

Decoding cognitive control in human parietal cortex

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Efficient execution of perceptual-motor tasks requires rapid voluntary reconfiguration of cognitive task sets as circumstances unfold. Such acts of cognitive control, which are thought to rely on a network of cortical regions in prefrontal and posterior parietal cortex, include voluntary shifts of attention among perceptual inputs or among memory representations, or switches between categorization or stimulus-response mapping rules. A critical unanswered question is whether task set shifts in these different domains are controlled by a common, domain-independent mechanism or by separate, domain-specific mechanisms. Recent studies have implicated a common region of medial superior parietal lobule (mSPL) as a domain-independent source of cognitive control during shifts between perceptual, mnemonic, and rule representations. Here, we use fMRI and event-related multivoxel pattern classification to show that spatial patterns of brain activity within mSPL reliably express which of several domains of cognitive control is at play on a moment-by-moment basis. Critically, these spatio-temporal brain patterns are stable over time within subjects tested several months apart and across a variety of tasks, including shifting visuospatial attention, switching categorization rules, and shifting attention in working memory.

fMRI | pattern classification | task switching | working memory

Effective goal-directed behavior requires organisms to manage and coordinate the perceptual, cognitive, and motor processes required by ongoing tasks. Efforts to unravel the neural circuits responsible for rapid and efficient cognitive control have revealed that regions of dorsolateral and dorsomedial prefrontal cortex and posterior parietal cortex subservise different aspects of control, including the maintenance of working memory representations of task sets (1, 2), detection and management of perceptual, cognitive, or response conflict (3) and the initiation of task set reconfiguration (4, 5).

Frequent reconfiguration of the mind/brain in one or more domains is required as goals and environmental demands change. These domains may include, for example, states of attention that select task-relevant sensory or mnemonic information; categorization rules that can be applied to an attended perceptual input; and/or stimulus-response mapping rules that specify a task-appropriate response after perception and categorization. Transitions between task sets (e.g., shifting attention or switching categorization rule) are accomplished through voluntary acts of cognitive control. The psychological and neurophysiological basis of task set shifting has been investigated with behavioral and neuroimaging techniques (4–8).

A critical unresolved question concerns whether task set reconfiguration in different cognitive domains is associated with multiple domain-specific control mechanisms or with a common, domain-independent control mechanism. According to the domain-specific account, distinct dedicated brain regions control task set shifts in different cognitive domains (9). According to the domain-independent account, a common cortical source of control signals initiates shifts in multiple (or all) cognitive domains (10). Shifting task set across several domains recruits a network of brain regions including the prefrontal cortex, superior parietal cortex, and the basal ganglia (4–6, 10). Studies have revealed at least partially distinct neural substrates for different domains of cognitive control, such as the intraparietal sulcus and frontal eye fields for shifts of

visuospatial attention (5, 10, 11), and prefrontal cortex for switching categorization rule (4, 6, 12, 13). Thus, a third possibility is that a common cortical locus initiates task set shifts within many domains of control by coordinating activity in brain regions that are specialized for representing and processing information within specific domains.

Several recent functional neuroimaging studies have reported that voluntary shifts of attention in multiple sensory domains are associated with transient shift-evoked activity in the medial wall of the superior parietal lobule (mSPL) and superior precuneus (5, 11, 14–17). This brain activity is time-locked to the initiation of the shift and is transient, suggesting that it plays a unique role in reconfiguring, rather than maintaining the state of attention. A recent meta-analysis of studies investigating different domains of control suggested that a common set of cortical regions, including posterior parietal cortex, tend to be associated with cognitive control (broadly construed) in each studied domain (18). Individual differences in behavioral switching performance correlate across tasks requiring both internal (mnemonic) and external (perceptual) loci of attentional control (19). Together, these lines of evidence implicate a domain-independent transient reconfiguration process associated with a neural signature that is consistently observed in mSPL. A recent neurophysiological investigation revealed that neurons in macaque area 7a, in the posterior parietal cortex, responded transiently to categorization rule reconfigurations (20); this finding is qualitatively similar to the signal observed in human mSPL with fMRI (e.g., ref. 10). However, few studies have investigated multiple domains of control simultaneously. One recent study that directly compared the neural basis of cognitive control in multiple domains reported that activation in a common region in mSPL was associated with both spatial shifts of attention and switches of categorization rule (10); no other brain region exhibited this domain-independent pattern of activity.

