the four possible button presses to control for possible motor confounds in the data. Third, movement parameters were added to the GLM as regressors of no interest to account for possible head movement during scanning. Regressors were time locked to the onset of the task screen and convolved with a canonical hemodynamic response function as implemented in SPM.

To account for the possible influence of task difficulty on MVPA results (Todd et al., 2013), we first calculated the mean RT for task 1 and task 2 for each subject individually. We then set the duration of each regressor to the mean task RT of the current trial (mean RT task 1 for trials with task 1 and mean RT task 2 for trials with task 2, as suggested by Woolgar et al., 2014). This accounts for task-specific RT-related effects in the data during GLM estimation, but does not remove task-switch-related variance from the data (Vandierendonck et al., 2010; for recent reviews about switch cost, see Kiesel et al., 2010).

Multivariate searchlight decoding

Analysis 1: Differences in task coding in switch and repeat trials. To test for possible differences of task representations in switch and repeat trials, we first identified regions that code for tasks and, in the following steps, assessed the differences of task-decoding in switch and repeat trials separately in these regions. Our analyses were designed to test whether task information is encoded similarly in switch and repeat trials. Put differently, can task information be read out in a similar way in switch and repeat trials? This type of question can be very well addressed using linear

classifiers (Kriegeskorte, 2011), which we used in every decoding analysis presented here.

Analysis 1A: Task information across all trials. In the first analysis, we used “searchlight” MVPA (Kriegeskorte et al., 2006; Norman et al., 2006) as implemented in TDT (Hebart et al., 2016) on the maps of GLM parameter estimates for each individual subject. For each voxel V in the volume, the searchlight classifier distinguishes between the two classes (here: tasks) based on the multivariate pattern formed by the local fMRI activity patterns in a small spherical cluster with the radius of 3 voxels surrounding V . We used a support vector classifier (SVC) with a linear kernel and a fixed regularization parameter ($C = 1$) as implemented in LIBSVM (<http://www.csie.ntu.edu.tw/~cjlin/libsvm>). As a result, searchlight decoding produces a whole-brain accuracy map representing which searchlights contained information about the two classes entered into the analysis. To identify which brain regions contain information about tasks, we performed this first searchlight decoding analysis, classifying task 1 versus task 2 and using data from both switch and repeat trials combined. Trials were collapsed across switch and repeat condition to increase power to identify regions of interests (ROIs) that contain information about tasks. To control for the effect of visual cue information, we performed cross-classification across visual cues. More specifically, we trained the SVC to discriminate “task 1 with cue 1” and “task 2 with cue 2” and tested its performance on trials from “task 1 with cue 3” and “task 2 with cue 4.” Only brain regions that use similar activation patterns to encode the same tasks with different cues will be visible in this analysis. Therefore, this analysis controls for effects that are merely due to the visual features of the cues used. There are a total of four different combinations of task and visual cues as a training and test dataset, so that we repeated this analysis three more times, once for every combination. To address the problem of overfitting (Kriegeskorte et al., 2009), we performed a fivefold leave-one-run-out cross-validation. Therefore, every run was the test dataset once. The results of the combinations of cross-validation and cross-classification were averaged for each subject.

The average accuracy maps were then spatially normalized to a standard brain (Montreal Neurological Institute EPI template of SPM8) to account for individual differences in brain structure. Accuracy maps were then smoothed with a Gaussian kernel (6 mm full-width at half-maximum) to account for differences in localization. At the group level, a random-effects analysis was performed using voxelwise one-sample t tests against chance level (50%). Results were initially thresholded at voxel level with $p < 0.001$, corrected for multiple comparisons at the cluster level for familywise error (FWE) ($p < 0.05$). Note that these threshold values are not problematic for cluster-level inference regarding the inflated FWE rates that have been discovered recently by Eklund et al. (2016).

Analysis 1B: Differences in task decoding for switch and repeat trials. In a second step, we performed two additional searchlight decoding analyses that were highly similar to Analysis 1A described above. This time, we performed two independent analyses for switch trials only and repeat trials only. We first entered only the data of switch trials into a SVC that was trained to classify task 1 versus task 2. We again applied cross-classification across cues and leave-one-run-out cross-validation and averaged across them. We also smoothed and normalized the resulting decoding accuracy maps, as described above. The same procedure was repeated for repeat trials only. This yielded a task-decoding accuracy map for switch trials and for repeat trials for each individual subject. To compare the task-decoding accuracies in switch and repeat trials, we created ROIs from the clusters that we defined in task decoding Analysis 1A. To avoid circular analysis (Kriegeskorte et al., 2009), we used a leave-one-subject-out ROI analysis (Esterman et al., 2010). For this, we excluded one subject and performed a group-level analysis as described above (Analysis 1A). The results were then thresholded at voxel level with $p < 0.001$ (corrected for multiple comparisons at the cluster level, FWE, $p < 0.05$). We extracted the resulting significant clusters from this analysis and created a ROI from each cluster (based only on the training subjects). For each ROI thus defined, we extracted the mean decoding accuracy for the left-out subject. The ROI should resemble the group level results of Analysis 1A, but ensure an independent dataset for extracting decoding accuracies. Accuracy values were extracted for the decoding of task in

