Brain Imaging and Behavior
https://doi.org/10.1007/s11682-024-00921-7

RESEARCH

Mapping common and distinct brain correlates among cognitive flexibility tasks: concordant evidence from meta-analyses

Zhanna V. Chuikova[1,2] · Andrei A. Filatov[3] · Andrei Y. Faber[3] · Marie Arsalidou[4,5]

Accepted: 3 September 2024

Abstract

Cognitive flexibility allows individuals to switch between different tasks, strategies, or ideas; an ability that is important for everyday life. The Wisconsin card sorting test (WCST) and task switching paradigm (TSP) are popular measures of cognitive flexibility. Although both tasks require switching, the TSP requires participants to memorize switching rules and retrieve them when they view a cue (rule-retrieval), whereas the classic WCST requires participants to discover the switching rule via trial-and-error (rule-discovery). Many functional magnetic resonance imaging studies have examined brain responses to these tasks. Extant meta-analyses show concordance in activation in a widespread set of areas including frontal, parietal, and cingulate cortices. Critically, past meta-analyses have not specifically examined brain correlates associated with rule derivation (i.e., rule-discovery vs. rule-retrieval) in cognitive flexibility tasks. We examine for the first time common and distinct concordance in brain responses to rule-discovery (i.e., WCST) and rule-retrieval (i.e., TSP), as well as TSP subtypes using quantitative meta-analyses. We analyzed data from 69 eligible articles with a total of 1617 young-adult participants. Conjunction results show concordance in common fronto-parietal areas predominantly in the left hemisphere. Contrast analyses show that rule-discovery required increased involvement in multiple cortical and subcortical regions such as frontopolar (Brodmann Area 10), parietal, insular cortex, thalamus and caudate nucleus predominantly in the right hemisphere. No significant differences in concordance were observed among the three, task switching paradigm sub-types. We propose a neuroanatomical model of cognitive flexibility and discuss theoretical and practical applications.

Keywords Cognitive flexibility · Meta-analysis · Rule-discovery · Rule-retrieval · FMRI · Wisconsin card sorting test · Task switching paradigm

Introduction

To successfully function in a constantly changing environment, we need to think flexibly. Cognitive flexibility, also called "set shifting", "task switching', "attention switching", is the ability to switch between different mental sets, tasks, or strategies (Miyake et al., 2000). It is an executive function that allows an individual to regard some aspects of a situation or an object from a new perspective (Diamond, 2013; Martin & Anderson, 1998; Miyake & Friedman, 2012). Popular tasks for assessing cognitive flexibility are the Wisconsin card sorting test (WCST; Berg, 1948) and the task switching paradigm (TSP; Jersild, 1927; Monsell et al., 2003). For these tasks participants are asked to switch rules during stimulus categorization (e.g., sort by color, number, shape). However, the classic WCST requires participants to come up or discover the switching rule after they receive negative feedback on a response (i.e., rule-discovery),

✉ Zhanna V. Chuikova
zhanna7496@mail.ru

✉ Marie Arsalidou
marie.arsalidou@gmail.com; arsalido@yorku.ca

[1] Centre for Cognition and Decision making, Institute for Cognitive Neuroscience, HSE University, Moscow, Russian Federation

[2] Department of Pedagogy and Medical Psychology, Sechenov University, Moscow, Russian Federation

[3] Laboratory for Cognitive Research, School of Psychology, Faculty of Social Sciences, HSE University, Moscow, Russian Federation

[4] York University, Toronto, Canada

[5] NeuroPsyLab.com, Toronto, Canada

whereas the TSP requires participants to remember the rule and retrieve it after a cue (i.e., rule-retrieval). Numerous neuroimaging studies examined neural correlates of cognitive flexibility showing that multiple frontal, parietal, insular and subcortical regions are active when switching among mental sets, tasks, or strategies (Buchsbaum et al., 2005; Kim et al., 2012a; Niendam et al., 2012; Rodríguez-Nieto et al., 2022; Wu et al., 2020; Zhang et al., 2021). Past meta-analyses combined switching tasks or examined them separately (e.g., Kim et al., 2012a; Rodríguez-Nieto et al., 2022; Wager et al., 2004) without considering the influence rule derivation (rule-discovery vs rule-retrieval) may have on brain correlates. From a constructivist theoretical viewpoint, mental operations needed to remember a rule versus discovering a rule via trial-and-error should place different demands on cognitive and brain mechanisms (Arsalidou et al., 2019). Specifically, the switching rule in WCST needs to be discovered after a wrong response, whereas the switching rule for a TSP is given by a cue. This rule uncertainty is one of the key differences between the WCST and TSP that has an impact on the speed and accuracy of responses (Lange et al., 2018). The purpose of the current meta-analyses is to identify common and distinct brain areas associated with the rule-discovery (i.e., WCST) and rule-retrieval (TSP), and its subtypes (i.e., TSP tasks that focus on different switching methods or contexts).

The first measure of cognitive flexibility is the WCST (Berg, 1948). The WCST has been primarily used to assess patients with frontal lobe damage (Eling et al., 2008; Miles et al., 2021; Milner, 1963). The classic WCST consists of 64 response cards and 4 stimulus cards (Grant & Berg, 1948), which display different types and numbers of colored geometrical figures (triangles, stars, circles, and crosses; Fig. 1(a). Participants are asked to determine the appropriate sorting principle (color, shape, or quantity) by receiving positive or negative feedback. After a particular number of consecutive correct answers, the sorting rule changes to a new one (e.g., from "color" rule to "shape" rule) requiring participants to think flexibly to adjust sorting strategies that are different from others (Heaton et al., 1993; Miles et al., 2021).

While the WCST remains widely used for evaluating cognitive flexibility, some identify challenges associated with performance outcomes due to other cognitive demands posed by the task (Figueroa & Youmans, 2013; Miles et al., 2021; Shallice, 2008). To address this issue, the task switching paradigm (TSP) was developed, the roots of which trace back to 1927 (Jersild, 1927). The TSP asks participants to switch between two or more tasks based on cues or sequences. Specifically, the classic TSP teaches participants the cues linked to specific switching rules and participants need to memorize them. For instance, participants are asked to perform odd/even tasks (trial A: Fig. 1b) or lower/higher than tasks (trial B) following corresponding cues (e.g., Monsell et al., 2003). If Test A is followed by the Test A, then it is considered a repeat trial, whereas transition to test B after test A is considered a switch trial (Karayanidis & McKewen, 2021). Modifications of the TSP can vary switching schemes by location, attribute, rule, task and object (Wager et al., 2004). TSP with a *location* switch asks participants to switch attention from one part of a screen to another following a target cue (e.g., covert attention direction switching task; Corbetta et al., 2000). *Attribute* switching tasks ask participants to shift their attention towards distinct characteristics of the same object. For instance, participants view a red circle and they are first asked to evaluate images based on color, and when a cue prompt appears they must switch their attention and evaluate subsequent images based on shape (e.g., color / shape task; Hakun et al., 2015). Tasks with a *rule* switch ask participants to reassign their category-response mappings while stimuli and response set remain the same. For example, participants are asked to press button A in response

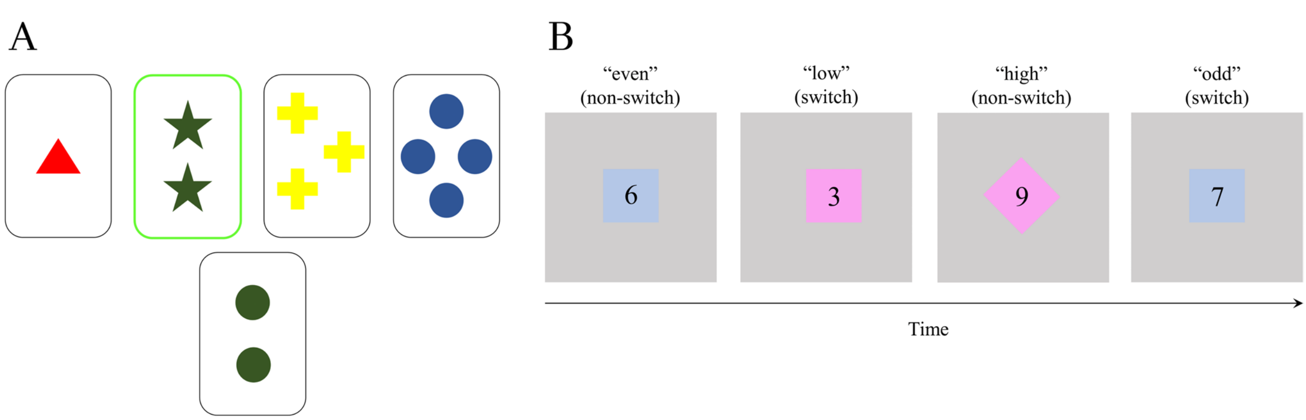

Fig. 1 An example of (**a**) the WCST and (**b**) the TSP tasks. *Note* Within the gray screen, the color of the central shape serves as a cue. A blue shape signals the need to proceed with an odd/even task, whereas a pink shape signals the need to classify numbers as higher or lower than 5 (low/high task)

to category X and button B in response to Y, and after the switch cue, participants need to change category-response mappings and to press button B in response to category X and button A in response to Y (e.g., finger-response reassignment task; Dove et al., 2000). *Object* switch entails switching attention from one object to another following a cue, whereas all of them are shown. For instance, tasks with overlapping figures (e.g., alternation of two univalent stimuli task; Crone et al., 2006). Finally, *task* switching implies shifting activity being applied to stimulus-category rules, such as between response sets or mental operations applied to stimuli. For instance, evaluating odd, even or evaluating vowel, consonant where a digit and a letter are shown simultaneously (e.g., syllables counting / sex identification task; Yeung et al., 2006).

