Reviewed Preprint
v1 • October 3, 2025
Not revised

Reviewed Preprint
v2 • February 18, 2026
Revised by authors

Reviewed Preprint
v3 • August 7, 2026
Revised by authors

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Competing interests: No competing interests declared

Reviewing editor: Qing Yu, Center for Excellence in Brain Science and Intelligence Technology, Chinese Academy of Sciences, China

Adaptive behavior is guided by integrated representations of controlled and non-controlled information

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eLife Assessment

This **useful** study uses creative scalp EEG decoding methods to attempt to demonstrate that two forms of learned associations in a Stroop task are dissociable, despite sharing similar temporal dynamics. However, the evidence supporting the conclusions is **incomplete** due to concerns with the experimental design and methodology. This paper would be of interest to researchers studying cognitive control and adaptive behavior, if the concerns raised in the reviews can be addressed satisfactorily.

https://doi.org/10.7554/eLife.108673.3.sa3

Abstract

Understanding how task knowledge is encoded neurally is crucial for uncovering the mechanisms underlying adaptive behavior. Here, we test the theory that all task information is integrated into a conjunctive task representation by investigating whether this representation simultaneously includes two types of associations that can guide behavior: stimulus-response (non-controlled) associations and stimulus-control (controlled) associations that inform how task focus should be adjusted to achieve goal-directed behavior. We extended the classic item-specific proportion congruency paradigm to dissociate the electroencephalographic (EEG) representations of controlled and non-controlled associations. Behavioral data replicated previous findings of association-driven adaptive behaviors. Decoding analyses of EEG data further showed that associations of controlled and non-controlled information were represented concurrently and differentially. Brain-behavioral analyses also showed that the strength of both associations was associated with faster responses. These findings support the idea that controlled and non-controlled associations are governed by an integrated task representation to guide adaptive behaviors simultaneously.

Introduction

Cognitive control coordinates our thoughts and actions with internal goals (Egner, 2017; Miller & Cohen, 2001) via the abilities of sustained task focus when faced with distractions (stability) and flexible adjustments between task sets based on varying situations (flexibility). Both stability and flexibility can be implemented in a proactive (Botvinick et al., 2001; Jiang et al., 2015) or reactive (Blais et al., 2007; Verguts & Notebaert, 2008) manner (Abrahamse et al., 2016; Braem & Egner, 2018; Braver, 2012; Brown et al., 2007; Egner, 2014, 2023; Jiang et al., 2018). For task focus indicating cognitive stability, conflict paradigms have been employed to explore how the brain focuses on task-relevant information while avoiding the distraction from potent task-irrelevant information (Eriksen & Eriksen, 1974; Simon & Rudell, 1967; Stroop,

1935). For example, in the Stroop task (Stroop, 1935), participants are shown a color word and asked to respond to the ink color of the word while ignoring the meaning of the word. The ink color can be consistent (congruent trials) or inconsistent (incongruent trials) with the meaning of the word, resulting in a conflict effect measured by worse performance on incongruent trials than on congruent trials. Some models of cognitive control postulate that the conflict effect reflects the involvement of cognitive control, which suppresses the habitual but inappropriate response to the word and/or boosts the novel and goal-directed response to the ink color to resolve the conflict on incongruent trials (Botvinick et al., 2001; Cohen et al., 1990).

A key question in the research on cognitive control is how the brain monitors control demands (i.e., how much control is needed). Recent research has demonstrated the importance of associative learning in guiding control demand (Bustamante et al., 2021; Jiang et al., 2020a; Jiang et al., 2020b; Wen et al., 2023). In particular, theories focusing on stimulus-control (SC) associations assume that the brain binds together a stimulus feature with the concurrent control demands (Bejjani et al., 2020; Blais et al., 2007; Bugg & Crump, 2012; Bugg & Hutchison, 2013; Bugg et al., 2011; Chiu et al., 2017; Colvett et al., 2025; Ileri-Tayar et al., 2024; Ileri-Tayar et al., 2022; Ileri-Tayar et al., 2025; Jiang et al., 2020a; Spinelli et al., 2022; Suh & Bugg, 2021). For example, in the Stroop task, if the color red is used on mostly congruent (MC) trials and the color blue is presented on mostly incongruent (MI) trials, then red would be associated with lower control demands relative to blue. This process has been proposed to account for the item-specific proportion congruency (ISPC) effect (Braem et al., 2019; Jacoby et al., 2003), whereby the conflict effect is reduced for stimulus features that predict higher control demands.

The ISPC effect is a natural prediction of stimulus-control learning, with the potential to provide a theoretical foundation for how cognitive control is scaffolded on structured representations of our environment. However, there have been theoretical challenges that the ISPC may arise from lower-level stimulus-response (SR) learning theory instead. This alternative account posits that associations may also form between stimulus and specific response (e.g., the most-likely response) in addition to more abstract SC associations (Atalay & Misirlisoy, 2012; Hazeltine & Mordkoff, 2014; Schmidt & Besner, 2008; Schmidt et al., 2016). Returning to the Stroop task, if the word blue is presented in red color (i.e., an incongruent trial), then the word blue will be associated with the 'red' response (in Stroop, often an assigned keypress or verbal response). Note that a stimulus may be associated with multiple responses. For example, if the word blue is presented in blue color (i.e., a congruent trial), then the word blue will also be associated with the 'blue' response. In this case, SR association is linked to the most-likely response. Following the example above, if the word blue is presented mostly on incongruent trials, then the word blue is paired more often with the red response than the blue response, and the SR is between the word blue and the red response. Subsequent responses to this stimulus will be biased towards the associated response, whether or not they are correct.

Since SC and SR accounts often predict similar behavioral patterns, previous studies have typically focused on one at a time through experimental controls, and current empirical evidence supports both SC (Bugg & Hutchison, 2013; Gonthier et al., 2016; Spinelli & Lupker, 2020a; Spinelli et al., 2019) and SR (Schmidt & Besner, 2008) associations. Additionally, studies of ISPC have differentiated the behavioral effects and neural substrates of SC and SR associations when either SC or SR associations are available (Bugg et al., 2011; Chiu et al., 2017). For example, Chiu and colleagues (Chiu et al., 2017) showed that the dynamics of SC and SR learning were captured by trial-wise prediction errors with a reinforcement learning model and that SC learning was encoded in the caudate nucleus while SR association was represented in the parietal cortex. Conceptually, SC associations affect behavior by modulating other cognitive processes via cognitive control, whereas SR associations drive behavior in a non-controlled manner by retrieving the associated response. These accounts provide competing explanations for what kind of knowledge is encoded in neural task representations. Task representations are often thought to be conjunctive, providing one-point access to all task-related information (Badre, 2024; Badre et al., 2021; Hommel, 2004, 2019; Kikumoto et al., 2024; Kikumoto & Mayr, 2020;

Kikumoto et al., 2022a; Kikumoto et al., 2022b; Sakai, 2008; Schumacher & Hazeltine, 2016a; Verguts & Notebaert, 2008). However, it remains unexplored whether and how controlled and non-controlled information can be integrated into a task representation to guide adaptive behavior. If controlled and non-controlled information are encoded in the same representation, then: (1) SC and SR representations should occur simultaneously; (2) the strength of SC and SR representations, being in the same task presentation, should covary (i.e., positively correlated) over time as the strength of the task representation fluctuates and (3) both SC and SR associations should exhibit behavioral relevance.

To test these predictions, we extended the classic ISPC paradigm to dissociate each of SC and SR associations from their associated stimuli (e.g., separating SC association from the stimulus and the linked control demand). Using this new ISPC paradigm in an EEG experiment, we tested whether SC and SR form integrated task representations using decoding, representational subspace analysis, and representational similarity analysis (RSA). We found three main results on task representations that integrate controlled (SC) and non-controlled (SR) associations. First, time-resolved RSA on the decoding results showed simultaneous representations of SC and SR associations. Second, the strength of SC and SR associations was positively correlated, consistent with the hypothesis that both SC and SR associations are integrated in a task representation. Third, both the strength of SC and SR associations were associated with faster responses at the trial level, indicating the behavioral relevance of the neural representations. These results provide convergent evidence of an integrated task representation that contains both SC and SR associations to jointly guide goal-directed behaviors.

Results

Task overview

EEG data were acquired while participants (N = 40) performed a 4-key Stroop task. On each trial, participants responded to the color of a word while ignoring the identity of the word (e.g., RED presented in blue color; Fig. 1a). Participants were encouraged to respond as quickly and accurately as possible. We applied three key manipulations to this experiment (Fig. 1b). First, each stimulus could be either congruent or incongruent, defined by whether the color was consistent with the word. Second, to test whether controlled and non-controlled information are encoded in a task representation, we manipulated the ISPC (Bugg et al., 2011; Bustos et al., 2024; Chiu et al., 2017; Jacoby et al., 2003) in Phase 1 to allow the associations between colors and their paired cognitive control demands (stimulus-control; SC) and the associations between words and their most-likely response (i.e., not necessarily the actual response on the current trial; stimulus-response; SR) to be induced at the same time. To keep the overall proportion of congruency at 50%, one set of colors was presented on 75% of congruent trials (mostly congruent trials, or MC), whereas the other set of colors was presented on 25% of congruent trials (mostly incongruent trials, or MI). The MC manipulation pairs color with low control state based on SC assumption (e.g., red-congruent) and word with the consistent response (e.g., red-red) based on the SR account. Similarly, the MI manipulation links color to high control state (e.g., blue-incongruent) and word to the inconsistent response (e.g., yellow-green, because each set has two colors, the inconsistent response is unique). This standard ISPC manipulation can test whether neural representations of controlled and non-controlled information are wrapped on the same trial by combing with the following EEG analysis (See Methods). However, it potentially mixes color identity with SC, word identity with SR, and the ISPC between SC and SR. To de-confound these factors when estimating SC and SR association representations on each trial, we modified this paradigm by flipping the ISPC contingencies across different phases of the task. For example, the color 'red' might be associated with 25% congruency in Phase 1, 75% congruency in Phase 2, and then return to 25% congruency in Phase 3 (see Methods). The color groups were counterbalanced across participants by red and blue as the color set of MC in one group while as the color set of MI in another group in the phase 1. Overall, these manipulations resulted in a 2 (Congruency: congruent vs. incongruent) × 2 (ISPC: MC vs. MI) × 3 (Phase 1 - 3) within-subject factorial design.

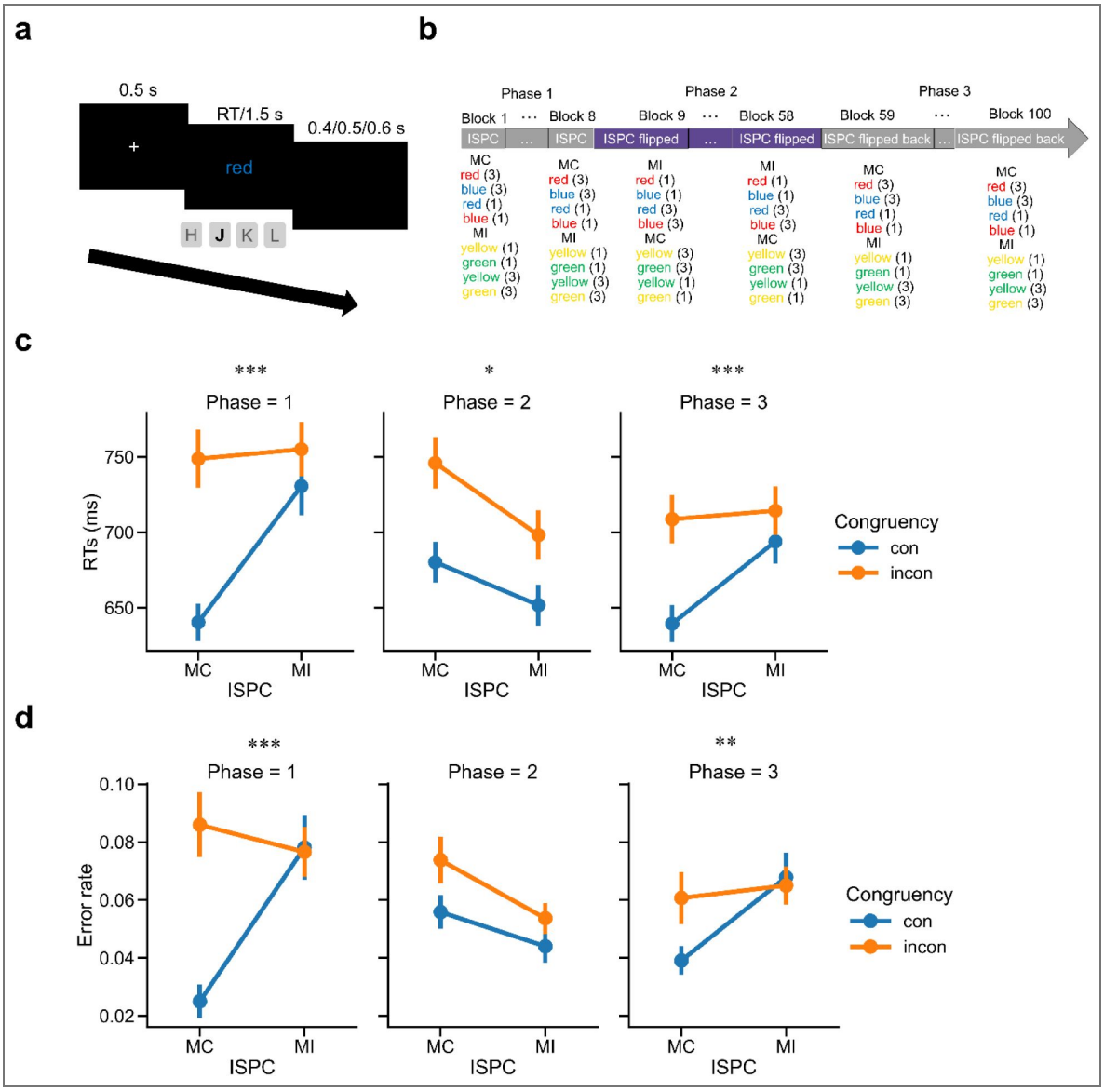


Figure 1. Experimental design and behavioral results (N = 40).