switch trials only, repeat trials only, and all trials together (Analysis 1A). We repeated this procedure until every subject was left out once. This ensures independence of the data used to define the ROIs from the data used for statistical assessment of the accuracy values inside these ROIs. The mean decoding accuracies from all three analyses and all ROIs were then entered into a two-factorial repeated-measures ANOVA (factor 1: 3 analyses; factor 2: ROIs) to identify possible differences between task coding in switch and repeat trials in each ROI. Furthermore, to assess whether decoding accuracies were significantly above chance in each analysis and ROI, planned one-tailed t test against chance level were performed. Results from these tests were Bonferroni corrected for the three analyses performed in each ROI.

To complement results of the traditional t tests, we also calculated Bayes factors (BFs) using R (RStudio version 1.0.136; RRID: SCR_001905, package: BayesFactor). Classical null hypothesis significance testing comes with several limitations, one of them being that these tests do not provide evidence for the null hypothesis (Wagenmakers, 2007; Dienes, 2014). Following these methods, the absence of a significant effect does not provide information whether there was an absence of an effect in the data or if the data were inconclusive in this regard. Bayesian hypothesis testing enables us to quantify evidence in favor for the null hypothesis (Rouder et al., 2009; Mertens and De Houwer, 2016). Following Jeffreys (1961), we considered BFs between 1/3 and 1 to represent anecdotal and thus inconclusive evidence and BFs smaller than 1/3 and 1/10 to indicate substantial and strong evidence for the absence of an effect, respectively. BFs larger than 1 were considered to represent substantial and BFs larger than 3 to represent strong evidence for the presence of an effect.

Analysis 2: Generalization of task coding between switch and repeat trials. Please note that the abovementioned analysis (1B) merely tests whether brain regions that encode tasks have different accuracies in switch and in repeat trials. If a given ROI indeed has a higher accuracy in one or the other condition, this would indicate a specialized role for task coding in either switch or repeat trials. If, however, no difference were to be found, this would not show directly that the ROI has a similar role in switch and repeat trials. To assess directly whether any brain regions encode tasks switching independently in these two conditions, a different type of analysis is necessary. Therefore, in Analysis 2, we aimed to identify brain regions that encode task information in the same way independently of whether subjects were repeating or switching between tasks, again using cross-classification (Reverberi et al., 2012a; Kaplan et al., 2015; Wisniewski et al., 2016). Similar to Analysis 1A, we first trained a searchlight classifier to distinguish between tasks in switch trials only and tested it on repeat trials only. We then trained a classifier on repeat trials only and tested it on switch trials only. Again, in both cases, we used leave-one-run-out cross-validation to avoid the problem of overfitting. Results from both analyses were first averaged for both cross-classification directions and then smoothed and normalized as in the previous analyses.

Please note that, in contrast to the Analysis 1, this analysis does not control for the effect of visual features of the task cues and results might reflect these. We also performed an exploratory task-decoding analysis with cross-classification across visual cue and across switch/repeat conditions at the same time. Specifically, we trained the classifier on “task 1 switch trials with cue 1” versus “task 2 switch trials with cue 3” and tested on “task 1 repeat trials with cue 2” versus “task 2 repeat trials with cue 4.” Such combined cross-classification should reveal task representations that are independent of switch and not confounded by visual cue information. This additional division of training data allows for 12 possible combinations of training and testing datasets. Therefore, we repeated this analysis for each combination and also applied cross-validation as described in the analyses above. The resulting decoding maps were averaged for each subject. However, because the trial number used to train the classifier in each decoding is again split in half compared with the previous cross-classifications, data are now divided across the cue and switch condition. That reduces the power of this analysis considerably, likely leading to reduced decoding accuracies.

To still control for the effect of visual cue information, we again used the ROIs defined in Analysis 1A using the leave-one-subject-out method. Within these clusters, we now extracted the mean task-decoding accuracies from Analysis 2, where we cross-classified across switch and repeat

trials. Please note that this is similar to a conjunction analysis and only voxels that show significant above-chance information in both task decoding cross-classified across visual cues and task decoding cross-classified across the switch and repeat conditions are interpreted. If tasks are encoded generalizably in these regions, then the mean decoding accuracies of task in both analyses should be significantly above chance. We tested this by applying a t test (against chance level, 50%) on the mean decoding accuracies for each cluster.