This classification into five switching types is well-supported by a definition of task-set and its components as provided by Vandierendonck et al. (2010). In order to reduce ambiguity in TSP switching types' nomenclature in Wager and colleagues classification (Wager et al., 2004), we will call rule switching '*response rule switching'* and task switching '*operation switching'*. For other TSP types, attribute, location, and object, we adopt the terms as proposed by Wager et al. (2004).

According to this classification, the WCST falls under attribute switching as it involves shifting between different features, such as color, shape and number of the same objects. Unlike the TSP, the WCST does not provide any explicit task sequence for participants, triggering switching by receiving negative feedback (Brass & De Baene, 2022). Thus, both TSP and WCST have a switch component, however, for the TSP the feature to switch to is known (i.e., rule-retrieval), whereas for the WCST the feature to switch to needs to be discovered via trial-and-error (rule-discovery). Within a constructivist theoretical viewpoint, (i.e., Theory of Constructive Operators) schemes that are known, but not automatized, do not pose high executive demands and would be supported primarily by the left-hemisphere (Pascual-Leone, 1995; Pascual-Leone & Johnson, 2021). Whereas executive schemes that need to be discovered and in other words novel, would favor involvement of the right-hemisphere (Arsalidou et al., 2018; Pascual-Leone, 1995) and implication of higher order cognitive regions such as frontopolar areas is expected (Pascual-Leone & Johnson, 2021). Further, according to the theory of constructive operators, figurative schemes that represent object and features should pose comparable cognitive demands and brain resources, whereas tasks with increased need for operative schemes such as those needed to plan the strategy for discovering the next switching rule would mobilize increased cognitive and brain resources (Pascual-Leone & Johnson, 2021).

Previous meta-analyses with adults showed that the WCST is associated with bilateral concordance in the inferior parietal lobule, inferior and middle frontal gyri (Buchsbaum et al., 2005; Rodríguez-Nieto et al., 2022), as well as bilateral insular cortex and thalamus (Rodríguez-Nieto et al., 2022). Left hemisphere concordance was found in the medial frontal gyrus, cuneus, postcentral, lingual (Buchsbaum et al., 2005), fusiform and middle occipital gyrus (Rodríguez-Nieto et al., 2022), as well as sub-cortical regions and the cerebellum (Buchsbaum et al., 2005). Extant TSP meta-analyses with adults also show that it is associated with the frontoparietal network, as well as the lingual gyrus (Buchsbaum et al., 2005), supplementary motor area (Worringer et al., 2019), superior parietal, frontal and occipital gyrus (Rodríguez-Nieto et al., 2022).

Meta-analyses also examined differences among the TSP switching types. Likely because of categorization differences Wager et al. (2004) reported comparable results among five switching types, whereas Kim et al. (2012a) showed both common and distinct brain areas for three of the switching types. Kim et al. (2012a) included the WCST with other switching tasks in the category 'operation' (what they called 'context'). Although the stimulus sorting in WCST is based on perceivable features (i.e., what can be theoretically referred to as figurative schemes; (Pascual-Leone & Johnson, 2005) like other TSP tasks, the switching strategy (i.e., what can be referred to as executive scheme, a type of operative scheme; (Pascual-Leone & Johnson, 2005) is discovered rather than memorized in WCST. Theoretically we would expect executive schemes that have a discoverable component to require more brain resources associated with coordinating multiple schemes and abstract thinking such as that observed when considering possibilities (e.g., Arsalidou & Pascual-Leone, 2016; Christoff et al., 2009).

Notably extant meta-analyses of cognitive flexibility tasks do not set age limits and included young and middle-aged participants. In light of neural and cognitive changes across adulthood (Ferguson et al., 2021; Ferreira et al., 2017; Hartshorne & Germine, 2015; Yaple et al., 2019) it is critical to map processes with age considerations. Therefore, we chose to focus only on young adults (18–35 years).

Our meta-analysis aims to distinguish brain correlates related to rule-retrieval and rule-discovery as observed in the tasks WCST and TSP, respectively, in young adults (18–35 years). Furthermore, we seek to determine whether common and distinct patterns exist among TSP switching types. Based on the aforementioned literature, we hypothesize that brain responses in the WCST and the TSP will exhibit common concordance in fronto-parietal, cingulate and insular cortices. Based on the right-left-right hypothesis (Arsalidou et al., 2018) we expect that the left hemisphere will be favored for switches that are known (i.e., TSP), whereas the right hemisphere will be favored for switches that are not known (i.e., WCST). Further, driven by the need to discover the switching rule we anticipate that the WCST will reveal increased implication of the frontopolar cortex and subcortical regions such as the basal ganglia and thalamus.

Materials and methods

Literature search and article selection criteria

We conducted literature searches in PubMed, Web of Science, BrainMap, Neurosynth, and PsycInfo databases using the following search string: ("cognitive flexibility" OR "set-shifting" OR "task-switching") AND (fMRI). The searches yielded a total of 5676 results published prior to January 2024. We conducted a manual search (i.e., by perusing) on the reference lists of past meta-analyses and identified two eligible articles from the meta-analysis conducted by Kim et al. (2012a). Figure 2 shows the PRISMA flow chart for the literature screening process. After removing 2298 duplicates, 3378 articles were subjected to the first screening. All article abstracts were screened for eligibility according to the following criteria: (a) utilized fMRI technology, (b) examined cognitive flexibility or relevant term (e.g., switching), and (c) conducted an original experimental study.

Four hundred ninety-four articles that survived the first screening were screened according to the following eligibility criteria: (1) written in English; (2) utilized a task-based fMRI approach; (3) conducted whole-brain analysis; (4) reported data in Talairach or Montreal Neurological Institute (MNI) standardized stereotaxic space; (5) included humans; (6) included either healthy participants (i.e., did not report mental or neurological disorders) as the primary group or as the control group; (7) involved participants older than 18 years and younger than 35 years on average; this criterion was included because past studies show cognitive performance changes in healthy adulthood (Cepeda et al., 2001; Hartshorne & Germine, 2015); (8) employed the subtraction method (e.g., task switching > control task). Articles were excluded if they employed correlation, multivariate pattern analysis, psychophysiological interaction, principal component analysis, and conjunction analysis; articles using the task-switching paradigm or the WCST (with task associated feedback) but did not focus on cognitive flexibility components (e.g., emotion, reward) or comparing different cognitive domains (switching vs. inhibition) were excluded, leaving only studies that focused on switch-related activity.

Two authors (Z.V.C. and A.A.F.) conducted the literature search and article screening. They read each identified article, applied eligibility criteria, and categorized the articles' characteristics into subcategories for data extraction. Whenever unclear aspects of data analysis, contrast or eligibility for inclusion criteria were encountered, issues were evaluated, and decisions were made in agreement with coauthors (A.Y.F. and M.A.). A total of 69 articles met the eligibility criteria for meta-analyses that included 94 experiments with data from 1617 participants. There were 14 WCST and 55 TSP articles containing 22 and 72 experiments, respectively.

Data extraction

For each experiment we recorded first author name, publication year, sample size, participant demographics, age and sex, task (i.e., WCST and TSP), experimental contrasts (i.e., experiments), and TSP switching type (i.e., attribute, response rule, operation; Tables 1 and 2). Note that not all TSP switching types had sufficient number of experiments ($n \geq 17$) recommended for meta-analyses (Eickhoff et al., 2016). Two authors (Zh.Ch. and A. Filatov) double-checked data entries for all experiments.

Data categorization

Data were organized by rule-discovery (WCST) and rule-retrieval (TSP) as well as by switching type (i.e., attribute, response rule, operation). Specifically, we defined our rule-discovery category as the WCST that did not provide retrieval rules for switching and required participants to use trial and error to identify the new sorting rule after negative feedback to a response. If the task provided participants with cues on rule-retrieval we considered the experiment as rule-retrieval which was comprised by TSP task.

The rule-retrieval category was further sub-categorized into experiments that assessed switching attention between locations (location switching), objects (object switching), attributes of objects (attribute switching), as well as shifting between response set, mental operations (operation switching), and response mappings (response rule switching).

Within the TSP we identified three of the most frequently used switching types for sub-analyses. There were 19 articles with attribute switching (25 experiments), 22 articles with operation switching (22 experiments), and 13 articles with response rule switching (13 experiments). Although the response rule switching does not satisfy the minimum number of experiments needed for a meta-analysis ($n \geq 17$; Eickhoff et al., 2016), we choose to perform the analyses to identify potential patterns as it was only 4 experiments away from the recommendations. Across 55 articles, there were only two eligible articles with experiments for location and object switching.