(a) Trial structure. **(b)** Procedure of the main experiment. The number following each stimulus indicates its trial count within a mini-block. (**c**) Group mean RT as a function of the ISPC effect. **(d)** Group mean error rate as a function of the ISPC effect. Error bars show standard errors of the mean (SEM). MI: mostly incongruent trials; MC: mostly congruent trials; incon: incongruent trials; con: congruent trials. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Behavioral patterns track manipulations of varying ISPC

RTs on correct trials within ±3 standard deviations (SD) of the mean and error rates were analyzed separately in each phase using a 2 (Congruency: congruent vs. incongruent) × 2 (ISPC: MC vs. MI) repeated-measures ANOVA. For RT data, there was a statistically significant interaction between Congruency and ISPC in each phase (Phase 1: $F_{(1,39)} = 36.36$, $p < 0.001$, $\eta_\rho^2 = 0.482$; Phase 2: $F_{(1,39)} = 6.63$, $p = 0.014$, $\eta_\rho^2 = 0.145$; Phase 3: $F_{(1,39)} = 53.27$, $p < 0.001$, $\eta_\rho^2 = 0.577$), which replicated the ISPC effect of smaller congruency effect in the MI condition compared with that in the MC condition in each phase (Phase 1: $t_{39} = 6.03$, $p < 0.001$, Cohen's $d = 1.174$; Phase 2: $t_{39} = 2.58$, $p = 0.014$, Cohen's $d = 0.476$; Phase 3: $t_{39} = 7.30$, $p < 0.001$, Cohen's $d = 1.317$; Fig. 1c). For error rate, the 2-way interaction was significant in Phase 1 ($F_{(1,39)} = 18.05$, $p < 0.001$, $\eta_\rho^2 = 0.316$) and Phase 3 ($F_{(1,39)} = 10.43$, $p < 0.01$, $\eta_\rho^2 = 0.211$) and was driven by smaller conflict effects in the MI condition than in the MC condition (Phase 1: $t_{39} = 4.25$, $p < 0.001$, Cohen's $d = 0.842$; Phase 3: $t_{39} = 3.23$, $p < 0.01$, Cohen's $d = 0.655$; Fig. 1d), but was not significant in Phase 2 ($F_{(1,39)} = 1.50$, $p > 0.05$). The above findings showed that the ISPC effect flipped from Phase 1 to Phase 2, and then reversed again in Phase 3, indicating that the experimental manipulations worked as expected. Additionally, we replicated the congruency effect (i.e., worse performance on incongruent than congruent trials) in both RT and error rate data in each phase (Supplementary Note 1 and Supplementary Table 1).

EEG analysis overview

We started by validating that the 16 experimental conditions (8 unique stimuli × MC/MI) were represented in the EEG data. Evidence of representation was provided by above-chance decoding of the experimental conditions (Fig. 2-3). We then examined whether the SC and SR associations were separable (i.e., whether SC and SR associations were different representations of equivalent information). As our results supported separable representations of SC and SR association (Fig. 4-5), we further estimated the temporal dynamics of each representation within a trial using RSA. This analysis revealed that the temporal dynamics of SC and SR association representations overlapped (Fig. 7a-b, Fig. 8a-b). To explore the potential reason behind the temporal overlap of the two representations, we investigated whether SC and SR associations were represented simultaneously as part of the task representation, independently from each other, or competitively/exclusively (e.g., on some trials only SC association was represented, while on other trials only SR association was represented). This was done by assessing the correlation between the strength of SC and SR representations across trials (Fig. 7c, Fig. 8c). Lastly, we tested how SC and SR representations facilitated performance (Fig. 9-10).

Decodable and separate representations of controlled and non-controlled associations

Before exploring the relationship between controlled and non-controlled representations, we first confirmed that each representation was encoded during task performance. We applied linear discriminant analysis (LDA) (James et al., 2013) with the features of 64-channel event-related potentials (ERP) data to decode the 16 experimental conditions (8 unique stimuli × MC/MI) at each time point. The decoding analysis was performed on a time window from 200 ms prior to stimulus onset to 1500 ms post-stimulus onset (cf., Fig. 1a). We found that the decoding accuracy was significantly above chance level from 60 to 1500 ms after stimulus onset (Fig. 2a). To illustrate the distribution of data in the feature space, we applied multi-dimensional scaling (MDS, see Methods) to the ERP data averaged over 60 - 1500 ms after trial onset and visualized the centers of the 16 experimental conditions using the first 3 dimensions. The cumulative explained variance of the first 3 dimensions in the MDS was 0.59, 0.76 and 0.87, respectively.

Both the 8 SC classes of 16 conditions and the conditions as 4 color clusters were categorized along dimension 1 and dimension 2 (Fig. 2b) or along dimension 1 and dimension 3 (Fig. 2c). We also performed the above analyses on response-locked data and found similar patterns (Fig. 3): decoding accuracy was significantly above the chance from ~ 800 to ~200 ms relative to response

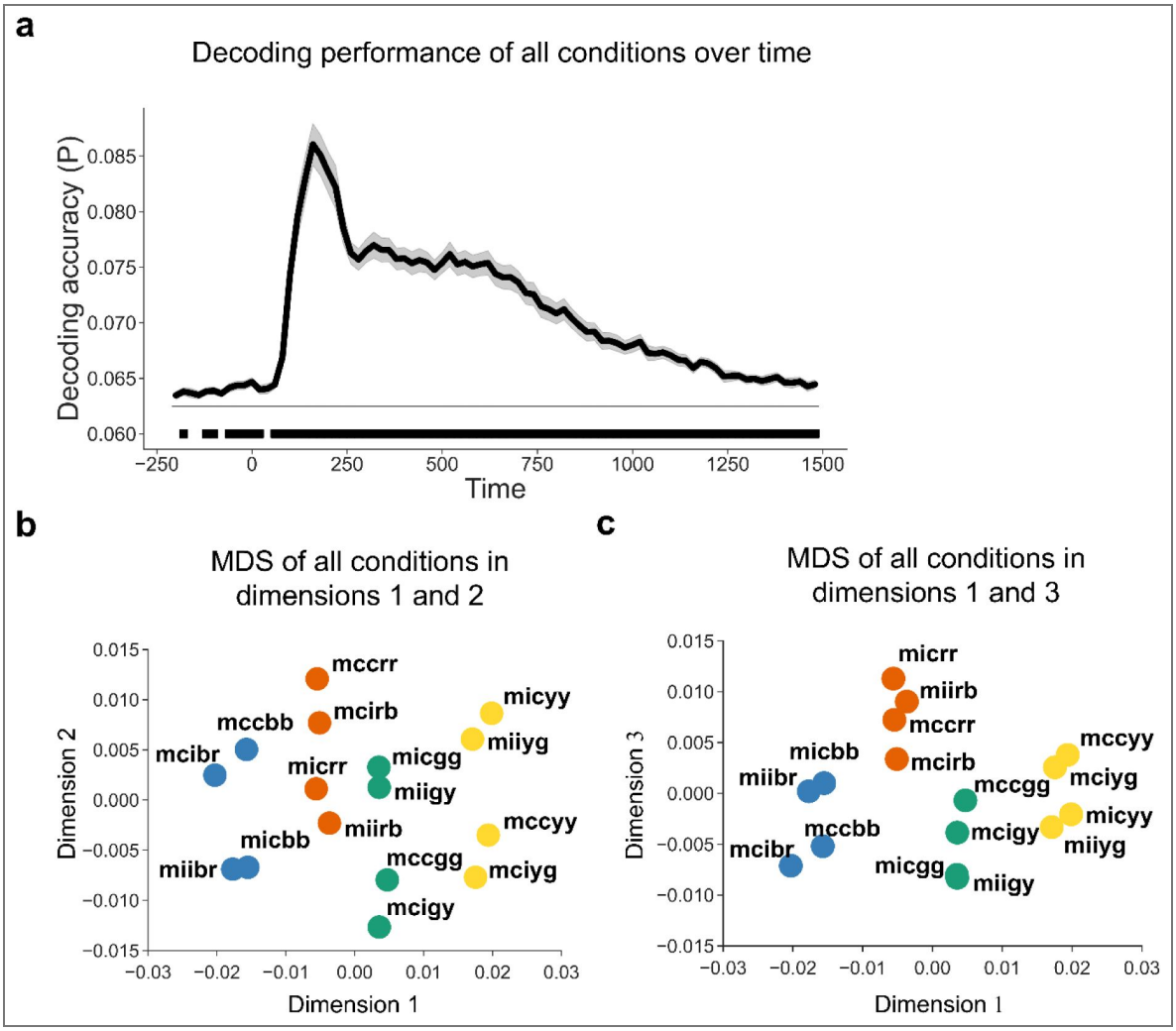


Figure 2. Decoding performance including both SC and SR latent subspaces (N = 40).

(a) Group average decoding accuracy of all 16 experimental conditions as a function of time after stimulus onset. Shaded regions represent SEM. The solid line above the time axis denotes the time points showing above-chance (0.0625, or 1/16) decoding accuracy (cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). **(b, c)** MDS of EEG data across all experimental conditions. The label of each dot encodes the condition in the experimental design in the order of ISPC, congruency, color, and word. For example, "mccbr" means the condition with MC, congruent trial, blue color, and the word "red". The color of each dot denotes the ink color of each condition.

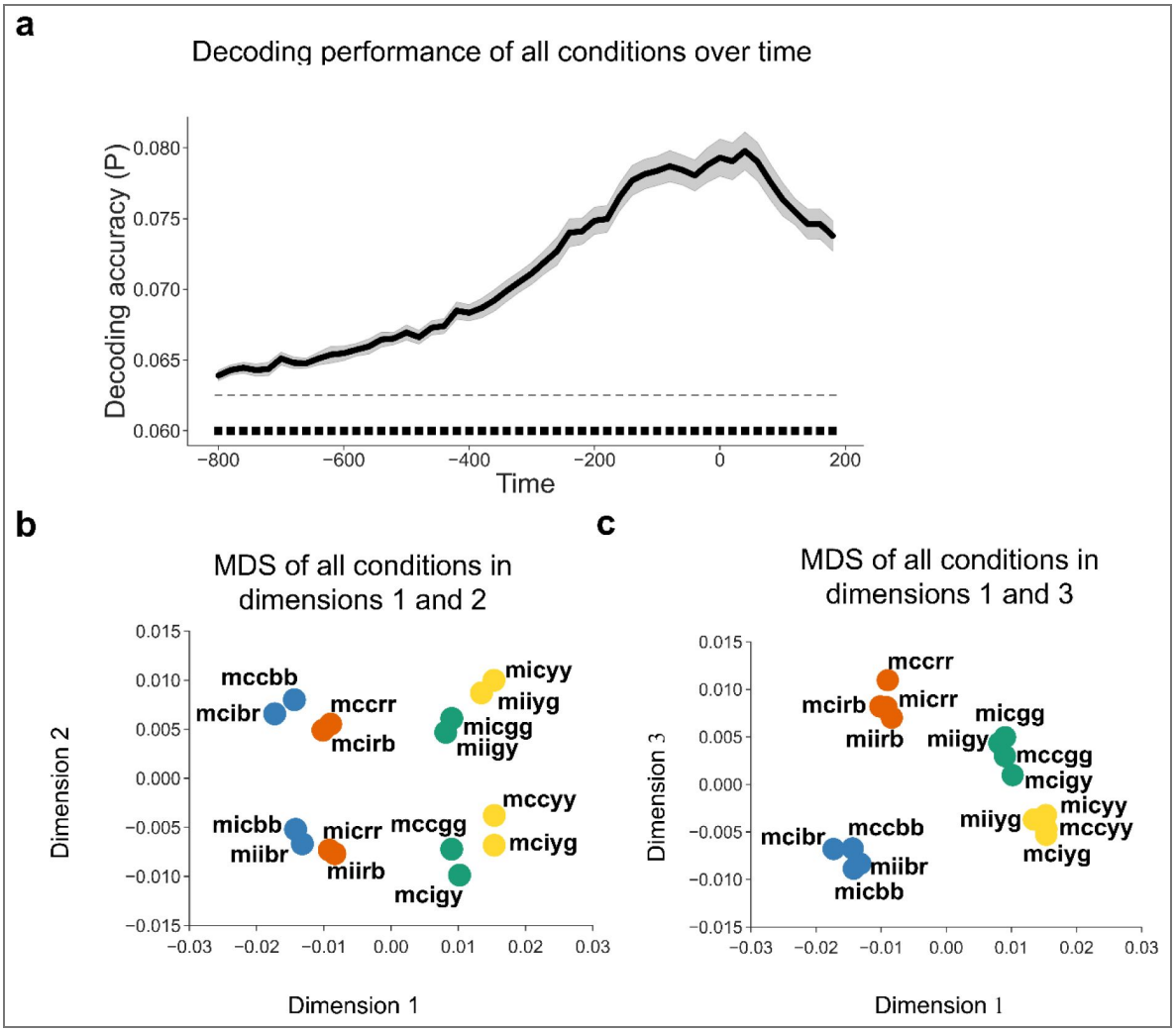


Figure 3. Decoding performance including both SC and SR latent subspaces using response-locked analysis (N = 40).

(a) Group average decoding accuracy of all 16 experimental conditions as a function of time after response onset. Shaded regions represent SEM. The solid line above the time axis denotes the time points showing above-chance (0.0625, or 1/16) decoding accuracy (cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). **(b, c)** MDS of EEG data across all experimental conditions. The label of each dot encodes the condition in the experimental design in the order of ISPC, congruency, color, and word. For example, "mccbr" means the condition with MC, congruent trial, blue color, and the word "red". The color of each dot denotes the ink color of each condition.