Results

Behavior

The mean RT across all correct trials was 1681 ms (SE = 30 ms). After removing trials following error trials, the mean RT changed significantly to 1664 ms (SE = 27 ms; paired t test: $t_{(37)} = 3.69$; $p < 0.001$; BF = 42). This effect could reflect post-error slowing (Dudschig and Jentsch, 2009). All fMRI and RT analyses are based only on correct trials also following a correct trial. On average, subjects were correct and fast enough in 95.5% (SE = 0.6%) of the trials. In 2.9% of the trials (SE = 0.3%) subjects pressed the wrong button and, in 1.6% (SE = 0.3%), they did not respond within the 3000 ms response window. The mean RT did not differ significantly between the two tasks (paired t test, $t_{(37)} = -0.30$, $p = 0.76$; BF = 0.18), nor did the accuracy of both tasks. Furthermore, there was no significant effect of cue on RTs, as tested using a one-way repeated measures ANOVA ($F_{(3,37)} = 0.31$, $p = 0.81$; BF = 0.05). No effects of tasks (paired t test, $t_{(37)} = 0.47$, $p = 0.74$; BF = 0.22) or cues (ANOVA, $F_{(3,37)} = 1.17$, $p = 0.32$; BF = 0.13) were found in accuracy rates. The average RT in switch trials was 1699 ms (SE = 32 ms). The average RT in repetition trials was 1656 ms (SE = 30 ms). The difference between these switch and repeat trials (switch cost) was significant (paired t test, $t_{(37)} = 5.04$; $p < 0.001$; BF = 1645). Average accuracy in switch trials was 94.59% (SE = 0.68%) and, in repeat trials, 96.36% (SE = 0.5%). This difference was also significant (paired t test, $t_{(37)} = -4.44$; $p < 0.001$; BF = 308). These results replicate previous findings of switch cost in RT and accuracy values (Monsell, 2003).

Multivariate searchlight decoding

Analysis 1: Differences in task coding in switch and repeat trials

Analysis 1A: Task information across all trials. First, we identified regions that encode tasks using data from both switch and repeat trials combined. Using cross-classification, we ensured that the visual features of the task cues cannot explain the results. Significant above-chance classification of task could be observed in three clusters ($p < 0.05$, FWE corrected at the cluster level, initial voxel threshold $p < 0.001$; Fig. 2A, Table 1). The first cluster is located in left inferior and superior parietal cortex spanning across angular gyrus, the second in right superior parietal cortex spanning across angular gyrus, and the third in left prefrontal cortex (PFC).

Analysis 1B: Differences in task decoding for switch and repeat trials. To compare the task-decoding accuracies in switch-only and repeat-only trials, we used a leave-one-subject-out approach to create the ROIs from the clusters identified in Analysis 1A. This procedure avoids the problem of double dipping (Kriegeskorte et al., 2009). We then extracted the task-decoding accuracy values in switch-only and repeat-only conditions. Figure 2B shows an overlay of all leave-one-subject-out-ROIs that were created. As expected, they closely resemble task-decoding results across all subjects in Analysis 1A. A two-factorial repeated-measures ANOVA on the mean task-decoding accuracies in these ROIs showed no significant main effect of the decoding analysis (all/switch-only/repeat-only task decodings, $F_{(2,74)} = 0.06$, $p = 0.94$; BF < 0.001), no significant main effect of the ROI ($F_{(2,74)} = 0.59$,

$p = 0.55$; BF < 0.001), and no interaction effect between ROI and the decoding analysis ($F_{(4,148)} = 1.08$, $p = 0.36$; BF = 0.06). This indicates that there are no strong differences in the task-decoding accuracies between switch and repeat trials in task-related brain regions. We thus have strong evidence for the absence of an effect in this analysis.

Average task decoding in the left parietal cortex in all trials was 52.44% (SE = 0.64%), which was significantly above chance level (50%, t test: $t_{(37)} = 3.82$; $p < 0.001$; BF = 60). In switch trials only, the average decoding accuracy was 52.46% (SE = 0.79%) and, in repeat trials only, it was 51.83% (SE = 0.89%). In right parietal cortex, the task-decoding accuracy in all trials was 52.1% (SE = 0.54%) and was significantly above chance level (t test: $t_{(37)} = 3.87$; $p < 0.001$; BF = 66). In switch trials only, it was 52.05% (SE = 0.69%) and, in repeat trials only, it was 51.75% (SE = 0.76). In left lateral PFC, the task-decoding accuracy in all trials was 51.85% (SE = 0.5%) and was significantly above chance level (t test: $t_{(37)} = 3.733$; $p < 0.001$; BF = 46). In switch trials only, it was 51.35% (SE = 0.6%) and, in repeat trials only, it was 52.18% (SE = 0.83%).

Please note that, due to the physical limitations of fMRI, we cannot exclude that additional information is present at finer spatial scales. The absence of differences between task-decoding accuracies in switch and repeat trials is thus limited by the spatial resolution of fMRI.