Activation likelihood estimation meta-analysis

The activation likelihood estimation (ALE; GingerALE, version 3.0.2; https://brainmap.org/ale/) is a coordinate-based meta-analysis method used in neuroimaging research for the quantitative evaluation of brain activation patterns

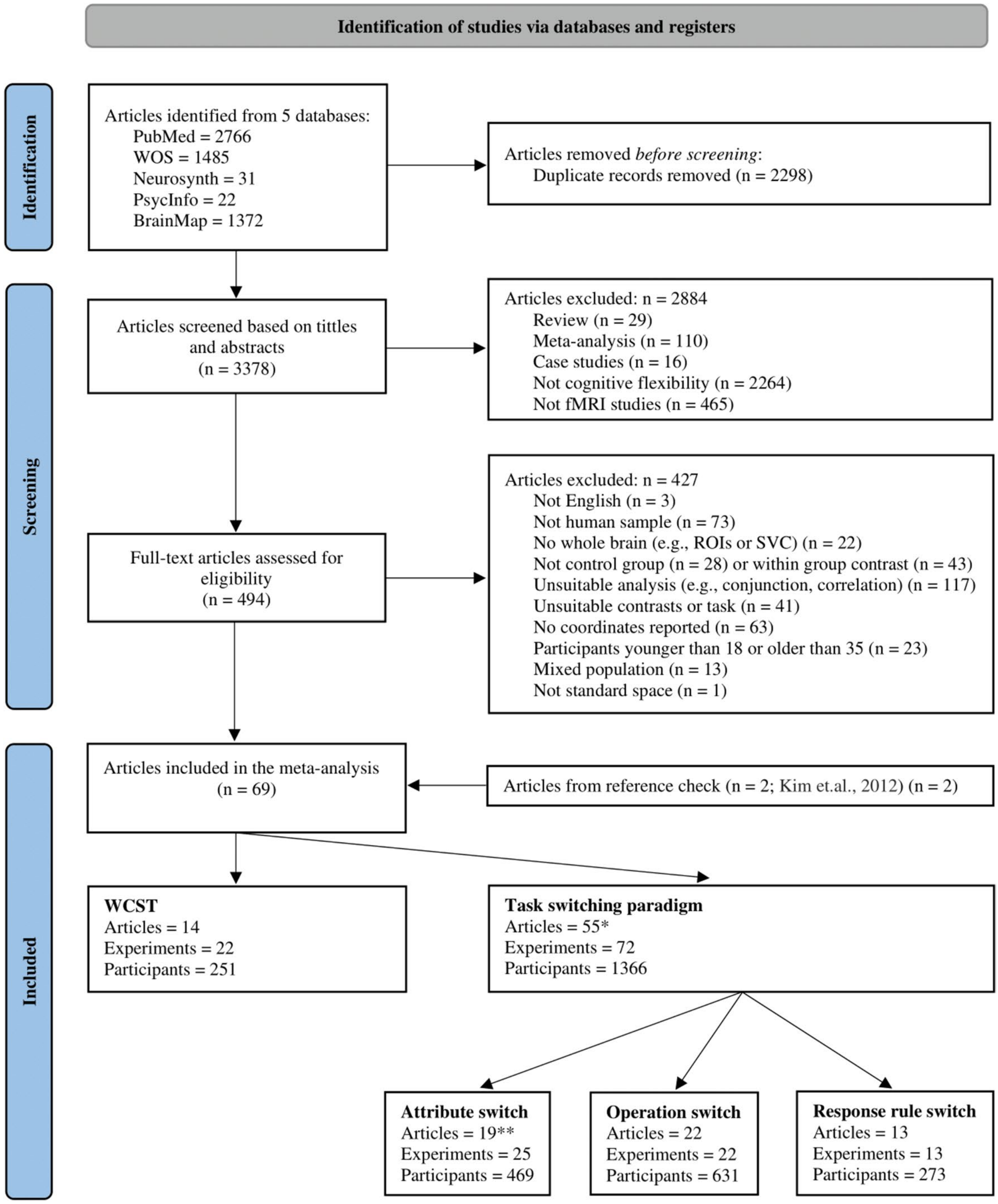

Fig. 2 Prisma flowchart for identification and eligibility of articles. *Note* n = number of articles. *Seven articles from task switching were not distributed by types of switching due to mixed types of switching (Cubillo et al., 2019; DiGirolamo et al., 2001; Armbruster et al., 2012; Yeung et al., 2006; Jamadar et al., 2010; Kim et al., 2012b; Sohn et al., 2000).**Six articles included data for two types of switching such as attribute and response rule switching (Philipp et al., 2013; Ravizza & Carter, 2008; Rushworth et al., 2002), operation and response rule switch (Stelzel et al., 2011, 2013) and attribute and operation switch (Vallesi et al., 2015)

(Eickhoff et al., 2009). It involves collecting data from different experiments and using coordinates (foci) to create 3D maps that show the probability of activation within a given voxel of a template brain. These maps are then compared to random spatial distributions to determine the likelihood of significant clusters. The ALE method generates a statistical map of ALE scores that assess the probability of the significance of brain regions being active during specific cognitive functions (Eickhoff et al., 2009; Turkeltaub et al., 2012). For all tasks, we include only contrasts that reflect brain

Table 1 Information on source datasets included in the meta-analysis for task switching paradigm

Study	*N*	Mean age ± SD (range)	F	Task	Contrast	Attribute switch	Operation switch	Response rule switch
Armbruster et al. (2012)	20	23.5 (20–32)	15	Task switching paradigm	Task Switching > Baseline			
Barber and Carter (2005)	13	20–35	4	A cued S-R incompatibility task	Switch > Repeat			●
Braem et al. (2013)	35	26 ± 6	7	Task switching paradigm	Task switch > Task repetition		●	
Brass and Cramon (2004)	14	24.4 ± 1.9	3	Task switching paradigm	Meaning switch > Cue switch		●	
Braver et al. (2003)	13	21 (19–26)	3	Semantic classification tasks	Switch > Repeat		●	
Buss et al. (2021)	20	23.8 ± 3.8	5	Task switching paradigm	Switch > Repeat trials	●		
Buss et al. (2021)	20	23.8 ± 3.8	7	Task switching paradigm	Shifting dimensions > Repeat dimensions	●		
Calcott and Berkman (2015)	19	22.63 ± 3.59 (19–30)	1	Modified version of composite letter task	Switch > Non-Switch	●		
Chiu and Yantis (2009)	16	20–32	3	A cued task-switching paradigm	Rule Switch > Rule hold		●	
Chiu and Yantis (2009)	16	20–32	6	A cued task-switching paradigm	Attention Shift > Attention hold			
Crone et al. (2006)	20		2	Task switching paradigm	Univalent switches > Repetitions			
Crone et al. (2006)	20		23	Task switching paradigm	Bivalent switches > Repetitions			●
Cubillo et al. (2019)	30	24 ± 2	3	Incentivized switch task	Switch > Repeat			
Dang et al. (2012)	16	25 ± 2.5	6	Set-shift task	Object shift > No shift	●		
De Baene and Brass (2011)	19	22 ± 1.8	5	Task switching	Task-switch > Cue-repeat	●		
DiGirolamo et al. (2001)	8	25 (20–30)	68	Task switching	Switch > Non-switch			
DiGirolamo et al. (2001)	8	25 (20–30)	31	Task switching paradigm	Switch > Fixation			
Dove et al. (2000)	16	21–29	13	Task switching paradigm	Task switch > Task repetition			●
Dreher and Grafman (2003)	8	25 (20–31)	14	Task switching paradigm	Switching > Baseline		●	
Dreher et al. (2002)	8	25 (20–31)	9	Task switching paradigm	Switching > Baseline		●	
Eich et al. (2023)	71	26.10 (20–31)	5	Cued task switching paradigm	Switch > Repeat		●	
Fuentes-Claramonte et al. (2015)	28	24.21 ± 4.08 (19–32)	20	Task switching	Switch > Repeat	●		
Gu et al. (2007)	21	24.8 ± 3.7	18	Task switching	Switch > Repeat	●		
Hakun and Ravizza (2012)	20	21.47 ± 2.95 (18–29)	3	Task switching	Rule-Catch Switch > Repeat			●
Hedden and Gabrieli (2010)	17	21.6 (18–28)	1	Global-local task	Neutral Shifting > Incongruent Non-Shifting	●		
Hippmann et al. (2021)	23	23 (19–29)	5	Task switching paradigm	Switch > Repeat		●	

Table 1 (continued)