The functional properties of mSPL are not well understood. This cortical region is virtually absent from the neurophysiology or human focal lesion literature (21). Furthermore, although several functional imaging studies have implicated mSPL as a domain-independent locus of cognitive control, other interpretations of this activity are possible. For example, mSPL may contain distinct domain-specific subpopulations of neurons that are recruited for different types of reconfigurations (10), a pattern that conventional univariate statistical techniques may fail to detect. No neurophysiological data have been collected to address this question.

Methods in multivariate analyses and machine learning have recently been deployed to investigate the voxelwise spatial pattern of activity within functional regions of interest (22). Multivoxel pattern classification (MVPC) applied to BOLD fMRI data supports inferences about functional organization at the subregion level, as follows. If a given cortical region contains two or more intermixed subpopulations of neurons with distinct functional se-

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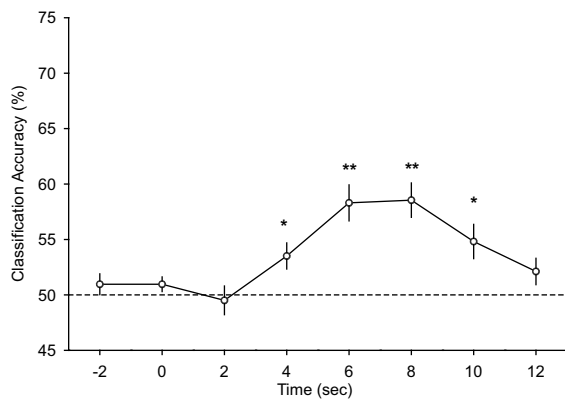


Fig. 2. Event-related classification performance in Experiment 1: decoding attention shift vs. categorization rule switch. Classification performance is presented for each time point relative to the onset of a switch cue, based on voxels in medial SPL (see *Methods*). *, $P < 0.05$; **, $P < 0.001$.

MVPC supports inferences about the relative contribution, or importance, of individual voxels to successful classification (22). This allows us to explore the response properties of the most important voxels, as well as the spatial pattern of voxel selectivity. To this end, mSPL voxels were rank-ordered according to how much they contributed to the classification accuracy (using the SVM weights derived from classifying the mean of the BOLD signal at time points 6 and 8 s after the relevant shift cue), separately for each subject (see *SI Methods*). MVPC was carried out repeatedly within subsets of voxels, starting with a subset of the two most important voxels and then with increasingly large subsets of the N most important voxels ($n = 2, 10, 25, 50, 100, 150, 200$, and 300). Classifier performance peaked when MVPC was restricted to the most important 100 voxels, and sharply decreased with 200 voxels or more (Fig. S2). The reduction in classification performance that emerges when increasing numbers of voxels are added reflects the addition of low-importance voxels that contain noise.

Approximately 54% of the 100 voxels that yielded the best classification performance were assigned positive weights (i.e., when these voxels were highly active, they contributed to an ‘attention shift’ classification) and 46% were assigned negative weights (i.e., when these voxels were highly active, they contributed to a ‘rule shift’ classification). To visualize the response properties of these voxels, the mean shift-cue-evoked BOLD response was examined. The distribution of the most discriminating voxels reveals subpopulations that respond preferentially to attention shifts and

rule switches, respectively (Fig. 3A shows a single representative subject). This illustrates that the classifier is relying on mSPL voxels that are recruited selectively for each type of cognitive reconfiguration. The spatial pattern of a subset of these 100 voxels (on a single slice plane) is displayed in Fig. 3B for four representative subjects.

Pattern classification reveals that the mSPL contains voxels that respond selectively during acts of control in different cognitive domains. The overall mean BOLD response of mSPL was greater after attention shift cues than after rule switch cues [$t(15) = 4.23$, $P < 0.01$], despite the fact that the distributions of peak BOLD response magnitudes for each type of shift were highly overlapping (see Figs. S3 and S4). A large mean difference in activity between conditions within an area could provide a partial basis for accurate classification. We therefore took several steps to determine whether the observed mean difference was a significant source of classification accuracy.