Although this is not the focus of our study, we also performed a univariate contrast of switch—repeat and repeat—switch trials and a multivariate decoding of switch versus repeat trials. Neither the univariate contrasts nor the multivariate decoding of switch versus repeat yielded significant results at $p < 0.05$ FWE cluster correction and initial voxel threshold of $p < 0.001$. The univariate results are consistent with previous research (Cavina-Pratesi et al., 2006; Gruber et al., 2006), although results on this topic have been heterogeneous (Ruge et al., 2013).

Analysis 2: Generalization of task coding between switch and repeat trials

In Analysis 1, we did not find evidence for a difference in task coding between switch and repeat trials. In a next step, we assessed directly whether regions that encode task do so invariant to switch and repeat condition. We thus performed a task-decoding analysis, training on switch trials and testing on repeat trials. To ensure an independent test dataset, we again used the ROIs extracted from Analysis 1A using a leave-one-subject-out approach. We extracted the mean decoding accuracy in these ROIs from the task-decoding analysis cross-classified across the switch/repeat conditions. Mean decoding of task was significantly above chance level (50%) in the left parietal (t test: $t_{(37)} = 4.84$; $p < 0.001$; BF = 940), right parietal (t test: $t_{(37)} = 5.05$; $p < 0.001$; BF = 1719), and left prefrontal (t test: $t_{(37)} = 2.83$; $p < 0.001$; BF = 5.31) regions. We thus have strong evidence for the presence of an effect in this analysis. This finding indicates that all identified task-related brain regions encode tasks generalizably regardless of the current switch/repeat condition.

To assess whether any other regions outside of the ROIs investigated above also encode tasks similarly invariant to switch and repeat conditions, we performed an additional explorative whole-brain analysis of the task decoding using cross-classification across switch/repeat trials.

Results were thresholded at voxel level with $p < 0.001$, corrected for multiple comparisons at the cluster level (FWE, $p < 0.05$). Task information was found in bilateral inferior and superior parietal cortex, bilateral precuneus, right angular gyrus, and