Study	*N*	Mean age ± SD (range)	F	Task	Contrast	Attribute switch	Operation switch	Response rule switch
Jamadar et al. (2010)	18	25 ± 7	9	Task switching paradigm	Switch > Repeat			
Kim et al. (2012b)	16	23.6 ± 2.9 (18–35)	20	Task switching	Switch > Non switch			
Liston et al. (2006)	19		7	Task switching paradigm	Shift > Repeat (color and motion)	●		
Liston et al. (2006)	19		2	Task switching paradigm	Shift > Repeat (color)	●		
Liston et al. (2006)	19		2	Task switching paradigm	Shift > Repeat (motion)	●		
Liu et al. (2023)	48	20.65 ± 2.1	5	Task switching paradigm	Switch > Repeat	●		
Muhle-Karbe et al. (2014)	44	1 study: 21.1 (21.1); 2 study: 23.3 (18–32)	13	Task switching paradigm	Switch > Repeat (Task switch)			
Muhle-Karbe et al. (2014)	44	1 study: 21.1 (21.1); 2 study: 23.3 (18–32)	12	Task switching paradigm	Switch > Repeat (Full Switch)			
Muhle-Karbe et al. (2014)	44	1 study: 21.1 (21.1); 2 study: 23.3 (18–32)	10	Task switching paradigm	Switch > Repeat (SR Switch)		●	
Nir-Cohen et al. (2023)	43	25.05 ± 2.5	5	The procedural reference-back task	Switch > Repeat		●	
Orr and Banich (2014)	28	21.6 ± 3.8	19	Task-switching	Switch > Repeat			●
Parris et al. (2007)	22	25 (21–52)	20	Task switching	Flip - Hold	●		
Philipp et al. (2013)	23	26	2	Task switching paradigm	Stimulus-categorization switch > Stimulus-categorization repetition			●
Philipp et al. (2013)	23	26	1	Task switching paradigm	Response-modality switch > Response-modality repetition	●		
Piguet et al. (2013)	18	24.9 ± 5.46	5	Task swithcing paradigm	Switch > Repeat			●
Pollmann et al. (2000)	11	22–27	6	Task-switching paradigm	Switch > Baseline			●
Ravizza and Carter (2008)	14	27.14	3	Task-switching paradigm	Rule Shift > Rule repetition	●		
Ravizza and Carter (2008)	14	27.14	3	Task-switching paradigm	Perceprual shift > Perceprual repeat		●	
Rubia et al. (2006)	22	28 ± 6 (20–43)	7	Switch task	Switch > Repeat		●	
Ruge et al. (2005)	18	25.5 (21–35)	2	Switch task	Task switch > Task repeat	●		
Rushworth et al. (2002)	10	19–31	2	Visual-switching paradigm	Switch > Stay			●
Rushworth et al. (2002)	10	19–31	4	Response-switching paradigm	Switch > Stay		●	
Sali et al. (2024)	24	26.25 ± 5.4 (21–39)	6	Numerical task-switching paradigm	Switch > Repeat		●	
Sekutowicz et al. (2016)	108	26.26 ± 3.75	22	Task switching paradigm	Task switch > Repetition			
Shi et al. (2018)	32	25.5 ± 3.9 (20–36)	21	Task switching paradigm	Task switching > Task repetition			●
Smith et al. (2004)	20	28.8 ± 7(20–43)	10	Switch task	Switch > Repeat		●	
Sohn et al. (2000)	12	18–36	4	Task-switching paradigm	Repetition and switch x Scan			

Table 1 (continued)

Study	*N*	Mean age ± SD (range)	F	Task	Contrast	Attribute switch	Operation switch	Response rule switch
Stelzel et al. (2011)	48	Female (22 ± 1.99); male (22.6 ± 1.99)	5	Task switching paradigm	Task switch > Task repetition		●	
Stelzel et al. (2011)	48	Female (22 ± 1.99); male (22.6 ± 1.99)	13	Task-switching paradigm	Hand switch > Hand repeat			●
Stelzel et al. (2013)	18	Female (25.6 ± 2.8); male (26.5 ± 6.7)	4	Task switching paradigm	Rule switch > Rule repeat		●	
Stelzel et al. (2013)	18	Female (25.6 ± 2.8); male (26.5 ± 6.7)	7	Task switching paradigm	Hand switch > Hand repeat			●
Tei et al. (2023)	24	31 ± 6.6 (20–46)	10	Task-switching paradigm	Switch > Repeat	●		
Tsumura et al. (2021)	27	18–23	40	Task switching	Switch > Repeat	●		
Vallesi et al. (2015)	31	23 (21–30)	10	Task switching paradigm	Task switching > Single task (Spatial)	●		
Vallesi et al. (2015)	31	23 (21–30)	8	Task switching paradigm	Task switching > Single task (verbal)		●	
Ward et al. (2019)	30	22 (18–32)	2	Task switching paradigm	Switch Only > Baseline		●	
Weissberger et al. (2015)	19	20.45 ± 1.9	6	Task switching paradigm	Switch trials > Baseline (color-shape)	●		
Whitmer and Banich (2012)	27	20.04 ± 2.73	6	Task switching paradigm	Switch > Repeat		●	
Witt and Stevens (2013)	83	22 ± 2.7 (18–31)	23	Set switching paradigm	Switch > Non switch	●		
Wylie et al. (2006)	13	24.5 ± 4.4	11	Task-switching paradigm	Color switch > Color repeat (cues)	●		
Wylie et al. (2006)	13	24.5 ± 4.4	2	Task-switching paradigm	Speed switch > Speed repeat (cues)	●		
Wylie et al. (2006)	13	24.5 ± 4.4	19	Task-switching paradigm	Color switch > Color repeat (targets)	●		
Wylie et al. (2006)	13	24.5 ± 4.4	4	Task-switching paradigm	Speed switch > Speed repeat (targets)	●		
Xu et al. (2015)	18	26.4 ± 4.5	10	Switching task	Switch > Switch go			
Yeung et al. (2006)	15	19–24	12	Task switching paradigm	Switch > Repeat		●	
Yin et al. (2018)	26	21.3 (21–25)	15	Task switching paradigm	Switch > Repeat		●	

activity during switching. All coordinates in Talairach space were converted to MNI space using the Lancaster transform method (Lancaster et al., 2007).

Individual ALE meta-analyses

Individual meta-analyses were conducted for the rule-discovery and rule-retrieval categories, as well as three sub-categories of rule-retrieval (attribute, response rule, and operation switch separately). Permutation testing with 10,000 iterations was conducted. Results were thresholded at $p < .05$ cluster-level family-wise error (cFWE) corrected for multiple comparisons, with a cluster-forming threshold at voxel level ($p < .001$), according to empirical simulations indicating that this correction is the most suitable approach available for statistical inference using ALE (Eickhoff et al., 2016).

Contrast and conjunction ALE meta-analyses

Contrasts analyses between rule-discovery (WCST) and rule-retrieval (TSP), as well as the rule-discovery WCST versus rule-retrieval TSP-attribute, TSP-response rule and TSP-operation, were performed to reveal brain regions that exhibited differential concordance among conditions. This involved calculating the voxel-wise difference between the two ALE analyses and randomly shuffling experiments contributing to each analysis into two samples of equal size.

Table 2 Information on source datasets included in the meta-analysis for the WCST

Study	*N*	Mean age ± SD (range)	F	Task	Contrast
Aizawa et al. (2012)	30	21.4 ± 1.5	14	WCST	RNF > RPF
Asari et al. (2005)	16	27 ± 5 (20–37)	66	WCST	Dimensional change > No-change
Graham et al. (2009)	18	21 (19–25)	17	WCST	MNF > MPF
Graham et al. (2009)	18	21 (19–25)	14	WCST	2 + NF > 2 + PF
Konishi et al. (2002)	16	19–35	9	Modified WCST	Dimensional change > No-change
Lao-Kaim et al. (2015)	32	34 ± 8 (22–46)	5	WCST	MNF > MPF
Lie et al. (2006)	12	24 ± 5 (19–36)	10	WCST	A-HLB
Methqal et al. (2017)	20	24.85 ± 3.85 (19–35)	12	Word-matching task	MNF > MCF
Methqal et al. (2017)	20	24.85 ± 3.85 (19–35)	8	Word-matching task	MNF > MPF
Monchi et al. (2001)	11	24 (18–31)	30	WCST	RNF > RCF
Monchi et al. (2001)	11	24 (18–31)	6	WCST	MNF > MCF
Nagahama et al. (2001)	6	27.4 ± 8.1	14	Modified WCST	Set shifting > Reversal
Nagano-Saito et al. (2008)	19	22.6 ± 2.2 (18–27)	29	WCST	MNF > MCF
Nagano-Saito et al. (2008)	19	22.6 ± 2.2 (18–27)	24	WCST	RNF > RCF
Ren et al. (2012)	14	34.07 ± 14.4	6	WCST	2 + NF > 2 + PF
Ren et al. (2012)	14	34.07 ± 14.4	12	WCST	MNF > MPF
Sato et al. (2013)	15	22 ± 3	5	WCST	RNF > RPF
Simard et al. (2011)	14	26 ± 2.29 (22–31)	36	WWST	RNF > RCF
Simard et al. (2011)	14	26 ± 2.29 (22–31)	30	WWST	MNF > MCF
Simard et al. (2011)	14	26 ± 2.29 (22–31)	27	WWST	MNF > MPF
Simard et al. (2011)	14	26 ± 2.29 (22–31)	32	WWST	FNF > RPF
Vatansever et al. (2017)	28	26.8 ± 2.8 (22–34)	5	WCST	Task > Control

RNF receiving negative feedback, *RPF* receiving positive feedback, *MNF* matching after negative feedback, *MPF* matching after positive feedback, *2 + NF* receiving second negative feedback, *2 + PF* receiving second positive feedback, *A-HLB* no instruction of dimension (A) - High-level baseline, *B-HLB* Instruction of dimensional change (B) - High-level baseline, *C-HLB* Reminder of dimension prior to each trial (C) - High-level baseline

Conjunction analyses were performed to detect brain regions that were concordantly activated among the three types of switching and in both rule-discovery and rule-retrieval. Because first-level results, which are already corrected for multiple comparisons, are used in second-level conjunction and contrast analyses to directly derive the convergence and divergence of coordinates between conditions, we applied a typical threshold of $p < .01$ uncorrected (10,000 permutations, 200 mm^3 minimum volume, e.g., Arsalidou et al., 2020; Yaple et al., 2019).