First, we compared multivoxel classification to classification performance based only on the mean activity within the entire ROI (in effect, treating it as a single feature). Classification performance was significantly worse than MVPC (60.3% for MVPC vs. 54.5% for the mean activity, paired t test, $P < 0.01$). Removing the mean difference (mean-centering) by normalizing rule- and attention-shift BOLD signal (see *Methods*) (24) had no significant effect on classifier performance (60.9% correct classification with and 60.3% without normalization). Together, these controls validate the sensitivity of multivariate pattern analyses in detecting different voxel patterns for different reconfiguration signals and reveal the pattern specificity of the transient signal in mSPL after acts of task set reconfiguration.

Decoding Reconfiguration Signals Within Each Domain. In addition to assessing the degree to which MVPC could accurately classify which of two different domains of cognitive control was at play (spatial attention shift versus rule switch), we also examined the degree to which MVPC could accurately classify different types of shifts within a single domain. The SVM classifier successfully decoded shifts of spatial attention from left-to-right vs. right-to-left (59.5% correct overall, $P < 0.0001$). However, MVPC failed to correctly classify shifts between the two digit categorization rules (shifts from the magnitude categorization rule to the parity rule and vice versa; 49.8% correct classification overall). This suggests that the neurons in mSPL encode the direction of spatial shifting but not necessarily the nature of the specific task rule reconfiguration. However, it is also possible that mSPL voxels represent the cue location or the location to which attention is directed (opposite of the cue), rather than the direction of the shift itself. These are not mutually exclusive

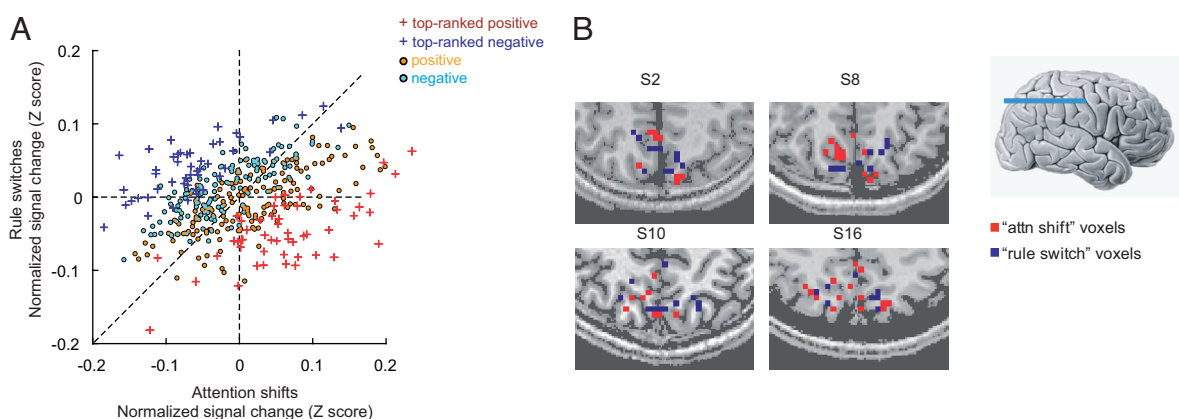


Fig. 3. Illustration of response properties and spatial pattern of important voxels (A) Scatterplot (data from Subject 8) of mean normalized BOLD response evoked by attention shift or rule switch cues in each of 402 mSPL voxels. Plus signs are the 100 most important voxels, and circles are the rest of the voxels. Dotted line indicates equivalent relative response to attention and rule reconfigurations. (B) Voxels projected on brain by importance value, in four subjects.

alternatives, and the resolution of fMRI and current experimental design does not allow us to distinguish between these alternatives.

The voxels selective for left-to-right versus right-to-left shifts did not correlate with left-right position in the brain (correlation of importance values and left-right position, $r = 0.01$), which constitutes evidence against a lateralized organization in this medial brain region. Furthermore, the classification of shift direction is not entirely driven by the highest magnitude “attention-weighted voxels” from the attention shifts vs. rule shifts classifier. Specifically, the most important 50 or 100 positively weighted “attention shift voxels” classified direction of shift (left-to-right vs. right-to-left) no better than the most important 50 or 100 negatively weighted “rule shift voxels” (50 voxels: 55.0% vs. 54.5%; 100 voxels: 57.5% vs. 54.8%; $P > 0.1$). However, among these subsets of voxels, only classification with the best 100 “attention shift voxels” (57.5%) was not significantly worse than classification using all SPL voxels (59.5% accuracy). This leaves open the possibility that “attention shift voxels” preferentially contain direction-specific information.