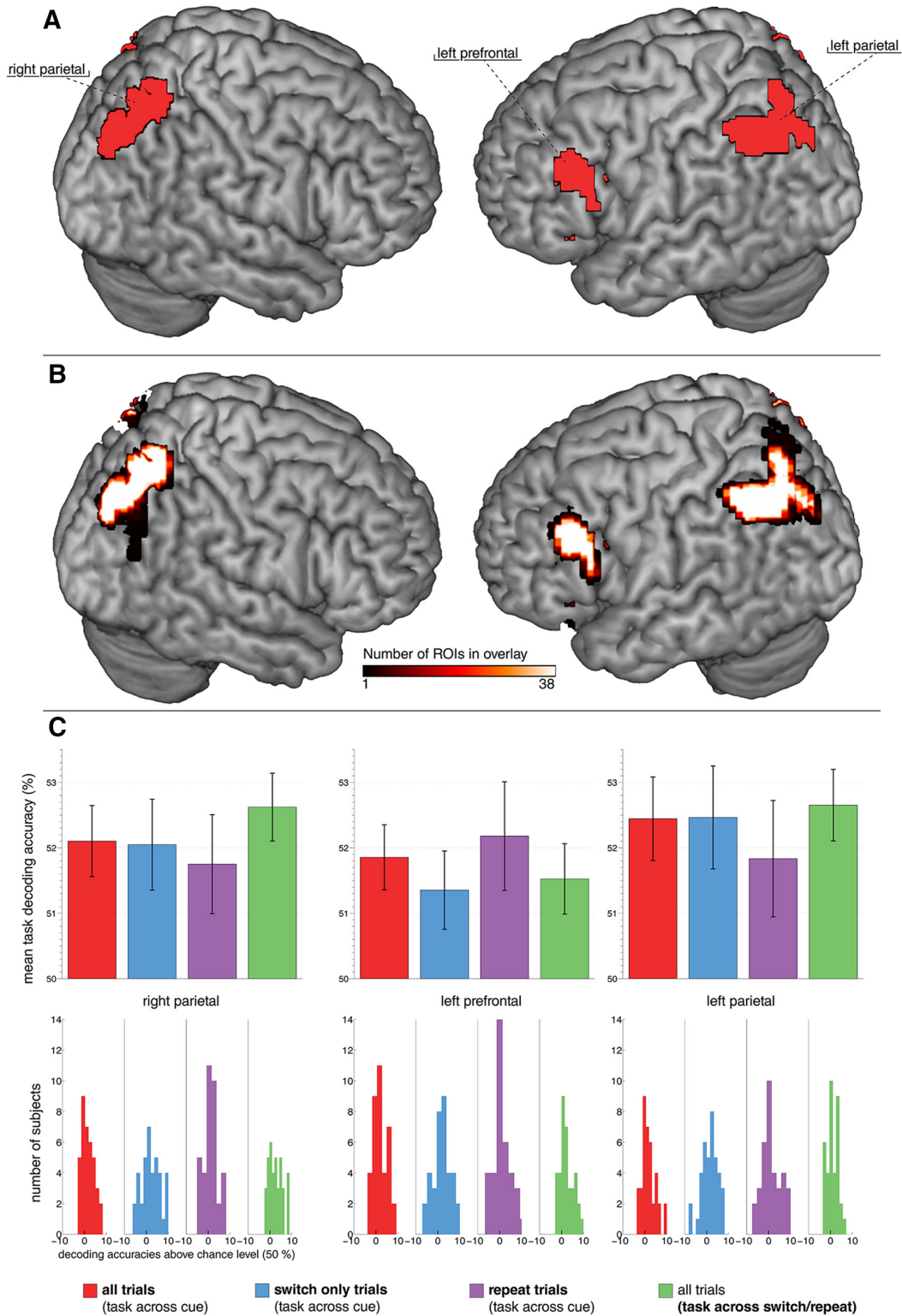


Figure 2. Task decoding. **A**, Task decoding across cues in all trials and all subjects. Tasks were encoded in bilateral superior parietal cortex, left inferior parietal cortex, and left lateral PFC ($p < 0.05$, FWE corrected at the cluster level, initial voxel threshold $p < 0.001$). **B**, Overlay of all 38 leave-one-subject-out ROIs. All ROIs were created leaving out one subject at the group-level statistic ($p < 0.05$, FWE corrected at the cluster level, initial voxel threshold $p < 0.001$) and later used for extraction of mean decoding accuracy values in that subject. **C**, Mean task-decoding accuracies extracted from the ROIs depicted in **B**. We extracted values from four different decodings: task across cues in all trials (red), task across cues in switch trials only (blue), task across cues in repeat trials only (violet), and task across switch (green). Chance level in these plots is 50%. The distribution of mean decoding accuracies across subjects is shown in the histograms below.

Table 1. Results of analysis

Brain region	Side	Cluster size	MNI coordinates (peak voxels)			t score peak
			x	y	z	
Task across cues in all trials ^a						
Parietal lobe	Left	383	−51	−52	49	4.75
Parietal lobe	Right	293	36	−61	64	4.87
Prefrontal lobe	Right	261	−39	35	−2	5.51
Task across switch in all trials ^b						
Parietal lobe	Left	1053	−48	−55	49	5.17
Parietal lobe	Right	597	27	−64	46	5.71
Occipital lobe	Left	440	−21	−91	−2	4.69
Cerebellum	Left	173	−39	−64	−23	5.34
Occipital lobe, cerebellum	Right	135	45	−64	−11	4.8

^aBrain regions where tasks could be decoded in an analysis collapsed across switch and stay trials independently of visual cue.

^bBrain regions where classifiers trained on switch trials could be used to decode the task in repeat trials and vice versa.

bilateral occipital cortex spanning into bilateral cerebellum (Fig. 3, green). Please note that, in contrast to Analysis 1, this analysis does not control for the effect of visual features of the task cues and results might reflect these. We therefore performed a conjunction analysis with the regions identified in Analysis 1A. This analysis explicitly controls for the influence of visual cue features on task decoding results. Voxels found in both Analysis 1A and Analysis 2 thus encode tasks in a generalizable format invariant to different visual cues and different switch/repeat conditions. This conjunction analysis identified the bilateral parietal cortex (Fig. 3, yellow). In contrast to Analysis 1A, we did not find a prefrontal cluster. Please note that this whole-brain analysis is less sensitive than our leave-one-subject-out ROI approach, potentially explaining the absence of prefrontal findings. This analysis suggests that the task information in parietal cortex generalizes across multiple different contexts.

To further test whether tasks are encoded in a switch-independent fashion, we compared the accuracies of task decoding within and across switching conditions directly. If a task representation is encoded independently of the switch/repeat condition, then it should yield comparable decoding accuracies in decoding in which the classifier is trained on switch and also tested on switch trials and the classifier is trained on switch but tested on repeat trials. For this comparison, we averaged the individual subjects' task-across-cue-decodings for switch only and repeat only trials from Analysis 1B and compared them with the task decoding across cue and across switch conditions simultaneously. Please note that the number of trials used to train the classifier for all of these analyses is the same in both analyses. Decoding accuracies did not differ significantly in left parietal (paired *t* test: $t_{(37)} = -0.8730$, $p = 0.3883$, BF = 0.25), right parietal (paired *t* test: $t_{(37)} = -0.9427$, $p = 0.3520$, BF = 0.26), or left prefrontal (paired *t* test: $t_{(37)} = -1.1629$, $p = 0.2523$, BF = 0.32) cortex.

The task decoding across cue and across switch condition simultaneously did not yield any significant results at FWE-corrected cluster level $p < 0.05$ with initial voxel threshold $p < 0.001$. This is likely due to the reduced number of trials that were used to train the classifier.