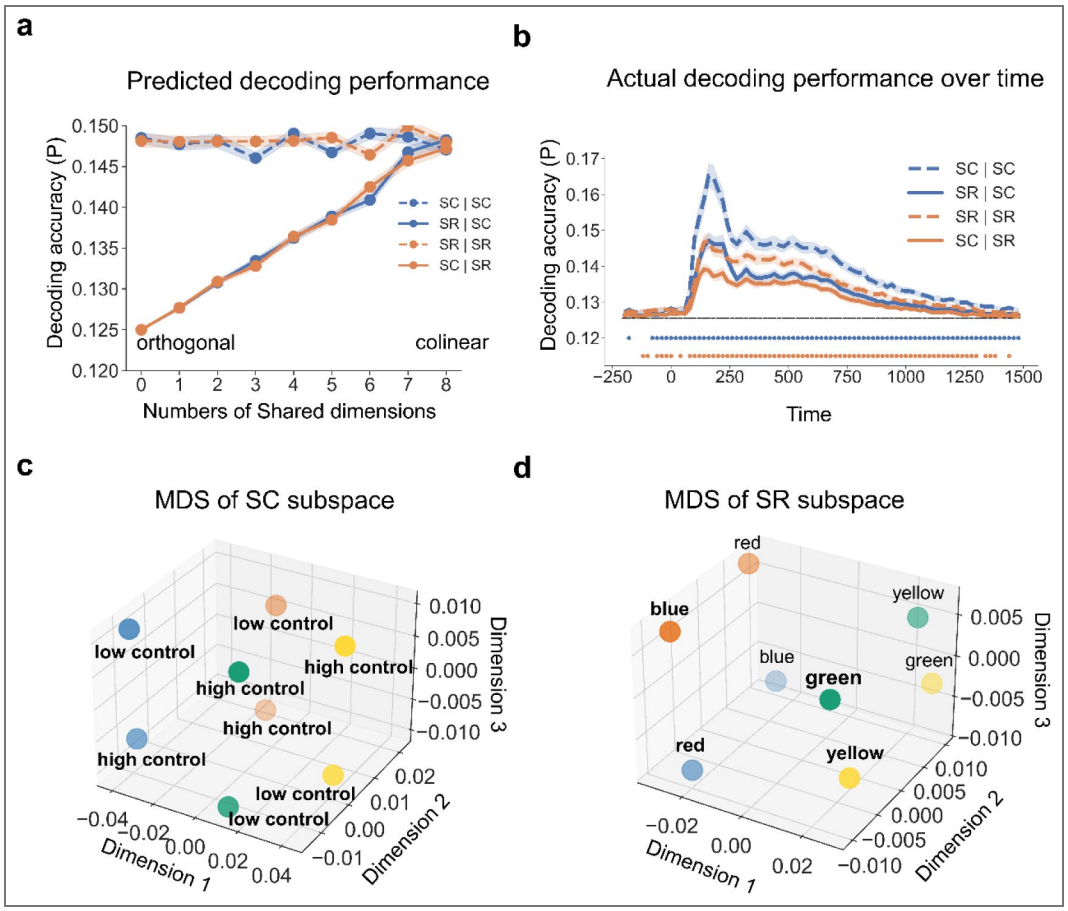


Figure 4. Partially overlapping SC and SR subspaces.

(a) Simulation results (N = 40) of decoding accuracy as a function of the degree of subspace overlap, subspace type, and decoder. Both SC and SR subspaces are 8-dimensional (SC: 4 colors × MC/MI; SR: 4 words × 2 possible responses per word). The number of Shared dimensions indicates how many dimensions overlap between SC and SR subspaces. Each condition label is encoded in the format of "subspace | decoder". For example, "SC | SR" means a SR decoder trained on the SC subspace. **(b)** Group average decoding accuracy over time as a function of which subspace the decoders are trained on. Shaded regions represent the SEM. Blue (orange) points denote the time points showing significantly better decoding accuracy when using the same subspace than when using the other subspace (cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). (**c**) MDS of the SC subspace. Each dot represents the center of a SC class. Dot color and label encode the ink color and cognitive control state, respectively. **(d)** MDS of the SR subspace. Each dot represents the center of a SR class. The label and dot color encode the word meaning and associated response, respectively.

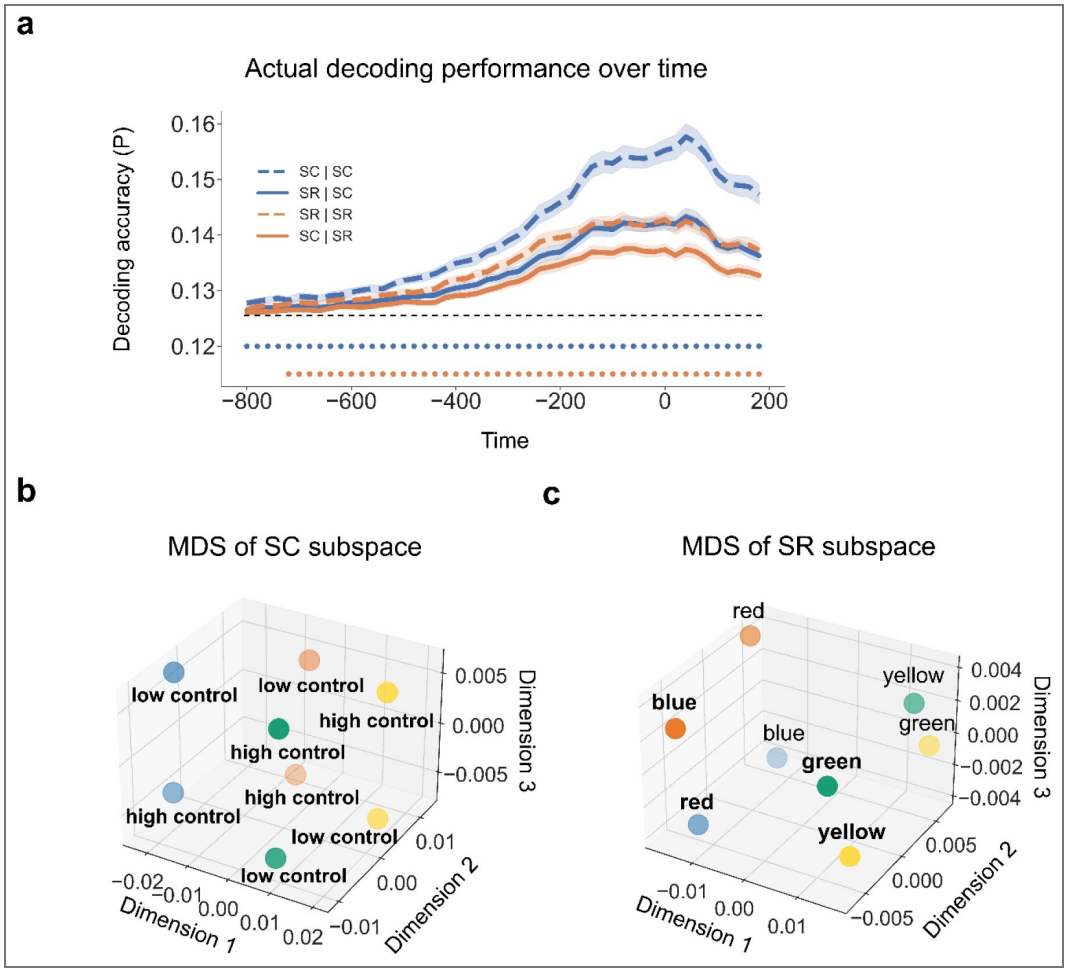


Figure 5. Partially overlapping SC and SR subspaces using response-locked analysis.

(a) Group average decoding accuracy over time as a function of which subspace the decoders are trained on. Shaded regions represent the SEM. Blue (orange) points denote the time points showing significantly better decoding accuracy when using the same subspace than when using the other subspace (cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). **(b)** MDS of the SC subspace. Each dot represents the center of a SC class. Dot color and label encode the ink color and cognitive control state, respectively. **(c)** MDS of the SR. Each dot represents the center of a SR class. The label and dot color encode the word meaning and associated response, respectively.

(Fig. 3a); The cumulative explained variance of the first 3 dimensions in the MDS was 0.53, 0.70 and 0.85, respectively, revealing that MDS separated 8 SC classes of 16 conditions along dimension 1 and 2 (Fig. 3b) and categorized the conditions as 4 clusters along dimension 1 and 3 (Fig. 3c).

Prior to testing whether controlled and non-controlled associations were represented simultaneously, we first tested whether the two representations were separable in the EEG data. In other words, we reorganized the 16 experimental conditions into 8 conditions for SC (4 colors × MC/MI, while collapsing across SR levels) and SR (4 words × 2 possible responses per word, while collapsing across SC levels) associations separately. If SC and SR associations are not separable, it follows that they encode the same information, such that both SC and SR associations can be represented in the same subspace (i.e., by the same information encoded in both associations). For example, because (1) the word can be determined by the color and congruency and (2) the most-likely response can be determined by color and ISPC, the SR association (i.e., association between word and most-likely response) can in theory be represented using the same information as the SC association. On the other hand, if SC and SR associations are separable, they are expected to be represented in different subspaces (i.e., the information used to encode the two associations is different). Notably, if some, but not all, information is shared between SC and SR associations, they are still separable by the unique information encoded. In this case, the SC and SR subspaces will partially overlap but still differ in some dimensions. To summarize, whether SC and SR associations are separable is operationalized as whether the associations are represented in the same subspace of EEG data. To test this, we leveraged the subspace created by the LDA (see Methods). Briefly, to capture the subspace that best distinguishes our experimental conditions, we trained SC and SR decoders using their respective aforementioned 8 experimental conditions. We then projected the EEG data onto the decoding weights of the LDA for each of the SC and SR decoders to obtain its respective subspace. We hypothesized that if SC and SR subspaces are identical (i.e., not separable), SC/SR decoding accuracy should not differ by which subspace (SC or SR) the decoder is trained on. For example, SC decoders trained in SC subspace should show similar decoding performance as SC decoders trained in SR subspace. On the other hand, if SC and SR association representations are in different subspaces, the SC/SR subspace will not encode all information for SR/SC associations. As a result, decoding accuracy should be higher using its own subspace (e.g., decoding SC using the SC subspace) than using the other subspace (e.g., decoding SC using the SR subspace). We used cross-validation to avoid artificially higher decoding accuracy for decoders using their own subspace (see Methods). We verified this hypothesis in computational simulations to understand how the representational subspace analysis should perform under different accounts (see Methods). The simulation results (Fig. 4a) showed that: (1) when SC and SR subspaces are completely separable (i.e., the two subspaces shared no dimensions), decoding accuracy using the other subspace is at chance level; (2) when the SC and SR subspaces partially overlap (i.e., share some but not all dimensions), decoding accuracy using the other subspace is above chance level but less than when using its own subspace; and (3) when the SC and SR subspaces fully overlap (i.e., share all dimensions), decoding accuracy using the other subspace is above chance level and is comparable to that when using its own subspace.

In the EEG data (Fig. 4b; See Fig. 5a from response-locked analysis), we observed that the decoders using the other subspace (i.e., SC | SR and SR | SC) showed significantly above-chance accuracy after ~100 ms following stimulus onset ($p < 0.05$, cluster-based permutation test). During the same time window, the decoder performance was significantly worse than the decoders using their own subspace (i.e., SC | SC and SR | SR). The empirical results are most consistent with the simulations of partially overlapped SC and SR spaces, suggesting that SC and SR association representations are separable in the EEG data. To show how each of the 8 conditions in the SC and SR subspaces are represented. The MDS approach was used for visualization to preserve dissimilarity between conditions when projecting from data from a high dimensional to a low dimensional space. The results showed that the 8 conditions were separate in both SC subspace (Fig. 4c, cumulative explained variance was 0.75, 0.88, 0.94 for the first 3 dimensions, respectively; See Fig. 5c from response-locked analysis, cumulative explained variance was 0.69, 0.86, 0.95 for the first 3 dimensions, respectively) and SR subspace (Fig. 4d, cumulative

explained variance was 0.84, 0.93, 0.98 for the first 3 dimensions, respectively; See Fig. 5d from response-locked analysis, cumulative explained variance was 0.82, 0.95,0.99 for the first 3 dimension, respectively), which revealed the different structures of SC and SR encoded in the brain. We conducted RSA on SR decoders on the SR subspace and confirmed that these word pairs were indeed linearly separable in the SR subspace (Supplementary Fig. 1, 2).

We performed control analyses to confirm whether decoding was confounded by temporally structured noise (TSN) due to different MC and MI assignments on different phases in the design. To reduce the influence of TSN, we maximized the temporal distance between training and test data (the distance between the centers of the training and test data of the same SC/SR manipulation is about 400 trials given the experimental design) by dividing the EEG data in phase 2 and phase 1&3 into the first and second half chronologically. Phases 1 and 3 were combined because they share the same MC and MI assignments. We then trained the decoders on one half and tested them on the other half. Finally, we averaged the decoding results across all possible assignments of training and test data. This approach, like cross-phase validation in concept, revealed similar patterns (Fig. 6a-b) to the above representational subspace analyses. Additionally, the idea that TSN biases decoding results would predict a distance effect, which predicts that if a test trial is closer to a training trial with the same trial type, the higher similarity in TSN between the training and test data would more strongly inflate the decoding accuracy of the test trial, resulting in a negative correlation between distance between a test trial and its closest training trial of the same type and the test trial's decoding accuracy. To test this predicted negative correlation, in each fold and each repetition of the cross-validation reported in the SC | SC and SR | SR decoders, we calculated the distance (mean=5.84 trials, SD=2.05, 5th percentile =2.87, 95th percentile=9.45, one trial = 2.4-2.6s) between each test trial and its closest training trial of the same trial type. This distance was used as the predictor to predict decoding accuracy in a linear regression. The regression coefficient is averaged across cross-validation folds and repetitions for each subject to match how the decoding accuracy was reported in the main text. Finally, the averaged regression coefficient was tested against 0 using a one-sample t-test. This analysis was conducted at each time point separately. As shown in the figure 6c, no time point exhibited the negative correlation as predicted by the TNS bias. In summary, our control analyses showed that the separable representations of SC and SR in the present project were not systematically biased by TSN.