Experiment 2: Spatial Shifts of Attention and Switching in Working Memory.

The degree to which these spatial patterns are consistent within subjects over time and across a range of tasks is of critical importance to their interpretation. One possibility is that these patterns are entirely task- and context-specific, such that changes in stimulus properties or configuration, for example, would alter this neural signature. Alternatively, these patterns may reflect stable properties of the neural subpopulations in different dimensions of cognitive control. In Experiment 1, the switches were spatial or nonspatial (i.e., rule) and involved an external or an internal locus of selection. To examine the stability of the multivoxel patterns within subjects across time and context, we examined data from a second experiment in which some of the participants in Experiment 1 subsequently participated (31).

Participants in Experiment 2 had to maintain two different counters in working memory (32) while viewing multiple rapidly changing RSVP streams (Fig. 1B, see *Methods*). One counter was “active” and the other “inactive,” but both counter values had to be maintained in WM at all times. Instructional cues appeared in the attended stream, which required the subject to increment the active counter, shift internal attention to the currently inactive counter (i.e., make it active), shift visuospatial attention to the other RSVP stream, or hold the current counter values, activation states, and focus of attention. A counter switch operation is both a nonspatial switch and one with an internal locus in WM rather than in external perceptual space. If the switch-related spatial patterns in Experiment 1 are able to accurately predict the switches in Experiment 2 (within an individual subject), it would indicate robust stability in the underlying neural subpopulations along some common dimension(s).

We first used SVM to train a classifier to discriminate between spatial attention and mnemonic shifts (Experiment 2) and found that the classifier was able to decode 70% of shifts correctly as either spatial attention or WM shifts at the peak time point of 6 s after the cue [$t(2) = 5.87, P < 0.05$; Fig. 4], using the same region and voxels as identified in Experiment 1 (see *Methods*). Thus, spatial attention shifts and working memory switches exhibited distinct spatial patterns of cortical activity in Experiment 2. In addition, we could classify shifts of left-to-right vs. right-to-left (77%, $P < 0.05$), but could not classify the two types of WM shifts (54%, $P > 0.2$).

To test the stability and generalizability of the multivoxel patterns, using the data from each of the three subjects who participated in both experiments, a classifier was trained to predict shifts of spatial attention vs. shifts of digit categorization rules using the patterns of activity in mSPL collected during Experiment 1, and was then tested with the data obtained from the same subject in Experiment 2. We decoded across experiments with the BOLD response at 6 s, since it represented the most informative time point for both experiments (see Figs. 2 and 4). Within-subject random-

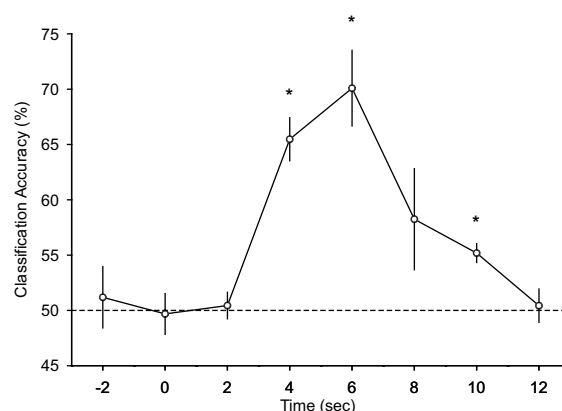


Fig. 4. Event-related classification performance in Experiment 2: decoding attention shift vs. working memory switch. Classification performance is presented for each time point relative to the onset of a switch cue, based on voxels in medial SPL (see *Methods*). *, $P < 0.05$; **, $P < 0.001$.