To further corroborate our findings, we repeated all analyses using correlation-based classifiers as implemented in TDT (Hebart et al., 2016). We compared the whole-brain results of the analyses above (linear SVC) with respective exploratory correlation-based classifier results using a *post hoc* paired *t* test as implemented in SPM8. Results did not differ significantly on a whole-brain level

(initial voxel threshold $p < 0.001$, FWE-corrected FWE cluster level $p < 0.05$). To test whether the classifier type had an influence on the results identified in more sensitive ROI analyses, we performed an additional ANOVA on the ROI results. We repeated the ANOVA described above, including the factors ROI (left parietal, right parietal, left prefrontal) and decoding analysis (task across cue for all trials, switch only trials, and repeat only trials). We added a third factor, classifier type, to this ANOVA (linear support vector classification, correlation-based classification). Results indicated that the main effect of classifier type did not reach significance ($F_{(1,37)} = 1.95$, $p = 0.17$, BF < 0.001). This ANOVA was designed to be as similar as possible to the original ANOVA performed in Analysis 1B. Because this did not include the decodings under Analysis 2, we assessed the influence of classifier on these analyses with two separate ANOVA, including the factors of classifier type and ROI (as described above). However, we found no significant effect of classifier type in either of the remaining analyses: task across switch condition ($F_{(1,37)} = 0.14$, $p = 0.71$, BF < 0.001) and task across cue and switch condition ($F_{(1,37)} = 1.62$, $p = 0.21$, BF < 0.001). Overall, we have strong evidence for the absence of any differences between the two classification algorithms used here, showing that our results are not specific to the method that we used.

Discussion

Summary

Effective goal-directed behavior requires humans to switch frequently between different tasks. To direct this behavior, cognitive control is required (Kok et al., 2006). Much previous research used task-switching paradigms to examine the role of cognitive control when changing between tasks (Monsell, 2003; Kiesel et al., 2010). Results show that performance is modulated by switching and switch costs are observed in both RT and accuracy (Jersild, 1927; Allport et al., 1994). However, the cognitive mechanisms and neuronal correlates of this behavioral switch cost are still under debate (Kiesel et al., 2010). Most previous fMRI research has focused on the neural correlates of task-switching processes (Ruge et al., 2013) and task-switching-related processes have been associated with a frontoparietal control network (Sohn et al., 2000; Braver et al., 2003; Brass et al., 2005; Crone et al., 2006). However, most of this research focused on the processes required to reconfigure the cognitive system from performing one task to performing a different task. Presumably, this includes changes to the neural representations of tasks, but effects on neural task representations have rarely been investigated (but see Waskom et al., 2014). However, task representations have been shown to be context dependent in some cases (Woolgar et al., 2015) and to remain context independent in others (Wisniewski et al., 2016). Here, we investigated the influence of cognitive control processes related to task switching on the neural representations of tasks.

In the current study, subjects were cued to perform one of two simple tasks, with the task being repeated or switched between successive trials. Behavioral results indicate that subjects showed switch costs (Rogers and Monsell, 1995), which suggests that cognitive control demands differed between switch and repeat trials. We first compared task-decoding accuracies in switch and repeat trials in these regions. Our results show that tasks were represented in bilateral parietal cortex and left lateral PFC. However, we found no differences in task-decoding accuracies between switch and repeat trials. Therefore, our data yielded no evidence that tasks are represented differently for either switch or repeat trials in the regions that we identified previously to maintain task information (but see Waskom et al., 2014). We also

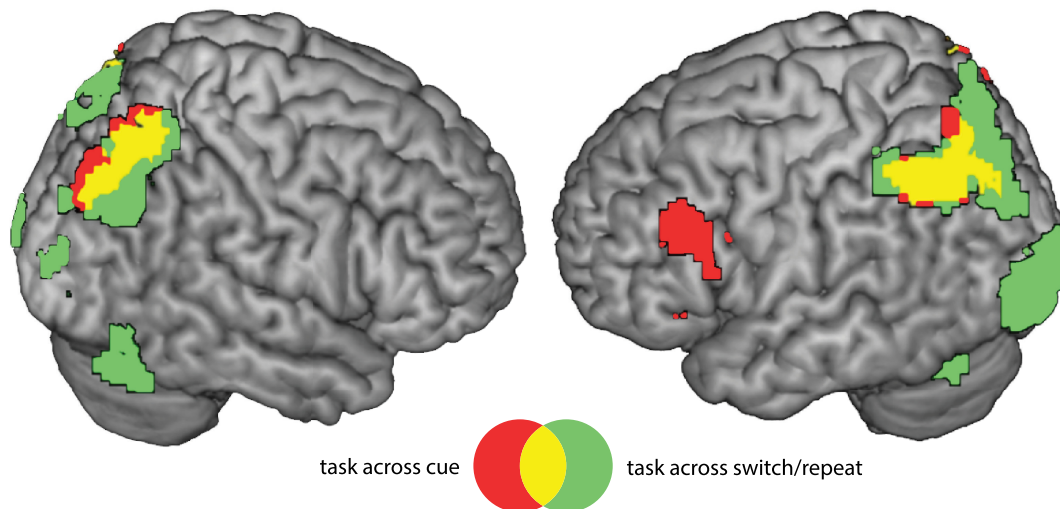


Figure 3. Task decoding in all subjects for the decoding of task across cues (red, Analysis 1A) and the decoding of task across switch/repeat (green, Analysis 2). Both regions overlap. Note that task decoding across switch/repeat does not control for the visual information contained in task cues (which might explain occipital task information) and is also less sensitive than the leave-one-subject-ROI approach, which might account for no prefrontal cluster surviving cluster correction (for both analyses: $p < 0.05$, FWE corrected at the cluster level, voxel threshold $p < 0.001$).