To characterize the nature of the shared features between SR and SC, we first identified which factors can be shared across SC and SR subspaces. For SC, the eight conditions are the four colors × ISPC. Thus, the possible shared dimensions are color and ISPC. Additionally, because the four colors and words are divided into two groups (e.g., red-blue and green-yellow, counterbalanced across subjects, see Methods), the group is a third potential shared dimension. Similarly, for SR decoders, potential shared dimensions are word, ISPC and group. Note that each class in SC and SR decoders has both congruent and incongruent trials. Thus, congruency is not decodable from SC/SR decoders and hence unlikely to be a shared dimension in our analysis. To test the effect of sharing for each of the potential dimensions, we performed RSA on decoding results of the SC decoder trained on SR subspace (SR | SC) (Supplementary Fig. 3a) and the SR decoder trained on SC subspace (SC | SR) (Supplementary Fig. 3b). The RSA results revealed that the contributions of group to the SC decoder (Supplementary Fig. 4a) and the SR decoder (Supplementary Fig. 4b) were significant. Meanwhile, a wider time window showed significant effect of color on the SC decoder (approximately 100 - 1100 ms post-stimulus onset, Supplementary Fig. 4a) and a narrower time window showed significant effect of word on SR decoder (approximately 100 - 500 ms post-stimulus onset, Supplementary Fig. 4b). However, we found no significant effect of ISPC on either SC or SR decoders. We also performed the same analyses on response-locked data from the time window −800 to 200 ms. The results showed shared representation of color in the SC decoder (Supplementary Fig. 4c) and group in both decoders (Supplementary Fig. 4c-d). Overall, the above results demonstrated that color, word and group information are shared between SC and SR subspaces.

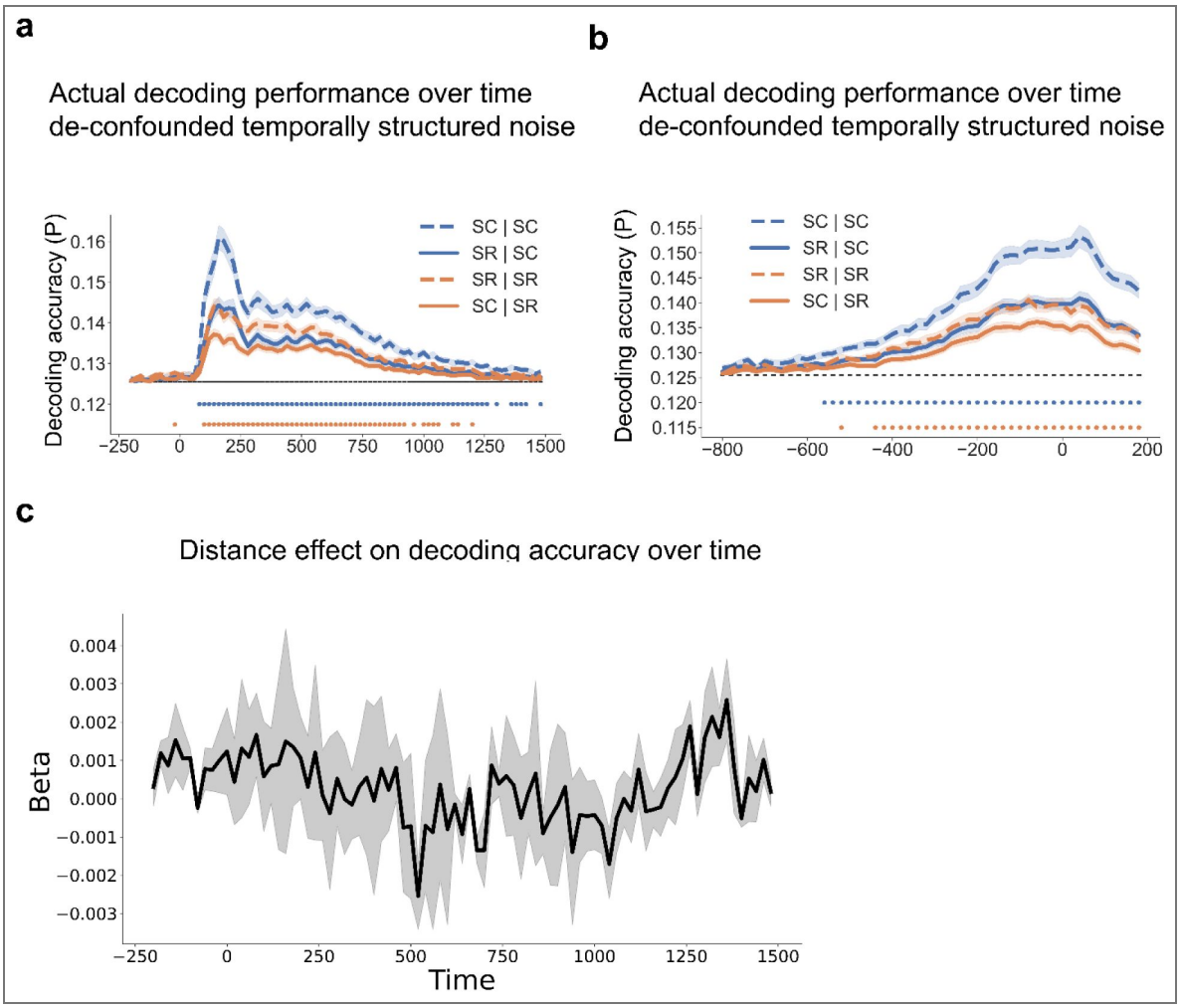


Figure 6. **Split-half decoding and distance regression support separable SC and SR subspace.**

(a, b) Group average decoding accuracy over time is plotted as a function of which subspace the decoders are trained on (stimulus-locked data (a), response-locked data (b)). Shaded regions represent the SEM. Blue (orange) points denote the time points showing significantly better decoding accuracy when using the same subspace than when using the other subspace (cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). **(c)** Slope of how much decoding accuracy changes as a function of the distance between each test trial and its closest training trial (group mean and SEM), plotted as a function of time relative to stimulus onset.

In summary, our main hypothesis for the cross-subspace decoding analysis is that SR and SC subspaces are not identical. This hypothesis was supported by lower decoding accuracy for cross-subspace than within-subspace decoders and enables following analyses that treated SC and SR as separate representations.

Simultaneously represented and positively correlated controlled and non-controlled associations

To further test whether SC and SR associations are simultaneously represented and contribute to adaptive task focus, we performed time-resolved RSA on decoding results to estimate the strength of representations of SC and SR associations while controlling for potential confounds (see Methods). In particular, since both SC and SR associations depend on the same ISPC condition, we included ISPC as a covariate in the same models as SC and SR associations to account for shared variability in the regression. The results showed that all the factors showed statistically significant effects on representational patterns (Fig. 7a). Notably, statistically significant representations of color and congruency were observed for about 1s. This long period of representation may be attributed to the trials with slow responses, as both color and congruency are crucial task information to produce the correct response and to suppress distraction from the word. Another non-exclusive possibility is that color and congruency information remained present for post-trial learning of the SC association. Crucially, both SC and SR effects remained statistically significant from ~250 to ~ 700 ms following the stimulus onset (Fig. 7a-b). To control for collinearity between the predictors in the RSA (see Fig. 12), we calculated the variance inflation factor (VIF) for each predictor and repeated the same analysis using predictors with VIF scores no greater than 5 (only the Identity predictor was removed). We observed similar patterns (Supplementary Fig. 5a-b), suggesting that SC and SR associations were simultaneously represented.

The integrated task representation hypothesis predicted that the representational strength of SC and SR associations should be positively correlated across trials. Alternatively, it remained possible that at the trial level SC and SR were not represented simultaneously. That is, a trial might only show an SR effect but no SC effect, or vice versa. If this were true, SC and SR effects should be negatively correlated across trials. A third possibility is that SC and SR association representations are independent from each other, leading to no correlation. To control for potential inflation of correlation coefficients due to inherent covariance between observations (Cai et al., 2019), we randomly shuffled the trial types within each block and repeated the same analysis using the shuffled data for 10 times. The results were averaged to form a baseline correlation coefficient. We observed significantly above-baseline positive correlation between ~100 and ~ 450 ms following stimulus onset (Fig. 7c) and between −180 and + 50 ms relative to response (Fig. 8c). These findings indicated that trials showing a strong SC effect tended to show stronger SR effects as well, supporting the hypothesis of simultaneously encoded SC and SR associations within an integrated task representation.

Controlled and non-controlled associations jointly predict behavioral performance

To test whether the SC and SR effects from the RSA exhibited behavioral relevance, we predicted RT using a linear mixed model (LMM, see Methods) that included the representational strength of SC and SR associations, as quantified by the t-statistic from a trial-wise RSA. This analysis was conducted at each time point (time-locked to stimulus onset) prior to the group average RT (700.56ms) to test the effect of SC and SR representations on behavioral guidance. We found that faster responses were correlated with stronger representations of SC in the time window 380 - 700 ms (peak time at 520 ms: b = −0.045, SE = 0.006, t = −7.02) and SR in the time window 440 - 580 ms (peak time at 560 ms: b = −0.020, SE = 0.007, t = −2.93, Fig. 9a-b; See Fig. 10a-b for response-locked analysis; See Supplementary Fig. 7 and Supplementary Fig. 8 for the effects on frequent and infrequent trials). These results suggest that controlled and non-controlled associations jointly influence performance before decision-making.

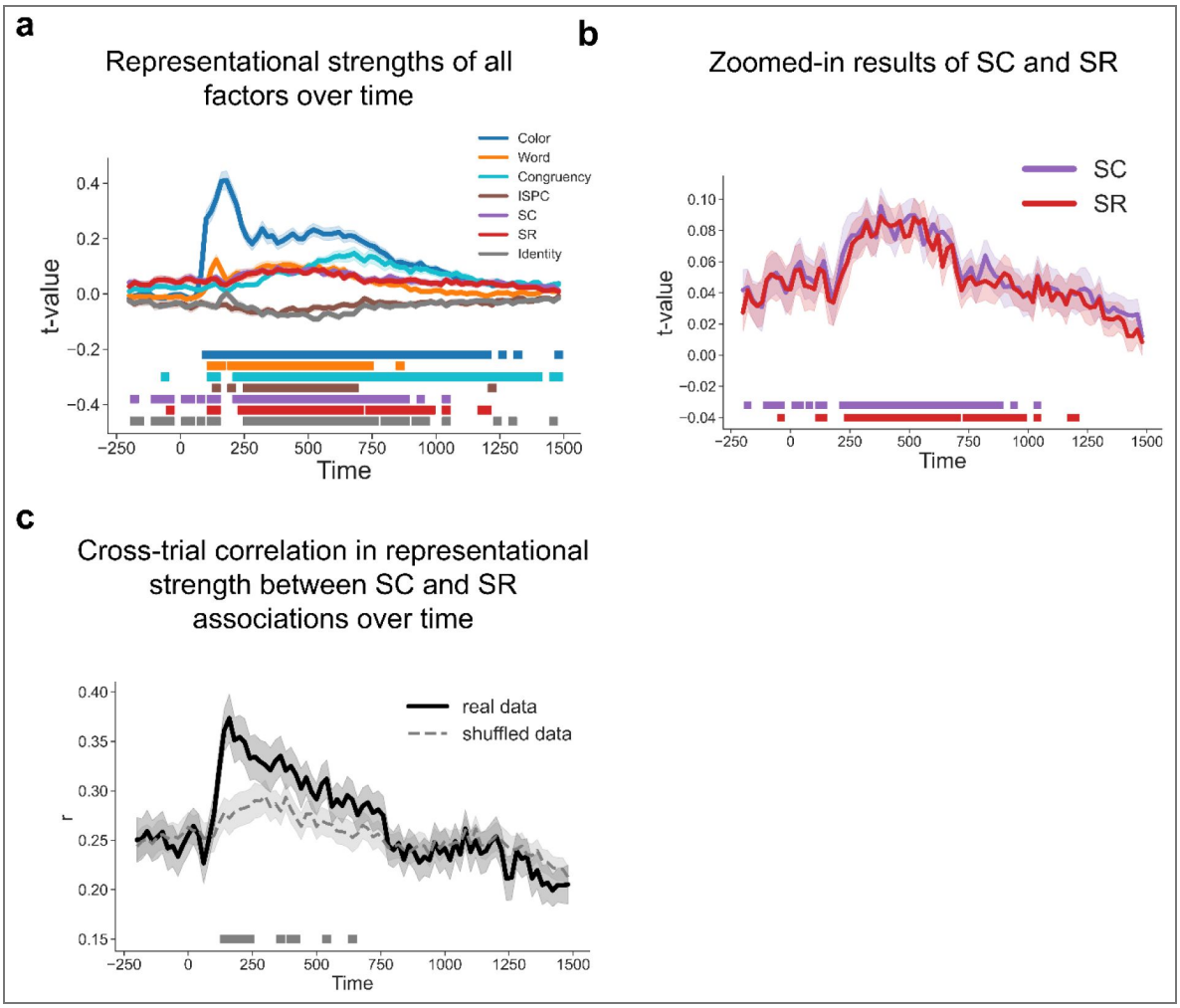


Figure 7. Simultaneous EEG representations of SC and SR associations.

(a) Group average t values of representational strength for each factor over time. Squares below the lines indicate the significant time points (cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). **(b)** SC and SR association results from Fig. 7a. Shaded areas denote SEM. **(c)** Cross-trial correlation coefficient of representational strength between SC and SR associations, plotted as a function of time after stimulus onset. Shaded areas indicate SEM. Squares below the lines indicate the time points significantly above the baseline correlation strength of shuffled data (Cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$).