ization tests were performed to evaluate statistical significance with an alpha of .05 (see *SI Methods*). The cross-experiment classification performance was significantly greater than chance (59.7%) for all three subjects (Fig. 5, Experiment 1- \rightarrow Experiment 2). The reverse classification (training on Experiment 2 and testing on Experiment 1) was also significantly greater than chance for two of three participants (56.8%, Fig. 5, Experiment 2- \rightarrow Experiment 1). In Subject 3, who failed to classify from Experiment 2 to Experiment 1 above chance (52.1%), within-Experiment 1 classification was the weakest of the three subjects (55.6%). Overall, the distribution of the domain-specific neural subpopulations recruited for task set reconfiguration exhibits robust stability within subjects across time, as five of six attempts to classify across experiments were significantly better than chance. This pattern of results is preserved when accounting for any mean-difference across the two conditions (see Fig. S5).

Discussion

We investigated the neural basis of task set reconfiguration in three distinct domains. Transient neural activity in mSPL is uniquely

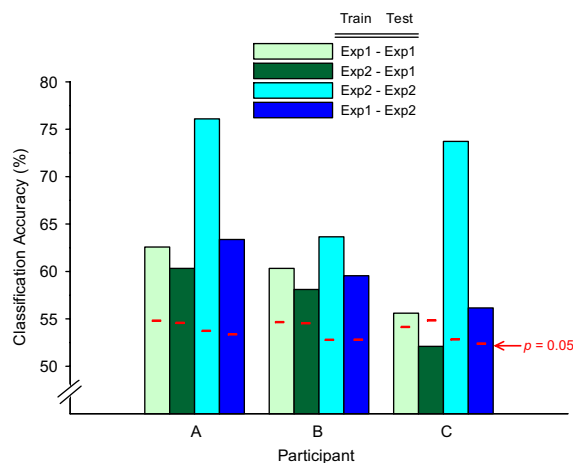


Fig. 5. Within and across experiment classification. In all three subjects, classification performance is significantly greater than chance (red lines indicate the critical value from a randomization test, $P = 0.05$; see *SI Methods*) for classification within Experiment 1 (light green) and within Experiment 2 (light blue). When data from Experiment 1 were used to train a classifier to predict switches in Experiment 2, decoding was significantly greater than chance in all three subjects (dark blue). When data from Experiment 2 were used to train a classifier to predict switches in Experiment 1, decoding was significantly greater than chance in subjects A and B, but not C (dark green).

associated with reconfiguration in multiple domains, including shifts of external attention between objects, locations, and features; shifts of attention between WM representations; and shifts of categorization rule (5, 10, 11, 14–17, 31). These results suggest that mSPL plays a domain-independent role in the initiation of task set reconfiguration. However, the conventional univariate statistical analyses used in these studies left open the possibility that mSPL contains two or more neural subpopulations that exhibit domain-specific patterns of activity. We used event-related multivoxel pattern classification (er-MVPC) to reliably decode shifts of spatial attention, switches of categorization rule, and switches between working memory representations. MVPC extracts information at a subregion scale of functional cortical organization and supports the inference that different neural populations respond selectively to different acts of cognitive control within this confined region of parietal cortex.

The spatiotemporal patterns we observed are stable over time and generalize across different types of reconfigurations. In Experiment 1, a classifier trained on attention shifts vs. categorization rule switches successfully classified attention shifts vs. working memory switches in the same subjects participating in Experiment 2 several months later. The functions of these neural subpopulations may vary along several possible dimensions. Given that both experiments examined spatial shifts of attention vs. another domain, the critical dimension could potentially be whether the reconfiguration is spatial or nonspatial. Although the importance of SPL in all manner of switches, including nonspatial ones, has been amply documented (5, 11, 14–17), spatial information may be specially represented in the parietal cortex (33, 34), and this explanation is bolstered by the accurate classification of shift direction (left-to-right vs. right-to-left), together with the failure to classify the nonspatial domains (e.g., magnitude-to-parity vs. parity-to-magnitude), as well as the overall mean activity difference between attention shift evoked response and rule shift evoked response. According to this explanation, classification, especially in the cross-experiment case, may rely on voxels that are either tuned to spatial shifts of attention, or “other,” nonspatial cognitive shifts.