Results

Individual ALE meta-analyses

Rule-discovery (WCST)

Results associated with brain concordance for rule-discovery in switching tasks are illustrated in Fig. 3.A and coordinates are listed in Table 3.. The WCST elicits concordance in bilateral fronto-parietal, cingulo-opercular areas, and BA 10, as well as subcortical regions in the right hemisphere.

Rule-retrieval (TSP)

Concordance for all TSP rule-retrieval tasks are illustrated in Fig. 3.B and coordinates are listed in Table 3.. The TSP shows concordance mainly in left hemisphere fronto-parietal areas and bilateral cingulo-opercular areas.

Sub-categories of rule-retrieval

Results are illustrated in Fig. 3.C-E, and concordant coordinates are listed in Table 4. All TSP subtypes show concordance in the left fronto-parietal areas. TSP attribute switching shows additional concordance in bilateral cingulate gyrus.

Conjunction ALE meta-analyses

Intra-paradigm conjunction analysis

Table 5 shows significant clusters common to TSP ∩ WCST, which include left hemisphere parietal (BA 7, 40) and

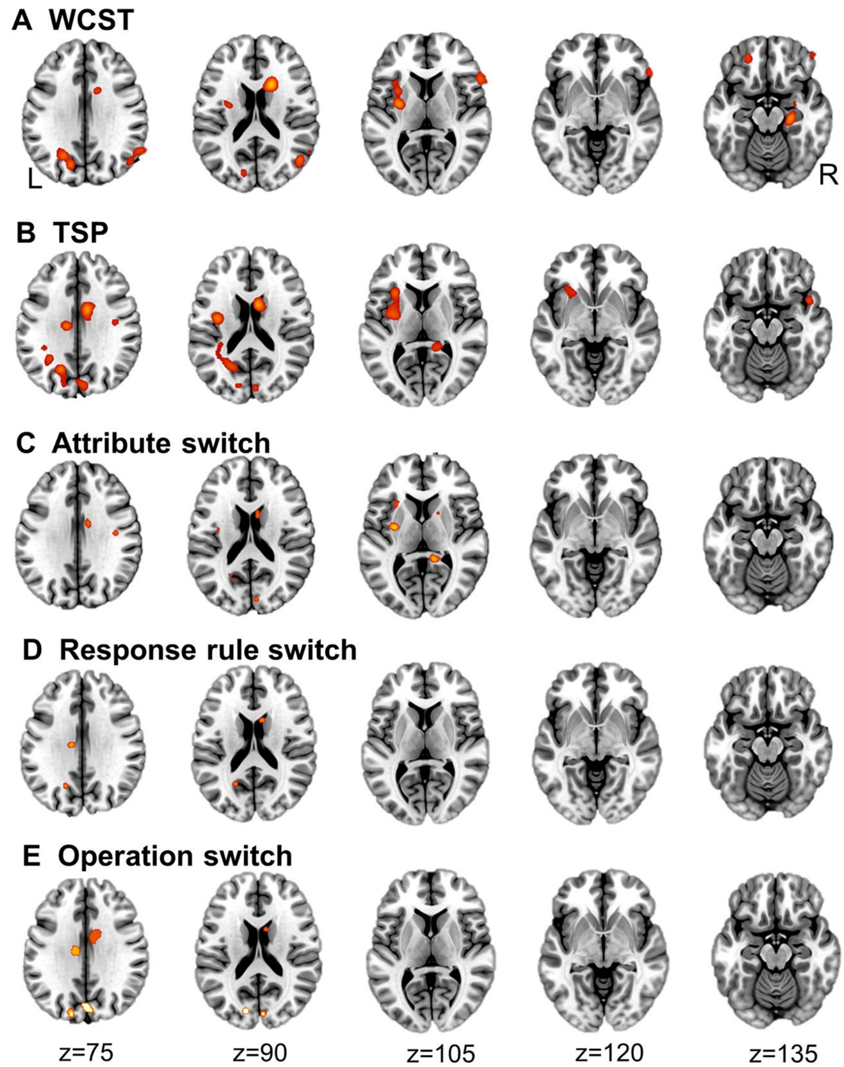

Fig. 3 ALE maps for (**A**) WCST, (**B**) TSP, (**C**) Attribute switch, (**D**) Response switch, and (**E**) Operation switch

prefrontal regions (BA 9) as well as right superior frontal gyrus and right claustrum.

Intra-switching subtypes conjunction analysis

A conjunction analyses of three switching subtypes (i.e., {[Attribute switch ∩ Operation switch] ∩ Response rule switch}) revealed concordance in mostly left lateralized fronto-parietal areas as well as in right cingulo-opercular areas (Table 5).

Contrasts

Rule-discovery (WCST) > rule-retrieval (TSP)

Rule-discovery showed concordance in numerous distinct bilateral clusters compared to rule-retrieval (Fig. 4; Table 5). Specifically, WCST showed increased involvement in bilateral inferior parietal lobule (BA 40, 39, 7), and middle frontal gyrus (BA 9, 10, 46), as well as increased concordance in insula, claustrum, and thalamus.

Rule-discovery (WCST) < rule-retrieval (TSP)

Comparison of the rule-retrieval greater than rule discovery revealed only one cluster in the left medial frontal gyrus (BA 6; Fig. 4; Table 5).

Contrast analyses among rule-retrieval (TSP) subcategories, namely attribute, response rule and operation switching subtypes showed no suprathreshold clusters.

Results of the contrast analyses between the rule-discovery (WCST) and each rule-retrieval (TSP) subcategory are listed in supplementary material (Table S1). All analyses produced consistent findings with respect to the comparisons between the WCST and TSP. Specifically, WCST showed increased concordance in multiple bilateral fronto-parietal and subcortical regions. Response rule switching and attribute switching did not yield any

Table 3 Brain correlates of the cognitive flexibility paradigms

WCST							
Cluster	Volume (mm³)	Region	BA	ALE Value	x	y	z
1	5672	L Inferior Parietal Lobule	40	0.035	-38	-50	50
		L Superior Parietal Lobule	7	0.031	-30	-60	50
		L Precuneus	19	0.022	-28	-76	34
2	5016	L Inferior Frontal Gyrus	9	0.037	-46	8	32
		L Middle Frontal Gyrus	46	0.027	-46	20	26
		L Middle Frontal Gyrus	46	0.019	-50	32	28
		L Middle Frontal Gyrus	9	0.017	-44	32	32
3	4968	R Inferior Parietal Lobule	40	0.029	36	-54	44
		R Inferior Parietal Lobule	40	0.029	44	-46	50
		R Superior Parietal Lobule	7	0.022	36	-58	56
4	4528	R Medial Frontal Gyrus	8	0.042	2	26	44
5	3232	R Thalamus		0.035	10	-10	6
		R Lentiform Nucleus		0.022	14	0	0
		R Caudate		0.019	16	16	-2
6	2712	R Inferior Frontal Gyrus	47	0.048	36	24	-4
7	2672	R Middle Frontal Gyrus	9	0.031	46	32	26
		R Middle Frontal Gyrus	46	0.022	44	40	20
8	2080	L Middle Frontal Gyrus	10	0.029	-36	56	-4
		L Middle Frontal Gyrus	10	0.022	-36	58	6
9	1936	L Insula	13	0.033	-32	24	-2
10	1032	R Middle Frontal Gyrus	10	0.019	34	54	-6
		R Middle Frontal Gyrus	10	0.018	36	62	4
TSP							
Cluster	Volume (mm³)	Region	BA	ALE value	x	y	z
1	9640	L Middle Frontal Gyrus	9	0.059	-50	6	36
		L Middle Frontal Gyrus	9	0.041	-44	32	28
2	9392	L Inferior Parietal Lobule	40	0.052	-34	-50	46
		L Inferior Parietal Lobule	40	0.042	-44	-40	48
		L Superior Parietal Lobule	7	0.030	-30	-70	50
		L Precuneus	7	0.027	-26	-70	42
		L Postcentral Gyrus	2	0.027	-50	-28	52
		L Postcentral Gyrus	2	0.027	-46	-24	38
		L Precuneus	19	0.025	-28	-70	36
3	7896	L Medial Frontal Gyrus	8	0.075	-4	18	46
		L Superior Frontal Gyrus	6	0.037	-4	6	58
		L Superior Frontal Gyrus	6	0.030	-2	0	70
4	3992	L Middle Frontal Gyrus	6	0.051	-28	-4	56
		L Middle Frontal Gyrus	6	0.045	-28	8	60
5	2584	L Precuneus	7	0.046	-8	-70	48
6	1288	R Middle Frontal Gyrus	6	0.032	28	0	56
7	1080	R Cingulate Gyrus	23	0.032	2	-28	30
8	1024	R Insula	13	0.032	32	24	6

Coordinates are in MNI space; R= right; L= left; BA = Brodmann Areas; Vol=volume

suprathreshold clusters in contrast to the WCST; however, operation switch revealed increased concordance in the left medial frontal gyrus (BA 32) and cingulate gyrus (BA 24), which was similar to the region associated with the region revealed in TSP > WCST.