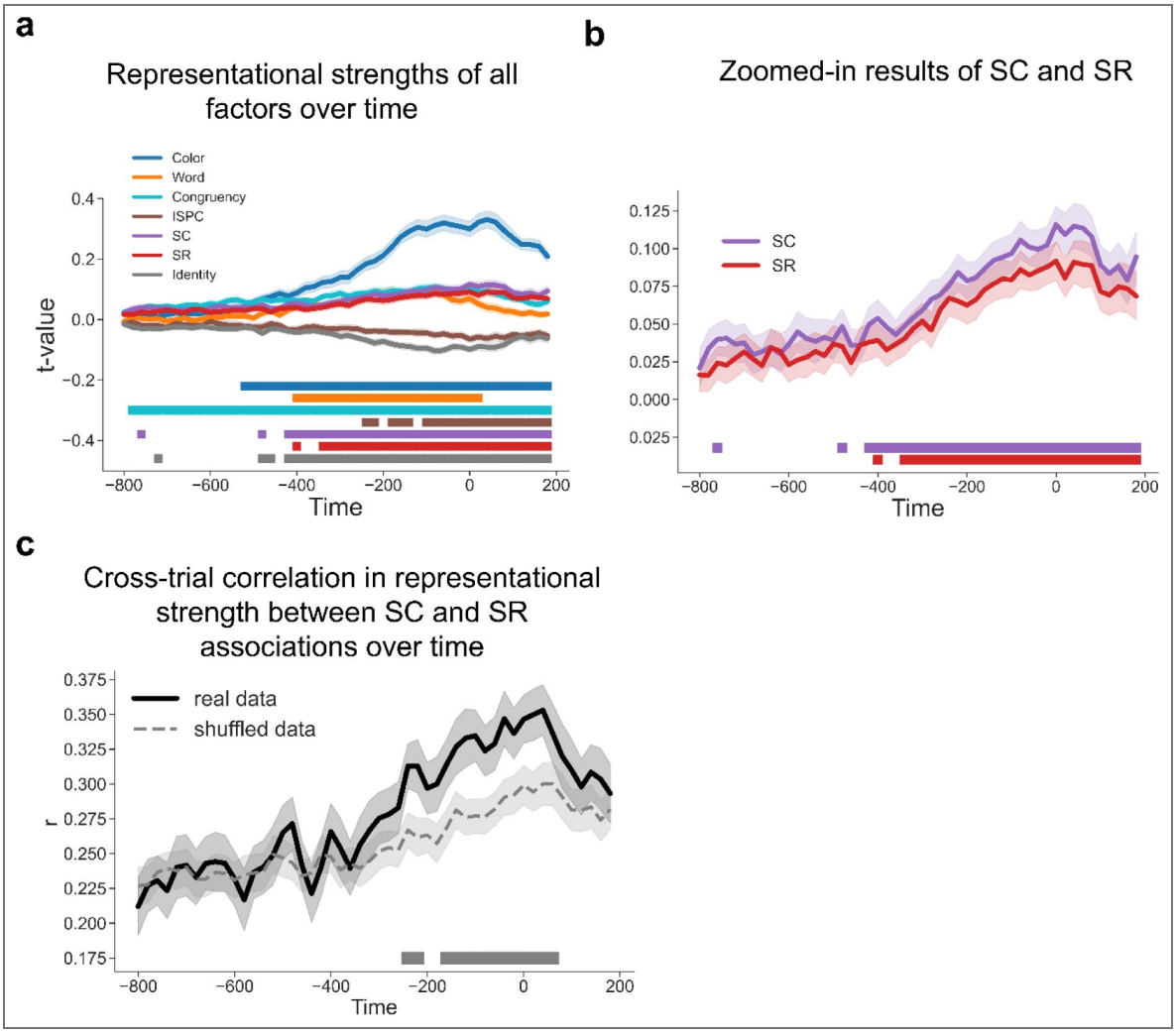


Figure 8. Simultaneous EEG representations of SC and SR associations using response-locked analysis.

(a) Group average t values of representational strength for each factor over time. Squares below the lines indicate the significant time points (cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). **(b)** SC and SR association results from Fig. 8a. Shaded areas denote SEM. **(c)** Cross-trial correlation coefficient of representational strength between SC and SR associations, plotted as a function of time after response onset. Shaded areas indicate SEM. Squares below the lines indicate the time points significantly above the baseline correlation strength of shuffled data (Cluster-based permutation test, cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$). The dashed line shows baseline correlation using shuffled data.

Figure 9. **Both the strengths of SC and SR associations are correlated with RT.**

(**a**) Group averaged t-values for each factor predicting RT in the LMM analysis. (**b**) SC and SR association results from Fig. 9a.

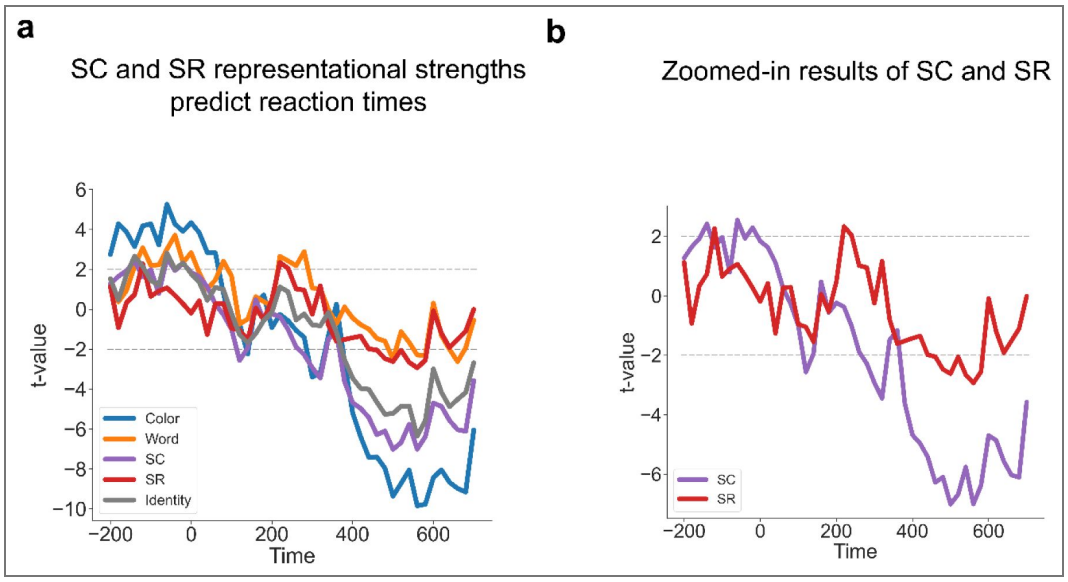
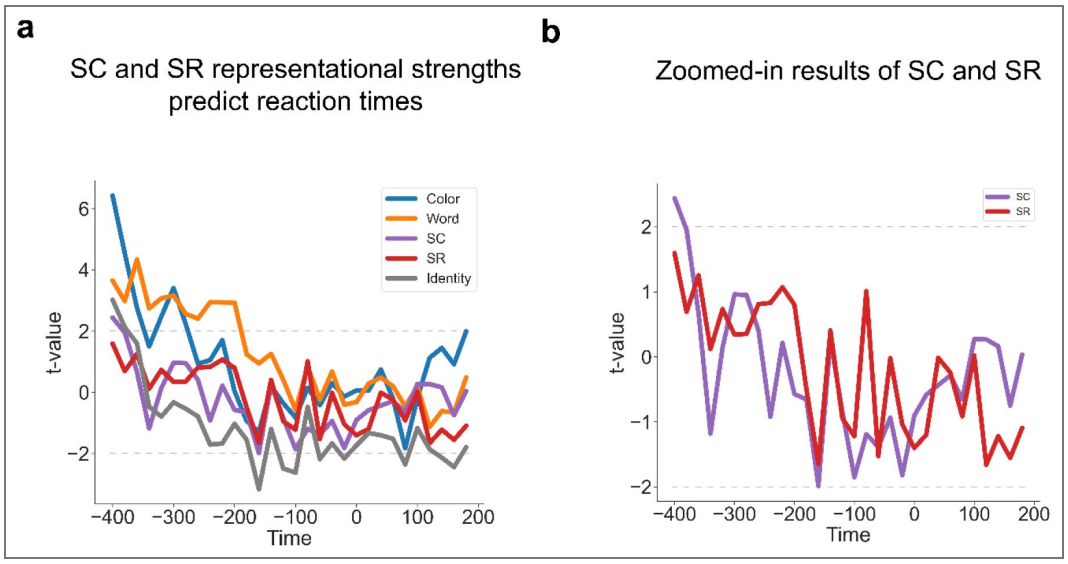


Figure 10. **Correlations of SC and SR association strengths with RT using response-locked analysis.**

(a) Group averaged t-values for each factor predicting RT in the LMM analysis. **(b)** SC and SR association results from Fig. 10a.



Discussion

Adaptive behavior can be guided by associations for controlled processing (e.g., stimulus-control associations) and non-controlled processing (e.g., stimulus-response associations). To explore the relationship between these representations, we combined (1) a novel extension of a classic assay of associative learning in cognitive control with (2) neural subspace analyses of the time-resolved task representations. We found consistent support for distinct neural representations of SR and SC associations, but these associations appeared to share a synchronized temporal profile consistent with them constituting a common task representation.

We found behavioral ISPC effect in each phase of our task, even after the ISPC manipulations were flipped. This suggests that participants adjusted to the local ISPC conditions, which critically allowed us to dissociate stimulus features from their SC/SR associations. The behavioral ISPC pattern was consistent with previous studies (Bejjani et al., 2020; Bugg & Hutchison, 2013; Bugg et al., 2011; Chiu et al., 2017; Ileri-Tayar et al., 2024; Ileri-Tayar et al., 2022; Jacoby et al., 2003; Spinelli et al., 2022). However, as both SC and SR associations are characterized by the same pattern of the ISPC effect, behavioral analysis and conventional contrasts between experimental conditions are insufficient to dissociate SC from SR effects. We addressed this issue with decoding, representational subspace analysis, and RSA on decoding results.

We also found that SC and SR associations were encoded in distinct representations but appeared to be temporally synchronized as a task representation. Brain-behavior analysis prior to the mean RT supported the prediction that SC and SR can jointly guide goal-directed behaviors. Previous fMRI studies with typical ISPC paradigms showed that the ISPC effect was related to cognitive control area including the dorsolateral prefrontal cortex (dlPFC), the dorsal anterior cingulate cortex (dACC) and the parietal cortex (Blais & Bunge, 2010; Grandjean et al., 2013). Therefore, the results showing that SC and SR had distinct subspaces but emerged in the same time window should not suggest a paradox of findings or functional equivalence of SC and SR; rather, they highlight the brain's ability to encode controlled and non-control information in parallel with partially overlapping representational subspaces to serve goal-directed behaviors. Additionally, the caudate nucleus associated with SC and the parietal cortex related with SR were observed in separate SC or SR conditions (Chiu et al., 2017). It is possible that SC and SR are supported by partially overlapping neural substrates with similar temporal dynamics. Direct evidence is needed to validate the possibility. The early onset of above-chance decoding accuracy may seem counter-intuitive. One potential confound that may cause this result is TSN. We did not find evidence that the TSN systematically biased the reported decoding results (Fig. 6). However, future research should consider orthogonalizing SC and SR classes from TSN at the source to prevent potential bias. Alternatively, because of the relatively high number of trials in each phase, it is possible that the participants (implicitly) learned the MC/MI manipulations and used the knowledge to guide proactive control, which is anticipatory and sustained (Braver, 2012; Khan et al., 2025) and then might be decoded early on or even before a trial.

We further explored how controlled and non-controlled associations jointly affect performance via brain-behavioral analyses with LMM. In general, we observed that the strength of SC and SR association representations are both negatively correlated with trial-level variability of RT. There could be one alternative explanation that either SC or SR, instead of both, occurs on each trial. If this were true, the coefficients of SC and SR from RSA results should be negatively correlated or not correlated across trials (i.e., some trials show strong SC effects and weak SR effects, while other trials show the opposite). However, we found the opposite pattern, which indicates that there is no competition between SC and SR to be represented. One possibility leading to this positive correlation is that both associations are encapsulated in an integrated task representation (Hommel, 2004, 2019; Schumacher & Hazeltine, 2016b). Specifically, if the task representation is strongly activated on a trial, both SC and SR associations will also be strongly triggered, leading to a positive correlation between SC and SR effects across trials. Note that we found the negative prediction of the strength of SC and SR to RTs did not reach statistical

significance in the response-locked analysis. It is possible that SC and SR representations have occurred before the stage of response processing, which is usually aligned with stimulus onset (Jiang et al., 2020a; Kang & Yu-Chin, 2024; Khan et al., 2025).

To interpret the ISPC effect, Bugg (2015) proposed the dual item-specific mechanisms whereby SC and SR associations learning dominate the ISPC effect under different situations, which was supported by behavioral and imaging evidence (Bugg & Hutchison, 2013; Bugg et al., 2011; Chiu et al., 2017). This means that SC associations would take over the adaptive effect when the frequency of incongruent trials is manipulated on task-relevant dimension, but SR associations would work when it is manipulated on task-irrelevant dimension. The results of the current study provide new temporal evidence for both control-driven ISPC and SR-driven ISPC and suggest that they can be represented simultaneously. Zooming in on the area of adaptive cognitive control, it has been debated whether adaptive task focus is actually involved with control or not, extending from ISPC to context/list-level PC (Brosowsky & Crump, 2016, 2021; Bugg, 2014; Bugg & Chanani, 2011; Bugg et al., 2022; Cohen-Shikora et al., 2019; Crump, 2016; Crump et al., 2017; Crump et al., 2006; Crump & Milliken, 2009; Crump et al., 2008; Crump et al., 2018; Hutchison, 2011; Schmidt, 2013b; Schmidt, 2014b; Schmidt, 2017; Schmidt et al., 2014; Spinelli & Lupker, 2021; Spinelli et al., 2019; Weidler et al., 2022) and the congruency sequence effect (Brosowsky & Crump, 2018; Schmidt, 2013a; Schmidt, 2014a; Schmidt, 2018; Schmidt & Weissman, 2016; Spinelli & Lupker, 2020b; Weissman et al., 2016). Researchers have gradually formed an associative learning view on adaptive task focus (Abrahamse et al., 2016; Egner, 2014, 2023). Egner (2014) assumed integrating different levels of abstraction about associations including SR and SC into the same learning scheme serves for adaptive behaviors. The current study supports this assumption directly with the finding of joint action of control and non-control within the same stimulus for adaptive behaviors.