Another possible axis of organization is external versus internal locus of selection. It has been demonstrated that even within the spatial domain, attention can be oriented to the external world (perceptually) or to internal representations in spatial working memory, and that these acts of control recruit only partially overlapping activity in the parietal and frontal cortex (35). In our experiments, shifting of counter selection and rule selection both require a change in the internal focus of attention to purely mental representations (counters or rules), while the spatial task requires attention toward external perceptual inputs that are continuously present (left or right visual stream). Therefore, the counter and rule switches may both require a change in priority of goals held in working memory, thought to be represented in prefrontal cortex (1, 2), compared to shifts of spatial attention toward perceptual inputs, which require change in top-down modulations in ventral visual cortex (5).

The spatial vs. nonspatial and external vs. internal possibilities are not mutually exclusive, and future studies considering the multiple internal or external domains of control within the same experiment will be required to further clarify these functional axes. In the first case (spatial vs. “other”), nonspatial switches of feature- or object-based attention should evoke patterns of activity that are similar to those evoked by categorization rule and memory switches. The second possibility (internal vs. external) would predict that spatial and feature- or object-based attention switches would evoke similar patterns of activity, because their locus is also external.

While cross-experiment decoding was significantly better than chance in most cases, it was not as accurate as within-experiment decoding. Several factors contribute to the attenuation of classification performance across experiments, including the possibility that the different contexts of these two experiments did yield

different multivoxel patterns and that the patterns changed with learning and experience in the task. Nevertheless, it is striking that classification was successful even in the face of the effective spatial smoothing that results from imperfections in coregistration of multiple fMRI sessions. The degree to which plasticity and learning influence the neural recruitment within mSPL remains unknown.

A challenge in the current study was that classification of transient shift events was attempted in a rapid event-related fMRI design. Most previous applications of MVPC have used blocked designs in which a single “trial” is the average BOLD response over several seconds of repeated stimulation (24) or slow event-related designs in which the trials are separated in time to prevent temporal overlap in the sluggish BOLD hemodynamic response (refs. 30 and 36; however, see ref. 28 for a notable exception and see ref. 37, which used a novel classification method). Successful application of er-MVPC in the face of a transient and non-deconvolved BOLD signal suggests the possibility of online, real-time decoding of subjects’ intentions and cognitive states during more naturalistic and overlapping cognitive demands.

Some voxels are assigned small weights (and therefore may be said to have low importance) in classification. There are several possible functional interpretations of these low-importance voxels. Voxels that contain redundant information (i.e., that are highly correlated with other voxels) may be assigned low weights. However, at least some voxels have little or no selectivity to these types of shifts (see Fig. 3A), and many only serve to impair classification performance (see Fig. S2). These unselective voxels may contain approximately equal numbers of neurons with selectivity to each type of shift, leading to no net selectivity. Alternatively, they could be dominated by neurons that are truly domain-independent. Last, they could contain neurons that are selective for other domains of control not explored in the current experiments.

While these results reveal that content of mSPL activity is process-specific, it is not yet known how this region communicates with other brain regions thought to be part of a cognitive control network, including lateral parietal and prefrontal cortex, and possibly subcortical structures such as the basal ganglia. EEG measurements have shown that, at least for spatial shifts of attention, posterior parietal activity precedes activity in the frontal cortex, suggesting a critical role for this region in the initiation of task set reconfiguration (38). Functional connectivity may reveal how the unique patterns of activity observed in the current study are related to domain-specific cortical activity. For example, Chiu and Yantis (10) found that spatial shifts of attention recruited mSPL and the inferior parietal cortex and frontal eye fields, a result that echoes other studies of visual spatial attention (11, 39). Conversely, they found that shifts of categorization rule were associated with activity in mSPL and in the left IPS, a region associated with alphanumeric categorization task switching (40). This analysis, like most fMRI analyses, does not support the inference of causality or necessity of this parietal region in acts of cognitive control. Because lesions of mSPL are so rare (21), cognitive neuropsychological methods are not well-suited to answer this question. Transcranial magnetic stimulation offers one possible method that could be used to explore the necessity and temporal properties of this region for cognitive reconfigurations.

Unlike other applications of MVPC that decode representational contents of perception, attention, and memory, we examined the spatial patterns of brain activity associated with different cognitive processes, independent of their representational content. This application could be valuable for other fMRI research investigating the neural organization of a specified brain region involved in cognitive control, such the rostral-caudate gradients in the prefrontal cortex (e.g., ref. 41).