tested for generalization of task coding across switch and repeat trials using cross-classification. Results indicate that the frontoparietal cortex represents tasks regardless of the current cognitive control demands in task switching and suggests that tasks are coded in a robust, switching-independent pattern.

Task representations in frontoparietal cortex

Recent MVPA research investigating the neural representations of tasks directly has shown that parietal (Bode and Haynes, 2009; Woolgar et al., 2011; Waskom et al., 2014; Etzel et al., 2016; Wisniewski et al., 2015), medial (Gilbert, 2011; Momennejad and Haynes, 2013), and lateral PFC (Cole et al., 2011; Reverberi et al., 2012b) hold information about tasks. We provide further evidence for these findings because we were able to discriminate between the two highly similar tasks in bilateral parietal and left lateral PFC. This is consistent with previous results highlighting the important role of these regions in task processing during task retrieval and maintenance (Bunge et al., 2003; Sakai and Passingham, 2003; Gilbert, 2011), processing rule and task compositionality (Woolgar et al., 2011; Reverberi et al., 2012a), adaptively coding tasks under different conditions (Woolgar et al., 2011), and their engagement over the course of development (Wendelken et al., 2012).

Influence of switching on task representation in frontoparietal cortex

Recent studies suggest that task representations can be modulated by different contextual variables: task representations have been observed to be modulated by rule complexity (Woolgar et al., 2015), rewards (Etzel et al., 2016), and skill acquisition (Jimura et al., 2014). This illustrates how higher cognitive functions might change flexibly the way tasks are processed in the brain, possibly reflecting adaptation of neuronal populations to different environmental demands (Duncan, 2010, 2013). However, other studies suggest that task representations also remain unaffected by experimental manipulation, such as task novelty (Cole et al., 2011), task difficulty (Wisniewski et al., 2015), or whether they are freely chosen or externally cued (Zhang et al., 2013; Wisniewski et al., 2016). It remains an open question

whether and how cognitive control processes modulate task representations. In a previous study, Waskom et al. (2014) found task information in the inferior frontal and intraparietal sulcus, as well as the occipitotemporal cortex. They found representations of rules regarding perceptual discriminations to be modulated by task switching because they had the highest decoding accuracy after a task switch. Such effects on context information might be driven by attentional processes (Liu and Hou, 2013). Also note that Waskom et al. (2014) did not observe behavioral switch costs. It thus remains unclear whether cognitive control demands differed between switch and repeat trials and if these neuroimaging results in fact reflect control-related processes. In contrast, our subjects did show switch costs, indicating different control demands between switch and repeat trials. Importantly, because we presented task cues simultaneously with the task stimuli, participants could not prepare in advance for the new task on switch trials. Therefore, switch costs presumably reflect both effects of task set inertia and proactive interference, as well as increased control demands due to the requirement to retrieve and implement the new task set and to reconfigure S–R accordingly. Nevertheless, our results suggest that control demands do not modulate task representations. Together, these findings indicate that tasks are represented using a general, context-independent neural code. At first glance, this finding might be taken to imply that these brain regions do not support flexible adaptation of behavior because they do not change flexibly under varying environmental conditions. It has been argued previously that frontal and parietal brain regions support flexible adaptation through flexible task representations that change under varying external demands (Duncan, 2001; Waskom et al., 2014; Woolgar et al., 2015). However, generalized coding under different conditions might also support adaptive behavior: invariant coding allows robust access to task information even if we are confronted with novel situations. This might enable fast transfer of abstract rules (Cole et al., 2011) and stable selective attention toward task-relevant information (Zhang et al., 2013). Stable task representations have also been observed under varying attentional loads (Chan et al., 2015), further highlighting the context-independent coding of tasks. Therefore, our findings of such invariant neural represen-

tations do not rule out a dynamic adjustment of task-specific neurons, as the adaptive coding hypothesis suggests (Duncan, 2001, 2010; Waskom et al., 2014). Flexible top-down signals may be reflected in different levels of task processing that merely access the robust context-independent representation without modulating it. In addition, we found no significant results in the analysis testing for context-dependent task coding. Although we used a highly sensitive ROI approach, this null finding cannot rule out in principle that there might also be neurons that do code tasks differently for different cognitive control demands.