Discussion

In a set of meta-analyses, we investigated common and distinct brain areas concordant in fMRI experiments that used cognitive flexibility tasks that required either

Table 4 Brain correlates of the TSP switching types

TSP attribute switching type							
Cluster	Volume (mm³)	Region	BA	ALE value	x	y	z
1	3320	L Superior Frontal Gyrus	6	0.022	-2	12	48
		L Superior Frontal Gyrus	6	0.020	-4	8	58
		R Cingulate Gyrus	32	0.019	4	20	32
2	1064	L Supramarginal Gyrus	40	0.018	-42	-42	34
		L Inferior Parietal Lobule	40	0.017	-36	-48	44
3	1056	L Middle Frontal Gyrus	6	0.022	-28	8	60
		L Middle Frontal Gyrus	6	0.016	-30	-2	58
4	1024	L Middle Frontal Gyrus	46	0.019	-42	26	24
5	1008	R Middle Frontal Gyrus	6	0.020	28	0	58
		R Middle Frontal Gyrus	6	0.013	30	8	60
6	960	L Inferior Frontal Gyrus	9	0.024	-46	6	30
7	888	L Cingulate Gyrus	31	0.021	-2	-30	30
8	704	L Precuneus	7	0.019	-8	-74	44
9	672	L Precentral Gyrus	6	0.018	-48	2	44
TSP operation switching type							
Cluster	**Volume (mm³)**	**Region**	**BA**	**ALE value**	**x**	**y**	**z**
1	2624	L Middle Frontal Gyrus	6	0.0296	-50	4	38
		L Inferior Frontal Gyrus	9	0.0198	-48	14	22
		L Inferior Frontal Gyrus	9	0.0152	-40	8	30
2	2512	L Superior Parietal Lobule	7	0.0192	-32	-52	54
		L Inferior Frontal Gyrus	40	0.0173	-40	-42	42
3	2432	L Superior Frontal Gyrus	6	0.0303	-4	14	52
4	2040	L Middle Frontal Gyrus	6	0.0267	-26	-4	56
		L Middle Frontal Gyrus	6	0.0161	-26	8	60
5	1448	L Precuneus	7	0.0210	-8	-72	44
		L Superior Parietal Lobule	7	0.0181	-14	-66	54
6	1208	L Superior Parietal Lobule	7	0.0226	-30	-72	48
		L Precuneus	19	0.0152	-28	-68	36
TSP response rule switching type							
Cluster	**Volume (mm³)**	**Region**	**BA**	**ALE value**	**x**	**y**	**z**
1	1256	L Inferior Parietal Lobule	40	0.019	-34	-50	48
2	1152	L Medial Frontal Gyrus	8	0.017	-6	18	46
		L Cingulate Gyrus	32	0.014	-4	24	38
3	800	L Middle Frontal Gyrus	6	0.017	-26	-6	50
4	656	L Middle Frontal Gyrus	9	0.015	-48	8	36
		L Middle Frontal Gyrus	6	0.011	-52	2	38
		L Middle Frontal Gyrus	6	0.011	-56	6	38

Coordinates are in MNI space, *R* right, *L* left, *BA* Brodmann Areas, *Vol* volume

rule-discovery (WCST) or rule-retrieval (TSP) in young adults. We highlight three key findings. First, rule-discovery associated with the WCST, and rule-retrieval associated with the TSP show concordance in a widespread set of brain areas. They share concordance in parietal and dorsolateral prefrontal cortices, and the claustrum. We emphasize that shared cortical concordance is identified mainly in the left hemisphere. Second, rule-discovery associated with the WCST implicates distinct brain regions including the right hemisphere in parietal and dorsolateral prefrontal cortex, and we note the concordance we observe in frontopolar regions (Brodmann Area; BA 10). The frontopolar cortex is involved in higher order abstract thinking (e.g., Christoff et al., 2009) that may play a role in maintaining a strategy for discovering the new switching rule needed when solving the WCST. Furthermore, rule-discovery-specific concordance is observed in several subcortical regions including the thalamus, claustrum and caudate nuclei, which some associate with higher demands such as working memory and

Table 5 Common and distinct brain correlates among tasks

TSP ∩ WCST							
Cluster	Volume (mm³)	Region	BA	ALE value	x	y	z
1	3792	L Inferior Parietal Lobule	40	0.034	-38	-52	50
		L Inferior Parietal Lobule	7	0.028	-32	-56	48
		L Superior Parietal Lobule	7	0.026	-28	-62	50
		L Precuneus	19	0.021	-26	-70	38
2	3744	L Inferior Frontal Gyrus	9	0.037	-46	8	32
		L Middle Frontal Gyrus	9	0.026	-44	22	26
		L Middle Frontal Gyrus	9	0.019	-50	32	28
		L Middle Frontal Gyrus	9	0.017	-44	32	32
3	1408	R Superior Frontal Gyrus	8	0.035	0	22	48
4	464	R Claustrum		0.026	32	24	0
TSP: (Attribute switch ∩ Operation switch) ∩ Response rule switch							
Cluster	**Volume (mm³)**	**Region**	**BA**	**ALE value**	**x**	**y**	**z**
1	8584	L Inferior Parietal Lobule	40	0.045	-34	-50	46
		L Superior Parietal Lobule	7	0.03	-30	-70	50
		L Precuneus	19	0.025	-28	-70	42
		L Precuneus	19	0.024	-28	-70	36
		L Postcentral Gyrus	2	0.024	-46	-26	40
2	7904	L Middle Frontal Gyrus	6	0.05	-50	4	38
		L Middle Frontal Gyrus	9	0.035	-44	30	28
		L Inferior Frontal Gyrus	44	0.024	-48	12	22
3	6368	L Medial Frontal Gyrus	8	0.058	-6	18	46
4	3688	L Middle Frontal Gyrus	6	0.047	-28	-4	56
		L Middle Frontal Gyrus	6	0.038	-28	8	60
5	2088	L Precuneus	7	0.04	-8	-72	44
6	1224	R Middle Frontal Gyrus	6	0.025	26	0	56
		R Middle Frontal Gyrus	6	0.02	30	6	60
7	1008	R Cingulate Gyrus	31	0.026	0	-30	30
8	984	R Insula	13	0.032	32	24	6
WCST ˃ TSP							
Cluster	**Volume (mm³)**	**Region**	**BA**	**ALE value**	**x**	**y**	**z**
1	4160	R Inferior Parietal Lobule	40	3.891	40	-49	48
		R Angular Gyrus	39	3.719	38	-56	42
		R Superior Parietal Lobule	7	3.239	36	-58	58
2	3264	R Cingulate Gyrus	32	3.891	4	29	41
3	2264	R Insula	13	3.891	36	25	-7
4	2232	R Middle Frontal Gyrus	9	3.891	50	35	30
		R Middle Frontal Gyrus	46	3.156	45	37	20
5	2048	L Middle Frontal Gyrus	10	3.891	-36	57	3
6	1632	R Thalamus		3.891	12	-8	5
7	1056	L Claustrum		3.891	-29	25	-6
		L Inferior Frontal Gyrus	47	3.291	-34	20	-10
		L Inferior Frontal Gyrus	47	3.121	-38	20	-10
8	904	R Middle Frontal Gyrus	10	3.719	33	57	-2
		R Superior Frontal Gyrus		3.432	30	52	-6
9	728	L Inferior Parietal Lobule	40	3.891	-42	-48	52
10	664	R Caudate		3.891	14	12	3
11	488	L Cuneus	19	3.719	-26	-80	33
12	440	L Inferior Parietal Lobule	39	2.848	-35	-60	48

Table 5 (continued)

TSP ∩ WCST							
Cluster	Volume (mm³)	Region	BA	ALE value	x	y	z
13	432	L Thalamus		3.062	-12	-8	6
		L Thalamus		2.929	-8	-8	8
14	424	L Middle Frontal Gyrus	9	3.036	-52	26	28
		L Middle Frontal Gyrus	9	2.770	-42	18	22
		L Middle Frontal Gyrus	46	2.716	-46	20	22
15	392	L Precentral Gyrus	6	2.989	-42	5	36
		L Precentral Gyrus	6	2.346	-41	0	30
TSP > WCST							
Cluster	**Volume (mm³)**	**Region**	**BA**	**ALE value**	**x**	**y**	**z**
1	328	L Medial Frontal Gyrus	6	2.687	-10	8	54
TSP: attribute > operation							
no suprathreshold clusters							
TSP: attribute < operation							
no suprathreshold clusters							
TSP: operation > response rule							
no suprathreshold clusters							
TSP: operation < response rule							
no suprathreshold clusters							
TSP: response rule > attribute							
no suprathreshold clusters							
TSP: response rule < attribute							
no suprathreshold clusters							