To better understand the role of complex associative learning in cognitive control, we developed a new way to test how representations are integrated, and how multiple representations of task information collaborate to guide goal-directed behaviors(Badre, 2024; Musslick & Cohen, 2021). Previous research has employed partially overlapping tasks to test the conjunctive nature. For example, when there are two tasks producing different responses to the same input stimulus, encountering the stimulus will retrieve both task representations, leading to interference between the incompatible responses and impaired performance (Hubner & Druey, 2008; Koch et al., 2011; Korb et al., 2017; Rogers & Monsell, 1995). However, this test is confounded by the retrieval of episodic memory (e.g., the last experiences performing the tasks, rather than the task representations), which is also conjunctive (Altmann, 2011; Hommel, 2004, 2019). Additional evidence supporting conjunctive task representation comes from studies showing that task identity is still decodable from electroencephalographic (EEG) data when accounting for individual task features such as stimulus, rule, and response (Kikumoto et al., 2024; Kikumoto & Mayr, 2020; Kikumoto et al., 2022a; Kikumoto et al., 2022b; Rangel et al., 2023). This approach relies on shared representations of task features across multiple tasks. It remained understudied how multiple task components within the same task are influenced by the conjunctive task representation. In this study, we extend the test of conjunctive task representation in two ways. First, we examine stochastic task features that must be learned from multiple episodes of task execution to tease apart retrieval of task representation from episodic retrieval. Second, we test the prediction that conjunctive task representation will simultaneously encode multiple task features instead of locating task-unique representations.

Despite the theoretical differences between SR and SC associations, our subspace analysis revealed a pattern that is consistent with partially overlapping subspaces for SC and SR representations. SC and SR are different in their concepts and information processing, but they shared variance in their operational definitions by both depending on the same ISPC conditions. While this may have resulted in the partially overlapping representations, it may also reflect simultaneous retrieval to guide behavior. Critically, our RSA analyses revealed concurrent representations of SC and SR associations even when controlling for ISPC confounds. The experimental design combined with the RSA method ensures that the predictors for SC and SR associations are different.

An SR association itself is automatic behavior, but it is sometimes included as a core component of cognitive control (Badre, 2024). We consider SC and SR as controlled and uncontrolled respectively based on the literature investigating the mechanism of ISPC effect. The SC account posits that the ISPC effect results from conflict and involves conflict adaptation, which requires the regulation of attention or control (Bugg & Hutchison, 2013; Bugg et al., 2011; Schmidt, 2018; Schmidt & Besner, 2008). On the other hand, the SR account argues that ISPC effect does not require conflict adaptation but instead reflects contingency leaning. That is, the response can be directly retrieved from the association between the stimulus and the most-likely response without top-down regulation of attention or control. As more empirical evidence emerged, researchers advocating control view began to acknowledge the role of associative learning in cognitive control regarding the ISPC effect (Abrahamse et al., 2016). SC association has been thought to include both automatic that is fast and resource saving and controlled processes that is flexible and generalizable (Chiu, 2019). Overall, we do not intend to claim that SC is entirely controlled or SR is completely automatic. We use SC-controlled and SR-uncontrolled representations to align with the original theoretical motivation and to highlight the conceptual difference between SC and SR associations.

In summary, we find evidence of neural representations of associations of both controlled and non-controlled information quantified by SC and SR. The neural representations are represented simultaneously in an integrated representation in partially overlapping neural subspaces shortly after stimulus onset and remain active after the response is made. Moreover, the strengths of the associations prior to the response can jointly predict performance. These results shed light on how an integrated task representation, which consists of multiple associations that can drive behavior, can retrieve multiple associations of controlled and non-controlled information to guide adaptive behaviors.

Methods

Participants

Sixty-one healthy adults participated in the EEG experiment. Sixteen participants with excessive muscle artifacts (6 subjects), too many corrupted EEG channels (5 subjects), and missed partial data (5 subjects), and five participants with accuracy below 75% were removed, resulting in a final sample of 40 participants (28 females, 12 males; age mean = 23.9, SD = 6.2, age information was not acquired for the first 25 participants). All participants had normal or corrected-to-normal vision. All participants gave informed consent prior to the experiment, and either were paid or received course credits for participation. All procedures were approved by the University of Iowa Institutional Review Board (UIIRB #202001345).

Stimuli

The experiment was programmed using PsychoPy (ver. 2022.2.5). The stimulus was a color word presented in the center of the screen (24 inch LCD display with resolution of 1920× 1080) on a black background. Four color words (red, blue, yellow, and green) and their corresponding colors were used. For each participant, the colors and their corresponding words were divided into two sets of red-blue and yellow-green. Within each set, the words and colors formed a 2 × 2 factorial design, resulting in eight unique Stroop stimuli (Stroop, 1935) in total (e.g., red in red or blue color, blue in red or blue color, yellow in yellow or green color and green in yellow or green color).

Design and procedures

Each trial started with the presentation of a fixation cross for 500 ms, followed by a color word at the center of the screen (specified in 'height' with 0.08 units where the full screen height equaled 1.0 unit) for 1500 ms or until a response was made (Fig. 1a). The four colors were mapped onto four keys ("H" for red, "J" for blue, "K" for yellow and "L" for green). Trials were separated by a black screen for the remainder of the 1500 ms response deadline plus a jittered (400/500/600 ms

with equal probability) interval. The trials were grouped into mini-blocks of 16 trials each. The participants first underwent a practice session with 3 mini-blocks of 50% congruent trials. During practice, participants received feedback for a correct, incorrect or too slow response on each trial. After reaching the 75% accuracy criteria across all blocks, they moved on to the main experiment (Fig. 1b) with 8 mini-blocks for phase 1, 50 mini-blocks for phase 2 and 48 mini-blocks for phase 3.

Behavioral analysis

Behavioral data from the main experiment were analyzed. For response time (RT) data, only correct trials within ±3 SD from each subject's mean RT were included in the analysis. Accuracy and RT were analyzed separately for each phase using a 2 (congruency) × 2 (ISPC) repeated-measures ANOVA.

EEG data acquisition and preprocessing

EEG data were recorded from a 64-channel active electrode cap with the ground at Fz and the reference at Pz using an actiCHamp amplifier (Brain Products) at a sampling rate of 500Hz with a hardware band-pass filter from 0.016 Hz to 1000 Hz. All electrode impedances werekept below 10 kΩ during the experiment. All EEG data were analyzed using the EEGLAB toolbox (*https://sccn.ucsd.edu/eeglab/index.php*) and custom MATLAB scripts. Preprocessing started with rejection and interpolation of noisy electrodes. Next, a 0.1–50 Hz band-pass filter was applied to the raw EEG data. The data were then re-referenced to the average of all electrodes and segmented into epochs spanning from −500 ms to 1500 ms relative to the stimulus onset. We used independent component analysis (ICA) to remove eye-blink and muscle artifacts from the epochs. These epochs were further segmented into smaller epochs ranging from −200 to 1500 ms relative to stimulus onset. These smaller epochs were also used to perform the response-locked analysis ranging from −800 to 200 ms relative to response. Epochs with amplitudes exceeding ± 80 μV were rejected. Fewer than 70% of all the epochs were excluded for each subject.

Decoding analyses

Decoding analysis was conducted on epoched EEG data without baseline correction to avoid potential bias in the decoding results (van Driel et al., 2021). To generate the dependent variable for the RSA, we first decoded the representations of all conditions using LDA (scikit-learn version 1.2.2 in Python (Pedregosa et al., 2011)). The preprocessed 64-channel ERP data were down-sampled to 50 Hz and were used as the features to decode the 16 experimental conditions (8 unique stimuli × MC/MI. Note that Phases1 and 3 shared the same ISPC manipulations). Decoding results were obtained by performing a 4-fold cross-validation procedure (Fig. 1I). To avoid the bias of unbalanced trial numbers among different classes on decoding results, the more frequent trial types were down-sampled to be consistent with the less frequent trial types. Specifically, given the 75%/25% proportion congruency used in the manipulation of ISPC, the more frequent trial types had three times as many trials as the less frequent ones. Thus, the more frequent trial types were randomly divided into three parts, and one part was used for the 4-fold cross-validation. The cross-validation was repeated 30 times (i.e., 10 random partitions of the frequent trial types and each part being used once within each random partition). The LDA decoding accuracy was averaged. The decoding analysis was performed at each time point of a trial for each participant.

To construct SC and SR subspaces, we trained 8-way SC (4 colors × MC/MI) and SR (4 words × 2 possible responses per word) LDA decoders and then transformed all training and test data into the subspaces of the LDA decoders. For each subspace, we built and tested SC and SR decoders using the same cross-validation approach as above. To avoid bias, all decoders used the same partition of training and test data, with the class label of each trial determined by its experimental condition. To test the statistical significance of decoding results, cluster-based permutation test (Maris & Oostenveld, 2007) with 1000 permutations was applied to address the issue of multiple comparisons. Clusters were formed with a threshold of $p < 0.001$ and cluster significance was

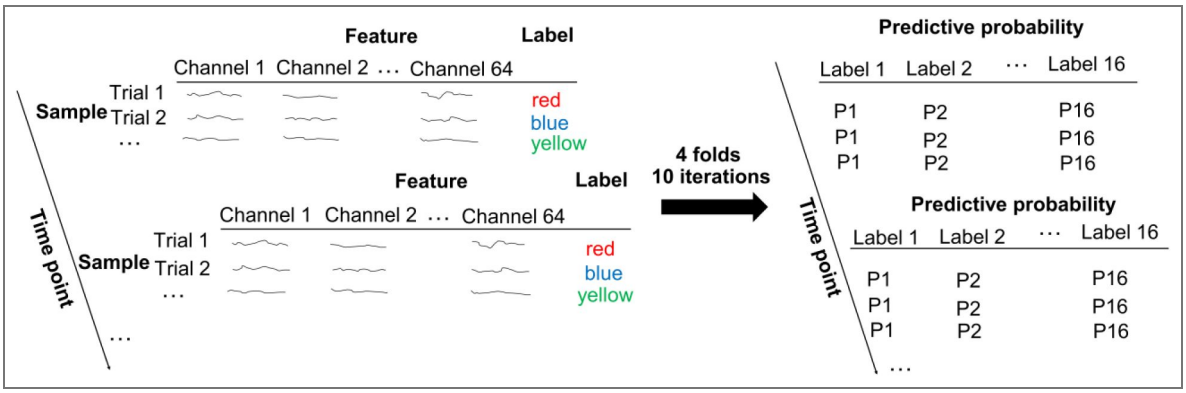


Figure 11. **Illustration of linear discriminatory analysis (LDA).**

assessed with a threshold of $p < 0.05$ (Collins & Frank, 2018). Additionally, classical multidimensional scaling (MDS) analysis (Wickelmaier, 2003) on a 16×16 matrix of probabilistic classification results from the 16-way decoders was applied to visualize the neural representations of all conditions potentially including both SC and SR associations. Similar MDS analyses were performed on the 8×8 matrix of probabilistic classification results from the SC decoder and the other 8×8 matrix of decoding accuracy from the SR decoder to visualize their neural representations.

Simulations of cross-decoding accuracy

To simulate SC and SR subspaces with different levels of overlap, we first constructed non-overlapping SC and SR subspaces, each having 8 dimensions and consisting of 8 classes of 100 data points each. The centers of the classes were equidistant, with the distance set to the mean between-center distance in the EEG subspace. For each class, the data points were randomly drawn from a multivariate Gaussian distribution using the class center as the mean and the within-class standard deviation from the EEG subspace (averaged across all time points). Both SC and SR decoding were then conducted on each of the SC and SR subspaces using 4-fold cross-validation. To examine how overlap in subspaces affects decoding accuracy, the overlap between the two subspaces was manipulated by the number of shared dimensions. That is, if n ($n \leq 8$) dimensions were shared, n dimensions of data were randomly chosen for SC_SR (i.e., SR decoder trained on the SC subspace) and SR_SC decoders. For SC_SC and SR_SR decoders, all 8 dimensions were used regardless of n.

RSA on decoding results

To further track the representational dynamics of SC and SR associations, we tested the hypothetical representational similarity patterns using the empirical representational similarity patterns from EEG data and linear regression-based RSA (Kikumoto & Mayr, 2020; Kikumoto et al., 2022a; Rangel et al., 2023). For each time point, its decoding results reflected the neural similarity between conditions (i.e., if two conditions have similar neural representations, the misclassification rate would increase) and were organized as the logit-transformed probability of a trial belonging to each of the 16 conditions to be the dependent variable. Six factors were considered, namely color, word, congruency, ISPC (MC/MI), SC (i.e., the pairing between color and ISPC), and SR (i.e., the pairing between word and ISPC), resulting in six hypothetical representational similarity patterns in the form of binary linear regressors (Fig. 12). Specifically, for each trial, each regressor was a column-vector of 16 cells, with each cell containing a binary value indicating whether each of the 16 conditions shared the feature (e.g., color) with the condition to which the current trial belonged to. Note that, as the SR association binds the word with the most-likely response rather than the actual response on the current trial, two trial types with different responses in the RDM (Fig. 12) may share the same SR association, as long as they share the same word and the same ISPC manipulation, which will produce the same most-likely response. Additionally, two nuisance binary regressors marking the condition and its frequency (i.e., whether a MC color on a congruent trial or a MI color on an incongruent trial) of the current trial were included. For each participant, the within-trial regressors formed a design matrix to regress against the empirical decoding results, resulting in trial-wise *t* values for each regressor. For each time point, individual mean *t* values for each regressor were submitted to a group-level one-sample *t*-test against 0. To test the significance of temporal representational strength, cluster-based permutation test (1000 permutations using identical cluster forming thresholds to the main analysis) was applied to address the issue of multiple comparisons. Additionally, we correlated those regression coefficients of SC with that of SR across trials at each time point to test the possibility that SC and SR were not simultaneously represented within a trial.