In summary, we used multivoxel pattern classification to show that mSPL supports the initiation of task set reconfiguration in multiple domains. Er-MVPC revealed that there are separable voxel-wise patterns of activity within mSPL evoked by different acts

of cognitive control. Decoding switches across multiple experiments conducted several months apart established the stability of these subpopulations across time and context. Together, these results support an emerging understanding of the neural basis of cognitive control involving both domain-specific and domain-independent mechanisms of task set reconfiguration.

Methods

Behavioral Task: Experiment 1. Subjects maintained central fixation while viewing two rapid serial visual presentation (RSVP) target streams of alphanumeric characters (4 Hz), each flanked by three distractor streams (Fig. 1A). At any given moment, the subject covertly attended to either the left or right stream and was prepared to categorize target digits that appeared in the attended stream according to one of two rules: odd vs. even (Parity Task) or high (6–9) vs. low (2–5) (Magnitude Task). Forty-eight critical events were randomly intermixed among filler items (non-cue letters) in each run; 24 target digits (2–9) and 24 cue letters ('L,' 'R,' 'M,' and 'P'). The cues respectively specified "attend Left," "attend Right," "prepare Magnitude Task," and "prepare Parity Task." See ref. 10 and *SI Methods* for further details.

Behavioral Task: Experiment 2. The display was similar to that in Experiment 1 (Fig. 1B). Subjects attended the left or right target stream, and maintained two counters in working memory, one active and ready to be incremented and the other inactive. The four cue letters were 'L,' 'C,' 'P,' and 'H' that respectively specified "shift the locus of spatial attention" "switch from one WM counter to the other," "increment the selected WM counter's value (plus)," and "hold the current state." At the end of the run, subjects verbally reported the values of the two counters. See *SI Methods* for further details.

mSPL Voxel Selection. The unsmoothed images were Talairach-transformed and resampled into 3-mm isotropic voxels for voxel selection. Sixteen separate random-effects group GLMs were performed, leaving each subject out. For each of these GLMs, a conjunction analysis (attSh>attHd AND rulSw>rulHd) defined an ROI in mSPL. For the purposes of voxel selection, the threshold was reduced to include a larger set of voxels with potentially weaker selectivity at the group level

($t = 2.00, P < 0.06$). This region was subsequently projected back into the native space of the subject left out of that GLM. Thus, the ROI selection process was independent of the data that were subsequently classified. We verified that these ROIs were still attention- and rule shift-selective (versus their respective hold trials; $t_{15} = 6.47$ and $3.66, P < 0.01$). These voxels were used for Experiment 2 as well.

Classification with Support Vector Machines. Decoding analyses were performed using OSU SVM toolbox (adaptation of libsvm: <http://www.csie.ntu.edu.tw/~cjlin/libsvm/>) for MATLAB and in-house MATLAB code. All analyses used linear SVM. The signal in each voxel was z-transformed for each of the runs. Initially, each TR after attSh and rulSw cues (WMSw for Experiment 2) was classified separately. The event-related fMRI signal associated with attSh and rulSw/WMSw cues starting 2 s before the event until 12 s after the event (i.e., TRs –1 to 6) was used for classification, as was the mean of the BOLD signal at 6 and 8 s after the event for follow-up analyses. In the mean-centered analysis, the mean of all of the voxels for each type of switch (attention or categorization rule) was subtracted from every voxel on each trial. This resulted in the overall voxel population mean being equated for the two types of shifts.

To estimate within-experiment classification rates, a leave-one-run-out cross-validation scheme was used. For cross-experiment decoding, all Experiment 1 or 2 data from a given subject were used as the training set, while Experiment 2 or 1 data, respectively, from that subject served as the testing set. The time point selected for cross-experiment SVM input was 6 s postcue. This was based on the observation that the event-related classification accuracy was greatest for that TR across the two experiments (Figs. 2 and 4).

Importance Map. With linear SVM, the absolute value of each voxel's weight provides a quantitative index of the importance of that voxel in the decision function (22); the most discriminating voxel has the largest absolute weight (See *SI Methods* for more details).

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