Coordinates are in MNI space, *R* right, *L* left, *BA* Brodmann Areas, *Vol* volume

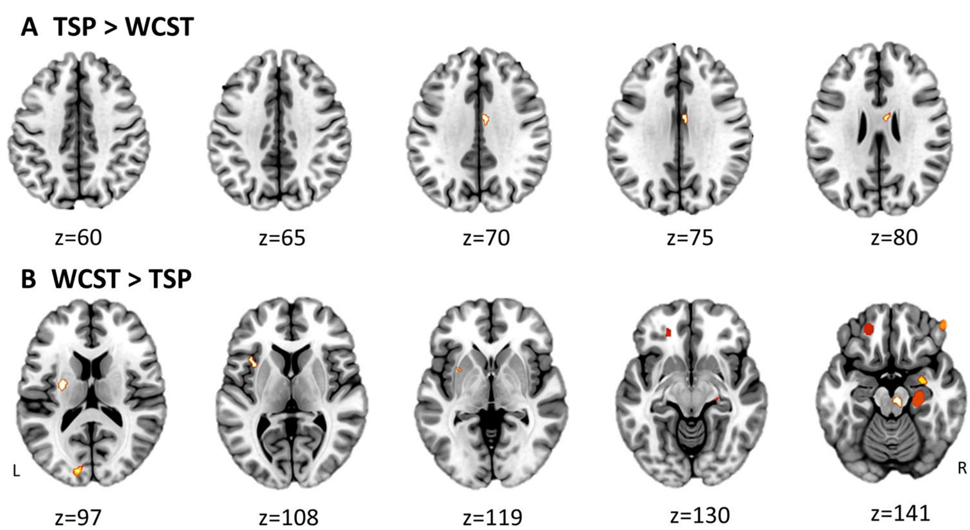

Fig. 4 ALE maps for (**A**) Rule-retrieval (TSP) > rule-discovery (WCST) and (**B**) Rule-discovery (WCST) > rule-retrieval (TSP)

inhibition processes (Rodríguez-Nieto et al., 2022). Third, contrasts among attribute, response rule and operation switching TSP subtypes of rule-retrieval did not show any suprathreshold differences, indicating a domain general nature for rule-retrieval. Overall, our results provide new knowledge on brain areas associated with different aspects of cognitive flexibility in healthy, young adults (18–35 years-old). We propose a topographical model of cognitive flexibility in standard stereotaxic space based on the findings of these meta-analyses that can serve as a framework for future research.

Common activation for the rule-discovery WCST and rule-retrieval TSP

Areas in the fronto-parietal network showed significant likelihood of being detected for both cognitive flexibility categories. The fronto-parietal areas are implicated in all sorts of cognitive processes such as working memory (Niendam et al., 2012; Rodríguez-Nieto et al., 2022; Yaple et al., 2019; Zhang et al., 2021), inhibition (Buchsbaum et al., 2005; Niendam et al., 2012; Rodríguez-Nieto et al., 2022; Zhang et al., 2021), as well as cognitive flexibility (Niendam et al., 2012; Rodríguez-Nieto et al., 2022; Wu et al., 2020; Zhang et al., 2021).

Our meta-analysis is the first to highlight the implication of the claustrum in cognitive flexibility. The claustrum is a thin strip of the cortex that borders the basal ganglia laterally and the insula medially. An early cognitive flexibility meta-analysis did not report concordance in the insula nor the claustrum (e.g., Kim et al., 2012a). A recent meta-analysis on cognitive flexibility implicates large clusters that encompass the insula, albeit it does not distinguish the claustrum (Rodríguez-Nieto et al., 2022), because the claustrum is a relatively small brain region, it can be a part of a large cluster that peaked on the insula. Although adjacent to the insula, the claustrum is distinct in terms of anatomy (Mathur, 2014) and structural connectivity (Park et al., 2012). Some suggest that the claustrum serves as a multisensory integrator (Bennett & Baird, 2006) that may underlie consciousness (Goll et al., 2015). Others point to its role in cognitive control (Krimmel et al., 2019; Madden et al., 2022; Niendam et al., 2012), social cognition (Zinchenko et al., 2018) and mathematical problem solving (Arsalidou et al., 2018). We suggest that the claustrum, situated within its sub-lobar location, serves a generic role in cognition for motivating goal-directed processes by coordinating interactions between cortical and subcortical regions.

Notably, common foci for both tasks are observed mainly in the left hemisphere. This finding is consistent with previous studies that highlight the role of the left hemisphere in response selection (Hammond & Fox, 2005; Rushworth et al., 1998). Indeed, the rule change in TSP is triggered by a cue, which is linked to a switching rule that was previously learned by the participants. In contrast, the WCST does not provide any cue; instead, the trigger for a rule change is negative feedback to a response to which participants need to consider their strategy and identify the next rule via trial-and-error. This is theoretically consistent with the hemispheric dominance hypothesis that predicts the left hemisphere being involved in familiar context within the participant's mental attentional capacity, whereas in an unfamiliar context the right hemisphere is favored (Arsalidou et al., 2018; Pascual-Leone, 1995).

Differences between rule-discovery (WCST) and rule-retrieval (TSP)

Our meta-analysis compares for the first-time brain coordinates associated with rule-discovery needed in the WCST and rule-retrieval needed in the TSP. Comparisons between paradigms revealed that rule-retrieval in the TSP showed increased engagement in a single brain region, in the left medial frontal gyrus (BA 6) adjacent to the cingulate gyrus, whereas rule-discovery in the WCST is associated with increased engagement in multiple cortical and sub-cortical regions in both hemispheres, including middle frontal gyri, inferior parietal lobule and thalami. Increased need for right hemisphere involvement is consistent with the theoretical notion of processes-driven hypotheses that implicate the right hemisphere in problem solving in highly novel situations and the left-hemisphere in familiar cognitive processes (Arsalidou et al., 2018; Pascual-Leone, 1995). Empirical data demonstrate that the right hemisphere corresponds with constructing plans, whereas the left one with supervising the execution of plans (Goel & Vartanian, 2005; Newman et al., 2009).

Rule-discovery in the WCST is associated with concordance in multiple cortical (e.g., frontopolar cortex) and subcortical brain regions such as the thalamus and caudate. The thalamus, for instance, is located between the midbrain and the cortex (Pinault, 2004) and is associated with multiple cognitive functions including learning and memory, decision-making, reward processing, monitoring, maintaining, and updating mental representations in response to changes in environmental conditions as well as selection of goal-directed action (Fama & Sullivan, 2015; Wolff & Vann, 2019). We propose that the thalamus helps assign priority values for coordinating cognitive processes in situations of high demand as in the case of rule-discovery.

The caudate nucleus, a subcortical region, part of the striatum or basal ganglia, has strong connections with the thalamus (Robinson et al., 2012). Although initially recognized for its role in motor behavior (Mattay & Weinberger, 1999; Ungerleider, 2002), the caudate nucleus has subsequently been implicated in a wide range of learning, executive and reward processing functions (Arsalidou et al., 2020, for meta-analyses). We propose that the caudate helps coordinate bottom-up and top-down (subcortico-cortico-subcortico) communication needed during rule discovery in the WCST.

Increased cortical concordance in favor of rule-discovery in the WCST was observed in the superior frontal gyri (BA 10). BA 10 is part of the frontopolar prefrontal cortex. The frontopolar cortex has been known for its involvement in strategy and planning processes. In the WCST, BA 10 involvement may be driven by the increase need for the identification of the new sorting principle, which is what we expected. BA 10 is associated with higher-order cognitive functions specifically with planning future actions and taking initiative (Christoff et al., 2009; Christoff & Gabrieli, 2000; Semendeferi et al., 2001) and has connections with the caudate nuclei. The implication of the frontopolar cortex emphasizes a key difference between rule-discovery and rule-retrieval in cognitive flexibility tasks.

In sum, although cognitive flexibility tasks share concordance in many brain locations primarily in the left hemisphere, rule-discovery in the WCST shows increased involvement of fronto-parietal and subcortical locations in both hemispheres. Notable is the implication of BA 10, the frontopolar cortex that is known for goal and strategy generation which is a primary procedural difference between cognitive flexibility tasks the TSP and the WCST.

Rule-retrieval (TSP): Attribute, operation, and response rule switching

We divided TSP tasks into sub-categories based on attribute, operation, and response rule. Conjunction results show concordance among TSP subtypes mostly in left hemisphere areas of the fronto-parietal network, namely dorsomedial prefrontal cortex, inferior frontal gyrus, as well as superior and inferior parietal lobules. Although the WCST shows several suprathreshold clusters in comparison with TSP subtypes, mainly in fronto-parietal and subcortical areas, TSP subtypes do not show increased involvement of brain region in the reversed contrasts, except for a single cluster in the dorsal cingulate for TSP operation switch. These results are consistent with our main analyses that combine all tasks and have been previously reported as involved in all sorts of cognitive tasks (Kim et al., 2012a; Niendam et al., 2012; Rodríguez-Nieto et al., 2022). The cingulate gyrus may be particularly implicated in TSP operation switch compared to WCST because it may be more effortful not in terms of rule-discovery but rather in terms of management of diverse types of information (e.g., syllables counting / sex identification task; Yeung et al., 2006).