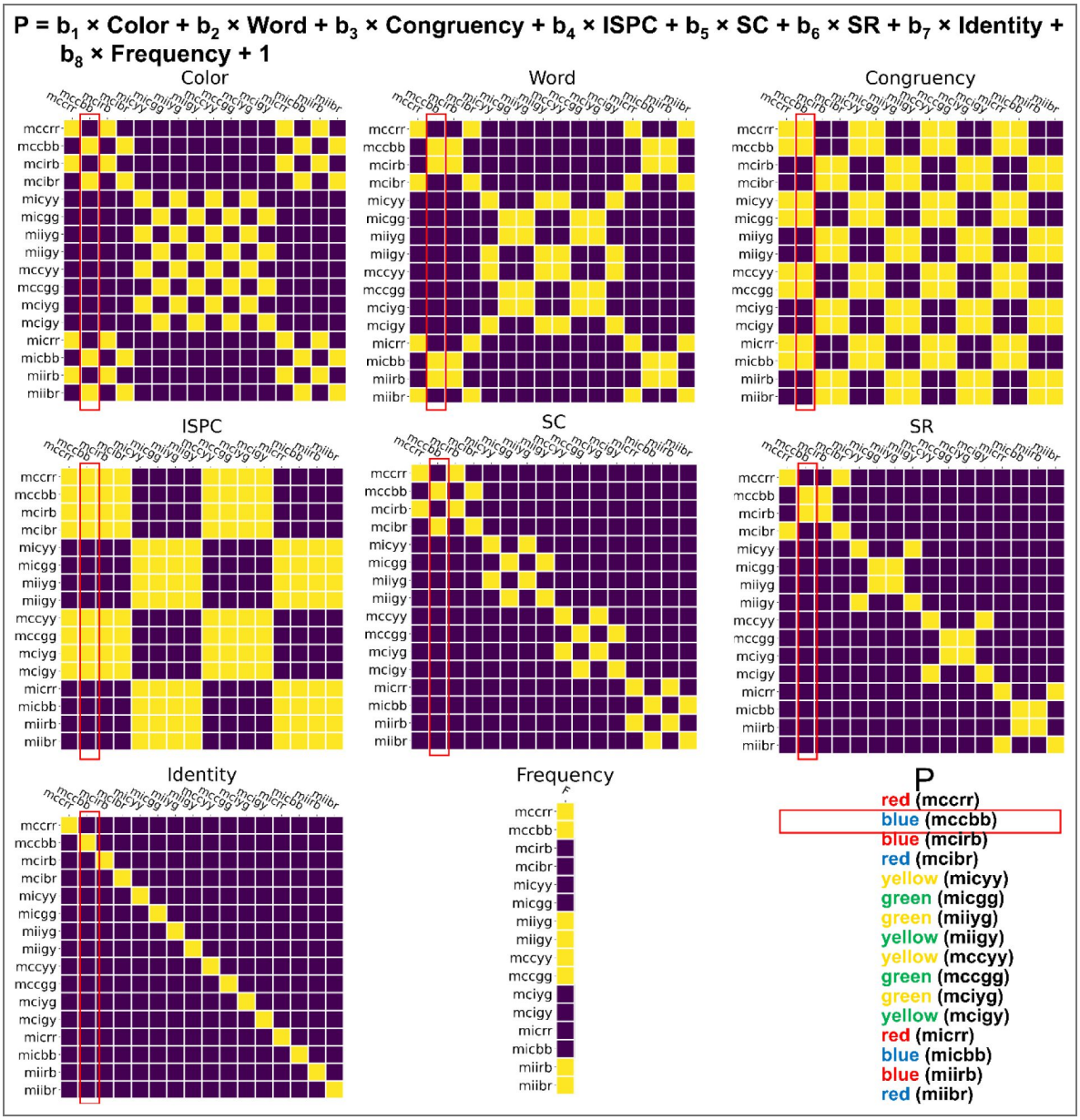


Figure 12. Illustration of RSA.

The label of each row/column represents the condition in the experimental design including ISPC, congruency, color and word. For example, "mccbb" means the condition with MC, congruent trial, color blue and word blue. For each cell in a matrix, the color indicates whether the row and column conditions share the same factor (yellow = yes, blue = no) encoded by the matrix. For example, the cell at the 4th row and the 2nd column in the "SC" matrix encodes that the 4th condition (i.e., mcibr) and the 2nd condition (i.e., mccbb) share the same SC association.

Linear mixed model (LMM)

We further performed LMM at each time point preceding the mean RT across all trials (700.56 ms) to test whether trial-wise RSA results could predict the RT variability (Kikumoto & Mayr, 2020; Rangel et al., 2023). The model predicted trial-wise RT using each of the eight trial types in SC or SR (t-values from the RSA regressors) as separate predictors with their own intercepts, while including random intercepts for subjects. Log-transformed RTs were used as the dependent variable. At each time point, we only included trials that have not generated a response (for stimulus-locked analysis) or already started (for response-locked analysis).

Data availability

Data and analysis scripts have been uploaded to *https://osf.io/tzcn8/files*

Acknowledgements

We thank Atsushi Kikumoto and the members of the Cognitive Control Collaborative at the University of Iowa for helpful comments and suggestions. We also thank Jordan Nicholson, Tommy Looi, Yong-Yao Cheng and Qiutong Hong for their help with data acquisition. This project was supported by the National Institute of Mental Health (R01MH131559 to J.J.), and the C.V. Starr Fellowship (H.R).

Additional files

Supplementary materials.

Additional information

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Peer reviews

Reviewer #1 (Public review):

Summary:

This study focuses on characterizing the EEG correlates of item-specific proportion congruency effects. In particular, two types of learned associations are studied. One association involves associations between stimulus features and control states (SC), and the other involves stimulus features and responses (SR). Decoding methods are used to identify time-resolved SC and SR correlates.

The authors conclude that SC and SR associations can independently and simultaneously guide behavior. This conclusion is based on results showing that SC and SR correlates are (1) not entirely overlapping in cross-decoding, (2) simultaneously observed on average over trials, (3) independently correlate with RT, and (4) have a positive within-trial correlation.

Strengths:

Fearless, creative use of EEG decoding to test tricky hypotheses regarding latent associations.

Nice idea to orthogonalize ISPC condition (MC/MI) from stimulus features.

Response:

In their last response to the reviewers, the authors write:

"... constructing a theoretically unbiased decoder requires perfectly counter-balanced training data (i.e., for every training trial of class A that is X trials away from the test data, there must be a training trial of all other classes that is exactly X trials away from the test data). As we were unable to achieve such a perfect design, we chose not to run an additional experiment."

This isn't really an issue about whether this design is "perfectly" orthogonal. It's an issue regarding a clear confound among the decoded classes for SC/SR decoders. To be clear: of the 8 classes in the SC decoder, 4 are overwhelmingly presented in the first half (PHASE 2) of the session, whereas the other 4 are overwhelmingly presented in the second half (PHASE 3). The same is true for the SR decoder. So, session-half correlated noise could readily contribute to distinguishing among these classes. And counterbalancing this across subjects won't help because decoders lose sign.

To me, the conducted control analyses don't really make strong contact with this issue. The split-half cross-validation is a nice idea but, as the authors acknowledge, it's also subject to slower cross-session noise, as is the original analysis. This sort of noise is not exactly exotic in EEG. Caps/hair/electrodes shift, gel dries and impedance changes, posture / muscle tension / skin conductance changes, fatigue may wax and wane (e.g., linked to increasing alpha), etc. And the newest analysis didn't really seem to engage with this issue either, as it only assessed minimum distances between classes, on the order of 5 +- 2 SD trials. This seems to assume that the dominant potential sources of noise will be scale-free, such that the strength of the relation at short time scales would generalize to longer ones. I'm not sure why that's expected here.

Here are some suggestions for alternative control analyses that I think would be more targeted to this issue:

(1) Explicitly train a decoder to separate the three levels of PHASE from each other. Successful decoding would provide positive evidence for the presence of structured noise at this timescale.

(2) Specify an RDM for the PHASE variable and regress this component separately from each time-point/trial of the SC and SR decoders. This is a post-hoc band-aid, but it is in the spirit of correcting for a known confound.

(3) In the spirit of the authors' distance analysis, but without assuming that the noise is scale-free: perform a time-series RSA like that in Alink et al. (2015; *https://doi.org/10.1101/032391*), Fig. 1 and 3. This would allow one, e.g., to estimate the structure & timescales of the noise processes across the session.

Other readers may, like me, be puzzled by the selection of this particular experimental design to test this question of SC and SR coding, given the temporal confound among SC/SR classes, and given that there would seem to be many possible designs that are less confounded. For example, why not use a design where ISPC was swapped/shuffled several more times within each subject, so that PHASE is more orthogonal to long-timescale noise? Isn't ISPC learning fast enough to support learning phases shorter than 700 trials? Such readers would likely appreciate a frank discussion of this dilemma, and a motivation for the choice of the present design, within the manuscript.

Pre-stimulus coding:

To explain the apparent pre-stimulus coding of several task variables, the newest version of the manuscript proposes that subjects were proactively coding these variables via predictive mechanisms. This is an interesting account of item-specific control. It is also surprising, given that item-specific control mechanisms are typically conceptualized as reactive or stimulus-driven phenomena. But I think support for a proactive control account was incomplete. The mechanistic logic was not presented, and no hypotheses under this account were developed or tested. So I would suggest pinning down some hypotheses here and actually putting this account to the test.

Outliers & t-values: thank you for checking this!

Random slopes were omitted due to convergence failure, but this can inflate false positive inferences (e.g., Barr et al. 2013), and doesn't really motivate a minimal model. I'd suggest trying a slightly reduced model (e.g., drop correlations via ŝlope || subject) using buildMer automated selection, or switching to brms.

https://doi.org/10.7554/eLife.108673.3.sa2

Reviewer #2 (Public review):

Summary:

In this EEG study, Huang et al. investigated the relative contribution of two accounts to the process of conflict control, namely the stimulus-control association (SC), which refers to the phenomenon that the ratio of congruent vs. incongruent trials affects the overall control demands, and the stimulus-response association (SR), stating that the frequency of stimulus-response pairings can also impact the level of control. The authors extended the Stroop task with novel manipulation of item congruencies across blocks in order to test whether both types of information are encoded and related to behaviour. Using decoding and RSA they showed that the SC and SR representations were concurrently present in voltage signals and they also positively co-varied. In addition, the variability in both of their strengths was predictive of reaction time. In general, the experiment has a solid design and the analyses are appropriate for the research questions.

Strengths:

(1) The authors used an interesting task design that extended the classic Stroop paradigm and is effective in teasing apart the relative contribution of the two different accounts regarding item-specific proportion congruency effect.

(2) Linking the strength of RSA scores with behavioural measure is critical to demonstrating the functional significance of the task representations in question.

Weaknesses:

I still have some doubts on the effectiveness of the experimental manipulation on Phase 2: although the ISPC effect is still present, it is much weaker in comparison, suggesting the participants did not learn the contingency statistics in Phase 2 as well as they did in the other phases, due to either the lingering effect of the previous phase or an inherent bias towards one color pairs. Perhaps by separately plotting the earlier and later blocks of Phase 2 any difference can be revealed if it exists. This behavioral difference could result in unequal levels of SC/SR representation across phases, which may raise problems when data were combined for analyses that assume the neural effects are equivalent.

https://doi.org/10.7554/eLife.108673.3.sa1

Author response:

The following is the authors' response to the previous reviews

> ***eLife Assessment***
>
> *This useful study uses creative scalp EEG decoding methods to attempt to demonstrate that two forms of learned associations in a Stroop task are dissociable, despite sharing similar temporal dynamics. However, the evidence supporting the conclusions is incomplete due to concerns with the experimental design and methodology. This paper would be of interest to researchers studying cognitive control and adaptive behavior, if the concerns raised in the reviews can be addressed satisfactorily.*

We thank the editors and the reviewers for their positive assessment and constructive feedback of our work, which led us to think more deeply about the conceptual and methodological aspects of this project and further strengthen the manuscript. Based on the comments, we included more control analyses and revised the manuscript accordingly. Please see below our responses to each comment raised in the reviews.

> ***Public Reviews:***
>
> ***Reviewer #1 (Public review):***

> *Summary:*
>
> *This study focuses on characterizing the EEG correlates of item-specific proportion congruency effects. Two types of learned associations are characterized, one being associations between stimulus features and control states (SC), and the other being stimulus features and responses (SR). Decoding methods are used to identify time-resolved SC and SR correlates, which are used to test properties of their dynamics.*
>
> *The conclusion is reached that SC and SR associations can independently and simultaneously guide behavior. This conclusion is based on results showing SC and SR correlates are: (1) not entirely overlapping in cross-decoding; (2) simultaneously observed on average over trials in overlapping time bins; (3) independently correlate with RT; and (4) have a positive within-trial correlation.*
>
> *Strengths:*
>
> *Fearless, creative use of EEG decoding to test tricky hypotheses regarding latent associations.*
>
> *Nice idea to orthogonalize ISPC condition (MC/MI) from stimulus features.*

Thank you for acknowledging the strength in EEG decoding and design. We have addressed all your concerns raised below point by point.

> *Weaknesses:*
>
> *I still have my concern from the first round that the decoders are overfit to temporally structured noise. As I wrote before, the SC and SR classes are highly confounded with phase (chunk of session). I do not see how the control analyses conducted in the revision adequately deal with this issue.*
>
> *In the figures, there are several hints that these decoders are biased. Unfortunately, the figures are also constructed in such a way that hides or diminishes the salience of the clues of bias. This bias and lack of transparency discourage trust in the methods and results.*
>
> *I have two main suggestions:*
>
> *(1) Run a new experiment with a design that properly supports this question.*
>
> *I don't make this suggestion lightly, and I understand that it may not be feasible to implement given constraints; but I feel that this suggestion is warranted. The desired inferences rely on successful identification of SC and SR representations. Solidly identifying SC and SR representations necessitates an experimental design wherein these variables are sufficiently orthogonalized, within-subject, from temporally structured noise. The experimental design reported in this paper unfortunately does not meet this bar, in my opinion (and the opinion of a colleague I solicited).*
>
> *An adequate design would have enough phases to properly support "cross-phase" cross-validation. Deconfounding temporal noise is a basic requirement for decoding analyses of EEG and fMRI data (see e.g., leave-one-run-out CV that is effectively necessary in fMRI; in my experience, EEG is not much different, when the decoded classes are blocked in time, as here). In a journal with a typical acceptance-based review process, this would be grounds for rejection.*
>
> *Please note that this issue of decoder bias would seem to weaken the rest of the downstream analyses that are based on the decoded values. For instance, if the decoders are biased, in the within-trial correlation analysis, how can we be sure that co-*

> *fluctuations along certain dimensions within their projected values are driven by signal or noise? A similar issue clouds the LMM decoding-RT correlations.*

We appreciate the reviewer's concern with the potential confound of temporally structured noise (TSN) in the EEG data. As we understand it, TSN refers to a process that the noise structure drifts over time. It follows that noise structure should be more similar for temporally closer trials and that the TSN's bias on decoding accuracy is stronger for test trials that are closer to the training data. In the previous round of revision, we conducted a control analysis that reduced the influence of TSN by maximizing the temporal distance between training and test data (the distance between the centers of the training and test data of the same SC/SR manipulation is about 400 trials given the experimental design) and showed comparable decoding accuracy with the main results. As the reviewer finds this analysis unconvincing, we reason that the reviewer believes that the TSN has a long-term effect, such that it remains relatively stable over time and can be picked up by trials temporally distant from the training data. With this assumption and the assumption that this effect may not be linear, constructing a theoretically unbiased decoder requires perfectly counter-balanced training data (i.e., for every training trial of class A that is X trials away from the test data, there must be a training trial of all other classes that is exactly X trials away from the test data). As we were unable to achieve such a perfect design, we chose not to run an additional experiment. Instead, we focused on testing whether and how much TSN systematically biased the reported decoding accuracy.