Role of task switch processes

Although this study focused on differences and generalizations of neural task representations during switching, we also observed behavioral switch costs. Our paradigm was not designed to determine the source of the underlying processes, but switch costs might arise for a number of reasons, including proactive interference due to task set inertia (Allport et al., 1994), the inhibition of previously executed task sets (Goschke, 2000; Mayr and Keele, 2000), and processes of rule retrieval (goal setting) and rule implementation (Rubinstein et al., 2001). Models of task switching that assume that part of the switch cost reflects proactive interference from previous and/or crosstalk from concurrently active but currently irrelevant task sets would presumably result in task representations that are degraded and less distinct on switch compared with repeat trials. Such an effect should show up in a reduced accuracy with which task representation can be decoded from spatial patterns of brain activity. However, the present findings of task representations that are independent of current switch demands do not suggest such a modulation from whichever source. Neurons in the frontoparietal cortex are able to encode tasks context invariantly under various different conditions such as high- and low-control demands (see also Wisniewski et al., 2016). Switch costs might then arise at a different stage, when task information from the parietal cortex is further processed by brain regions more closely associated with implementing cognitive control (Badre, 2008).

Conclusion

In summary, our results provide novel insights into the effects of task switching on the distributed neuronal representations of tasks. We did not find reliable differences in task coding between switch and repeat trials. However, task representations in bilateral parietal and left PFC generalized under conditions of high- and low-cognitive-control demands. These results provide further insight into the important function of the frontoparietal network for task representation. Control-independent task coding might enable robust access to task-relevant information under different environmental conditions to support flexible adjustment of behavior.

Notes

Supplemental material for this article is available at <http://neurovault.org/collections/2011/>. Included are unthresholded group-level whole-brain maps (spmT) that are presented in the manuscript. This material has not been peer reviewed.

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Komplette Publikationsliste

Originalarbeiten

Loose*, L. S., Wisniewski*, D., Rusconi, M., Goschke, T., & Haynes, J. D. (2017). Switch independent task representations in frontal and parietal cortex. *Journal of Neuroscience*, 3656-16.

* these authors contributed equally to this work (geteilte Erstautorenschaft)

Journal of Neuroscience (2017) Impact Factor: 5.970
Eigenfaktor: 0.265950

Kongressbeiträge

Loose LS, Wisniewski D, Rusconi M, Goschke T, Haynes J. Cognitive control modulates task representations in occipital and prefrontal cortex. Program No. 80.19/W6. 2015 Neuroscience Meeting Planner. Washington, DC: *Society for Neuroscience, 2015*. Online.

Loose LS, Wisniewski D, Rusconi M, Goschke T, Haynes J (2016) Task representations in the fronto-parietal network are not modulated by switching. *Bernstein Conference 2016*. doi: [10.12751/nncn.bc2016.0193](https://doi.org/10.12751/nncn.bc2016.0193)

Lebenslauf

Mein Lebenslauf wird aus datenschutzrechtlichen Gründen in der elektronischen Version meiner Arbeit nicht veröffentlicht.

Danksagung

Mein Dank gilt zuallererst Herrn Prof. Dr. John-Dylan Haynes, für die Betreuung meiner Arbeit, der freundlichen Aufnahme in seine Arbeitsgruppe, das in mich gesetzte Vertrauen und die stetige Motivation sowie die kompetente Hilfe in jeder Phase der Doktorarbeit.

Ich danke Herrn Prof. Dr. Goschke für die konstruktive Mitarbeit an unserer Studie und das in mich gesetzte Vertrauen.

Ein besonderer Dank gilt Dr. David Wisniewski für die umfangreiche und bereichernde Zusammenarbeit, das Erklären und Diskutieren auf Augenhöhe, das immer offene Ohr und die unkomplizierte und sehr beruhigende Art der Problemlösung, das Lob und die stets konstruktive Kritik, die Motivation und die Geduld. Danke auch für die wertvolle Perspektive und Einblicke in die Welt der Neurowissenschaft.

Ich danke auch Dr. Marco Rusconi für seine Einführung in die Welt von MATLAB, die oft akribische Kritik an unseren Methoden und den idealistischen wissenschaftlichen Geist.

Mein Dank gebührt außerdem dem gesamten Team des Haynes Lab, dem BCAN Team und insbesondere der BCCN-Gemeinde: Danke für die unkomplizierte und oft zeitintensive Hilfe und die Motivation auch mal den Kopf zu heben und über den eigenen persönlichen und wissenschaftlichen Tellerrand hinaus zu schauen. Im speziellen seien Dr. Carsten Bogler, Dr. Robert Deutschländer, Achim Meyer, und Dr. Fernando Ramirez für die vielen Denkanstöße und Diskussionen gedankt und Kai Görgens für seine unglaublich konsequente und uneigennützig Hilfsbereitschaft sich in fremde Problemkomplexe ein zudenken und jederzeit ohne zu zögern sein Wissen weiterzugeben.