Critically, no significant differences are observed among switching types. Similarly, Wager et al. (2004) reported comparable brain regions among switching types, whereas others did not (Kim et al., 2012a); albeit we must note that the latter used different task categorization criteria and mixed data from WCST and TSP. The lack of distinctions we observe among the three TSP types of switching supports that the general cognitive task demands are comparable (i.e., not significantly different). Our meta-analysis revealed that fronto-parietal brain regions associated with task-switching appear to be largely comparable across diverse task contexts and are not significantly influenced by them. This highlights the theoretical notion that operative schemes (executive schemes are a type of operative scheme: Pascual-Leone & Johnson, 2005) that we used to distinguish the cognitive flexibility tasks (e.g., rule-discovery) play a significant role in brain responses rather than content or context which primarily relies on figurative schemes (i.e., features or objects) as we see in the lack of difference observed among sub-categories of the rule-retrieval TSP. Further research with larger data samples is needed to confirm this finding.

Modeling cognitive flexibility

The most popular tasks of assessing cognitive flexibility are the WCST and the TSP. Both tasks evaluate switching properties during problem solving but they do so in a different way; in the TSP the rule is given and retrieved during problem solving, whereas in the WCST the rule needs to be discovered during problem solving. In a schematic brain model of cognitive flexibility, we illustrate key regions that are common between cognitive flexibility tasks ({rule-discovery ∩ rule-retrieval} in blue) and distinct to the rule-discovery in the WCST (in orange; Fig. 5). The model illustrates that that WCST is sensitive to multiple cognitive processes such as working memory, inhibition, and planning.

We speculate on the role each region plays in cognitive flexibility tasks. Specifically, we propose that the dorsolateral (middle frontal gyrus, BA 9, 46) is responsible for monitoring few or several items needed for problem solving, whereas frontopolar cortex (middle frontal gyrus and superior frontal gyrus, BA 10) is responsible for goal and strategy formation. We propose that the medial frontal gyrus (BA 6), which is adjacent to the dorsal cingulate, is involved in implementing cognitive goals, whereas BA 6 in the precentral gyrus plays a role in directing eye-movements. The inferior parietal lobule (BA 40) plays a role in visual-spatial representation, whereas the precuneus (BA 19, 7) and superior parietal lobule (BA 7) are responsible for recognizing perceptual characteristics of stimuli and associated visual-spatial processing. Sub-lobar structures: we propose that the claustrum integrates motivated goal-directed processes, and the insular cortex plays a role in balancing goal-directed and default mode processes. Sub-cortical structures: the thalamus plays a role in assigning priority values and the caudate nucleus is involved in coordinating top-down and bottom-up processes.

Considerations

Quantitative fMRI meta-analyses share general shortcomings associated with the lack of control over variability in statistical methodologies in original articles and publication bias, which should be considered when interpreting the results. Specifically, the TSP response rule category did not have sufficient power based on Ginger ALE recommendation of at least 17 experiments (Eickhoff et al., 2016). Although

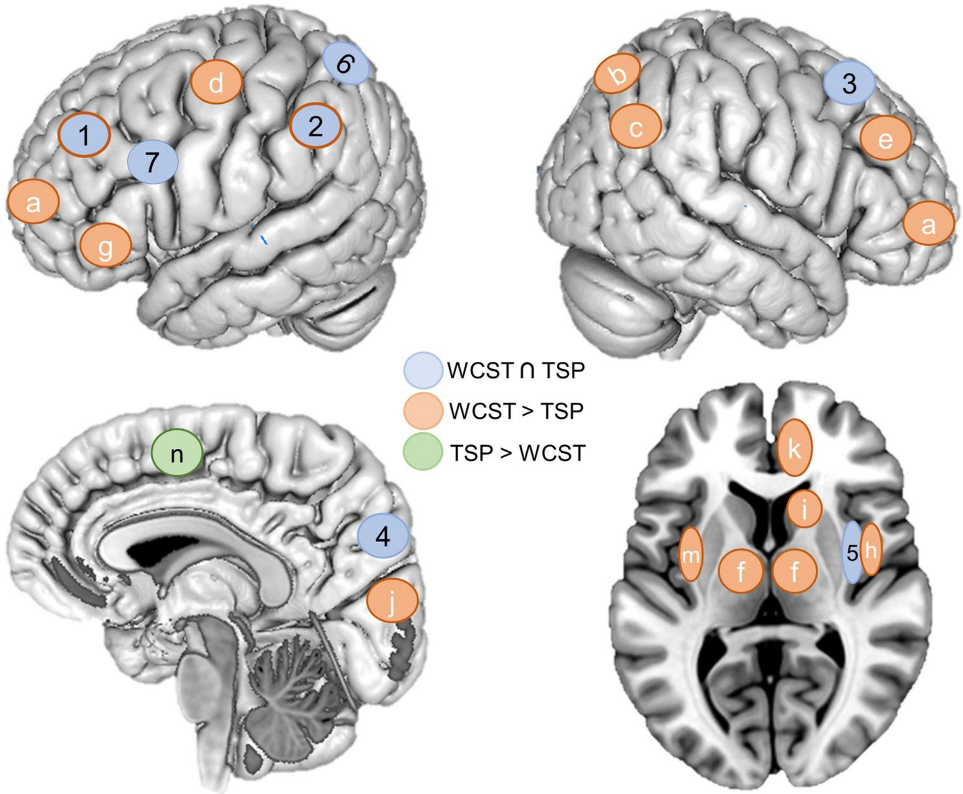

Fig. 5 A topographical model of cognitive flexibility. *Note* We schematized in blue cortical and subcortical locations common to WCST and TSP: (1) Middle frontal gyrus (BA 9): responsible for monitoring several items; (2) Inferior parietal lobule (BA 40; left hemisphere): involved visual-spatial representation; (3) Superior Frontal Gyrus (BA 8): plans eye movements; (4) Precuneus (BA 19): recognizes perceptual characteristics of stimuli; (5) Claustrum: integrates motivated goal directed processes; (6) Superior parietal lobule (BA 7): associated visual-spatial processing; 7); Inferior Frontal Gyrus (BA 9): responsible for monitoring few items. Blue areas that were identified through conjunction analysis and through contrast analysis were outlined in orange (e.g., (1) the middle frontal gyrus was significant for the WCST ∩ TSP conjunction and the WCST > TSP contrast). In orange, we schematized cortical and subcortical locations specific to WCST. **a**) Middle frontal gyrus (BA 10): engaged in goal, strategy formation; **b**) Superior parietal lobule (BA 7): handles visual-spatial processing; **c**) Inferior parietal lobule (BA 40): involved in visual-spatial representation; **d**) Precentral gyrus (BA 6): directs eye movements; **e**) Middle frontal gyrus (BA 9,46): monitors several items; **f**) Thalamus: assigns priority values; **g**) Inferior Frontal Gyrus (BA 47): synthesizes items needed for action outcomes; **h**) Insular cortex (BA 13): balance goal-directed and default-mode processes; **i**) Caudate nucleus: coordinates top-down and bottom-up processes; **j**) Cuneus (BA 19): recognizes perceptual characteristics of stimuli; **k**) Cingulate Gyrus (BA32): involved in task monitoring; **m**) Claustrum: integrates motivated goal directed processes. Using green color, we schematized cortical location specific to TSP; **n**) Medial Frontal Gyrus (BA 6): adjacent to the dorsal cingulate, involved in task monitoring

this analysis is underpowered, we chose to analyze data from 13 experiments in this category as they may be indicative of trends that may benefit future studies.

Conclusion

Our meta-analysis examined the common and distinct brain areas associated with two well-established cognitive flexibility paradigms. Both tasks shared fronto-parietal and cingulo-operculum locations mainly in the left hemisphere. Importantly, rule-discovery in the WCST showed increased concordance mainly in fronto-parietal and sub-cortical areas in both hemispheres, which may be associated with the increased task demands. Our results have theoretical and practical implications related to the underlying processes that give rise to performance in the two tasks. Specifically, our results support a process- rather than a material- based theoretical notion of the left and right hemispheres (Pascual-Leone & Johnson, 2005). Practically, we propose a model of cognitive flexibility with corresponding coordinates in stereotaxic space that will be useful for future studies that examine cognitive flexibility in samples with and without neurodevelopmental disorders.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11682-024-00921-7.

Acknowledgements This research was supported in part through computational resources of HPC facilities at HSE University to Z.V.C.

Author contributions Z.V.C., A.Y.F., and M.A. designed research; Z.V.C. and A.Y.F. analyzed data and prepared figures; Z.V.C. and A.A.F. wrote original draft; Z.V.C., A.A.F, and A.Y.F. performed research; Z.V.C. and M.A. interpretated results; A.Y.F. and M.A. reviewed manuscript; M.A., supervised.

Funding This work/article is an output of a research project implemented as part of the Basic Research Program at the National Research University Higher School of Economics (HSE University) that provided funding for Z.V.C.

Data availability Not applicable.

Code availability Not applicable.

Declarations

Consent for publication Was provided.

Competing interests The authors declare no competing interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

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