Please note that the existence of TSN in the EEG data is not sufficient to rule that the decoding results are biased. As TSN is stronger for trials closer to each other, the idea that auto-correlation biases decoding results would predict a distance effect, such that if a test trial is closer to a training trial of the same trial type, the higher similarity in TSN between the training and test data would more strongly inflate the decoding accuracy of the test trial, resulting in a negative correlation between distance between a test trial and its closest training trial of the same type and the test trial's decoding accuracy. To test this predicted negative correlation, in each fold and each repetition of the cross-validation reported in the SC-SC and SR-SR decoders in Fig. 4, we calculated the distance (mean=5.84 trials, SD=2.05, 5th percentile =2.87, 95th percentile=9.45, one trial = 2.4-2.6s) between each test trial and its closest training trial of the same trial type. This distance was used as the predictor to predict decoding accuracy in a linear regression. Note that even if the relation between distance and decoding accuracy is non-linear, the linear relation will be negative because the relation is monotonic (similarity in noise structure decreases monotonically with temporal distance between trials). Similarly, because the effect is monotonic, if a long-range effect exists, it should also exist in short-range and be picked up by the distance range in this analysis. The regression coefficient is averaged across cross-validation folds and repetitions for each subject to match how the decoding accuracy was reported in the main text. Finally, the averaged regression coefficient was tested against 0 using a one-sample t-test. This analysis was conducted at each time point (from -250ms to 1500ms) separately. As shown in the figure below, no time point exhibited the negative correlation as predicted by the auto-correlation account. An alternative explanation is that this result indicates that TSN remains stable over time. If this is the case, TSN will be shared by all trials and will be unable to bias decoding results. Together with the control analysis introduced previously, this new control analysis supports the notion that the decoding results are not inflated by TSN in the EEG data. We included all the control analyses in the revised manuscript (page 13-14). Please note that this analysis is specific for the present dataset and we strongly agree with the reviewer that TSN is a key confounding factor in EEG analysis in general and should be carefully addressed.

Lastly, we understand the concern with the early onset of above-chance decoding accuracy. Here, we provide an explanation: because of the blocked design (i.e., participants performed hundreds of trials with the same SC/SR associations), it is possible the participants learned the associations and used them to guide proactive cognitive control. As proactive cognitive

control is anticipatory and sustained (Braver, 2012; Khan et al., 2025), it may be able to be decoded early on a trial, or even before trial onset. In the revised manuscript, we discussed this account along with the TSN issue as a limitation of the current project and directions for future research (page 24).

> *(2) Increase transparency in the reporting of results throughout main text.*
>
> *Please do not truncate stimulus-aligned timecourses at time=0. Displaying the baseline period is very useful to identify bias, that is, to verify that stimulus-dependent conditions cannot be decoded pre-stimulus. Bias is most expected to be revealed in the baseline interval when the data are NOT baseline-corrected, which is why I previously asked to see the results omitting baseline correction. (But also note that if the decoders are biased, baseline-correcting would not remove this bias; instead, it would spread it across the rest of the epoch, while the baseline interval would, on average, be centered at zero.)*
>
> *Please use a more standard p-value correction threshold, rather than Bonferroni-corrected p<0.001. This threshold is unusually conservative for this type of study. And yet, despite this conservativeness, stimulus-evoked information can be decoded from nearly every time bin, including at t=0. This does not encourage trust in the accuracy of these p-values. Instead, I suggest using permutation-based cluster correction, with corrected p<0.05. This is much more standard and would therefore allow for better comparison to many other studies.*
>
> *I don't think these things should be done as control analyses, tucked away in the supplemental materials, but instead should be done as a part of the figures in the main text -- including decoding, RSA, cross-trial correlations, and RT correlations.*

Thank you for your suggestions. we have added the baseline period from 200 to 0 ms prior to the stimulus onset in all the stimulus-locked analyses and tested the significance with cluster-based permutation test (cluster-forming threshold $p < 0.001$, cluster-level $p < 0.05$, (Collins & Frank, 2018)) in all the analyses including decoding, RSA, cross-trial correlations and RT correlations. The results showed similar patterns, and they are all reported in the main text (please see all the figures and page 30-32 in the main text).

> *Other issues:*
>
> *Regarding the analysis of the within-trial correlation of RSA betas, and "Cai 2019" bias:*
>
> *The correction that authors perform in the revision -- estimating the correlation within the baseline time interval and subtracting this estimate from subsequent timepoints -- assumes that the "Cai 2019" bias is stationary. This is a fairly strong assumption, however, as this bias depends not only on the design matrix, but also on the structure of the noise (see the Cai paper), which can be non-stationary. No data were provided in support of stationarity. It seems safer and potentially more realistic to assume non-stationarity.*
>
> *This analysis was included in the supplemental material. However, given that the correlation analysis presented in the Results is subject to the "Cai 2019" bias, it would seem to be more appropriate to replace that analysis, rather than supplement it.*
>
> *Regardless, this seems to be a moot issue, given that the underlying decoders seem to be overfit to temporally structured noise (see point above regarding weakening of downstream analyses based on decoder bias).*

Thank you for this important point. We now replaced the previous control analysis with a new one that does not assume stationary noise structure (page 19 in the revised manuscript). In Cai et al (2019), the source of confound is the covariance between observations.

Specifically, as the observations in fMRI data are the BOLD signal at different time points, TSN can introduce covariance between nearby observations, which further biases the observed correlation between experimental conditions/trial types. In our case, the observations are decoding accuracy for different trial types. Thus, bias in the correlation may come from covariance between trial types. In this study, potential covariance between trial types includes the constrain that the decoding accuracy of all trial types adds up to 1 for a given trial (although we transformed the accuracy into logits prior to RSA, so the constrain may not hold), and the blocked design (as discussed above). Thus, to establish a baseline level of correlation between SC and SR representation strength, we took a similar shuffling approach as in Cai et al (2019) and randomly shuffled the trial types within each block. The reason to shuffle within each block is to preserve the covariance structure in the blocked design. We then repeated the same analysis using the shuffled data. The results of 10 shuffled analysis were averaged to form a baseline. Please note that (1) this control analysis was performed separately at each time point, hence removing the assumption of stationary noise structure, (2) this analysis also included as noise any covariance introduced by the proactive cognitive control guided by the learned SC and SR associations (see response to comment 1), thus it is more stringent than intended and (3) this control analysis started from decoding and was intended to provide a baseline for all downstream analysis. As shown in figures 2A, 3A, 7C and 8C, the reviewer was correct that the bias was not stationary, as the baseline of correlation coefficient varies over time. Additionally, the SC-SR representation strength correlation remained significantly above baseline between ~100 and ~ 450 ms following stimulus onset and between -180 and + 50 ms relative to response, suggesting that the noise structure (even when including potential proactive cognitive control) cannot fully explain the observed the SC-SR representation strength correlation. Considering the fact that this control analysis treated proactive control as a source of confound, this result does not necessarily contradict the absence of distance effect reported above.

> *Outliers and t-values:*
>
> *More outliers with beta coefficients could be because the original SD estimates from the t-values are influenced more by extreme values. When you use a threshold on the median absolute deviation instead of mean +/-SD, do you still get more outliers with beta coefficients vs t-values?*

Thank you for your suggestion. We calculated the proportion of outliers with a threshold of median absolute deviation (defined as values beyond median ± 5 median absolute deviation) for each subject. The outliers remained less frequent for t-values than for beta coefficients (t-values: mean = 1.08%, SD = 0.12%; beta-values: mean = 4.45%, SD = 0.28%). Based on these results and to maintain consistent with previous studies employing the methods (Cellier et al., 2022; Kikumoto & Mayr, 2020; Kikumoto et al., 2022a; Kikumoto et al., 2022b; Rangel et al., 2023), we still decided to stay with t-values.

> *Random slopes:*
>
> *Were random slopes (by subject) for all within-subject variables included in the LMMs? If not, please include them, and report this in the Methods.*

Thank you for your suggestion. The model failed to converge with random slopes of all variables. Thus, we chose not to add random slopes in the LMM. But we have added the random effects structure in the methods (see page 34).

> ***Reviewer #2 (Public review):***
>
> *Summary:*
>
> *In this EEG study, Huang et al. investigated the relative contribution of two accounts to the process of conflict control, namely the stimulus-control association (SC), which refers*

> *to the phenomenon that the ratio of congruent vs. incongruent trials affects the overall control demands, and the stimulus-response association (SR), stating that the frequency of stimulus-response pairings can also impact the level of control. The authors extended the Stroop task with novel manipulation of item congruencies across blocks in order to test whether both types of information are encoded and related to behaviour. Using decoding and RSA they showed that the SC and SR representations were concurrently present in voltage signals and they also positively co-varied. In addition, the variability in both of their strengths was predictive of reaction time. In general, the experiment has a sold design and the analyses are appropriate for the research questions.*
>
> *Strength:*
>
> *(1) The authors used an interesting task design that extended the classic Stroop paradigm and is effective in teasing apart the relative contribution of the two different accounts regarding item-specific proportion congruency effect.*
>
> *(2) Linking the strength of RSA scores with behavioural measure is critical to demonstrating the functional significance of the task representations in question.*
>
> *We thank you for acknowledging our work on design and brain-behavior analysis. We have addressed all your concerns raised below point by point.*
>
> *Weakness:*
>
> *(1a) The distinction between Phase 2 and Phase 1&3 behavioral results, specifically the opposite effect of MC/MI in congruent trials raises some concerns with regard to the effectiveness of the ISPC manipulation. Why do RTs and error rates under MC congruent condition in Phase 2 seem to be worse than MI congruent?*

Thank you for raising these issues. In Phase 1, one color set (red and blue) was assigned to the MC condition, whereas another color set (yellow and green) was assigned to the MI condition. In Phase 2, these assignments were flipped, and they were flipped back again in Phase 3. Thus, the MC condition consisted of red and blue in Phases 1 and 3 but yellow and green in Phase 2, whereas the MI condition consisted of yellow and green in Phases 1 and 3 but red and blue in Phase 2 (Fig. 1b in the manuscript). This manipulation leads to seemingly opposite patterns between Phases 1 & 3 and Phase 2.

However, when considering specific colors, the pattern is consistent across phases. In Phase 2, RTs and error rates for yellow and green (MC congruent) were worse than those for red and blue (MI congruent), which mirrors the pattern observed in Phases 1 and 3, where RTs and error rates for yellow and green (MI congruent) were worse than those for red and blue (MC congruent)

We interpreted the results in Phase 2 as reflecting a typical ISPC effect, which is defined as a smaller conflict effect in the MI condition (MI incongruent – MI congruent) compared with the MC condition (MC incongruent – MC congruent). To our knowledge, the ISPC paradigm does not impose a specific prediction regarding the relative difference between MC-congruent and MI-congruent conditions.

> *(1b) Could there be other factors at play here, e.g. order effect?*

We agree that order effect could play a role, such that memory from Phase 1 may influence the pattern in phase 2. For example, in phase 1, yellow and green were assigned to the MI condition, and participants therefore have associated these colors with a high control state (SC) and incongruent responses (SR). These prior associations could interfere with the newly learned mappings in Phase 2, where yellow and green were reassigned to the MC congruent condition (i.e., low control state and congruent responses). As a result, memory from Phase 1

may have weakened the expected MC in phase 2. A similar effect could also apply to the MI condition. Consequently, the same condition does not show parallel performance between phase 1 and phase 2, which may lead to different patterns in the difference between MC congruent and MI congruent conditions in phase 2.

> *(1c) How does this potentially affect the neural analyses where trials from different phases were combined?*

Thank you for the question. As we mentioned above, the order effect could slow down the newly learned associations. However, we still found the ISPC effect in each phase, suggesting that all kinds of both SC and SR associations were formed and could be applied to the decoding and the following analyses cross phases. Relatedly, there might be confounded with temporal structured noise (TSN) when the neural analyses on decoding were combined the trials from different phases. However, we have performed the control decoding analyses and distance effect tests and confirmed that our decoding results were not driven by TSN (Please see comment #1 of R1).

> *(1d) the manuscript does not mention whether there is counterbalancing for the color groups across participants, so far as I can tell.*

Thank you for the reminder. We have balanced the color groups by randomly dividing the participants into two groups and assigning different color sets to each group. The related interpretations have been included in task overview of the revised manuscript (page 6), which reads:

"The color groups were counterbalanced across participants by red and blue as the color set of MC in one group while as the color set of MI in another group in the phase 1."

Recommendations for the authors:

> ***Reviewer #2 (Recommendations for the authors):***
>
> *I commend the authors for addressing and clarifying my previous questions. One new comment regarding the newly added Figure 9: the response-locked behavioral correlation is much weaker compared to the stimulus-locked one, even never reaching the significance level. I think this difference should be discussed instead of simply glossing over it.*

Thank you for your suggestion. We discussed the difference in the discussion of revised manuscript (page 25), which reads:

"Note that we found the negative prediction of the strength of SC and SR to RTs did not reach statistical significance with response-locked analysis as stimulus-locked analysis. It is possible that SC and SR representations have occurred before the stage of response processing, which is usually aligned with stimulus onset (Jiang et al., 2020a; Kang & Yu-Chin, 2024; Khan et al., 2025)"

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