Neural evidence of switch processes during semantic and phonetic foraging in human memory

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Humans may retrieve words from memory by exploring and exploiting in "semantic space" similar to how nonhuman animals forage for resources in physical space. This has been studied using the verbal fluency test (VFT), in which participants generate words belonging to a semantic or phonetic category in a limited time. People produce bursts of related items during VFT, referred to as "clustering" and "switching." The strategic foraging model posits that cognitive search behavior is guided by a monitoring process which detects relevant declines in performance and then triggers the searcher to seek a new patch or cluster in memory after the current patch has been depleted. An alternative body of research proposes that this behavior can be explained by an undirected rather than strategic search process, such as random walks with or without random jumps to new parts of semantic space. This study contributes to this theoretical debate by testing for neural evidence of strategically timed switches during memory search. Thirty participants performed category and letter VFT during functional MRI. Responses were classified as cluster or switch events based on computational metrics of similarity and participant evaluations. Results showed greater hippocampal and posterior cerebellar activation during switching than clustering, even while controlling for interresponse times and linguistic distance. Furthermore, these regions exhibited ramping activity which increased during within-patch search leading up to switches. Findings support the strategic foraging model, clarifying how neural switch processes may guide memory search in a manner akin to foraging in patchy spatial environments.

foraging | memory search | verbal fluency | hippocampus | cerebellum

Efficient storage and retrieval of information from memory are critical for adaptive human behavior. Just as animals forage for resources such as food and mates by strategically deciding where, when, and how to search in physical space, a growing body of research is probing the question of whether humans retrieve information from memory by employing similar strategies to search in "semantic space" (1, 2).

An experimental task conducive to studying these cognitive search strategies is the verbal fluency test, in which people name as many distinct items as possible belonging to a particular category (e.g., animals, foods), or beginning with a particular letter (e.g., F, S), in a limited time. In this task, people tend to "cluster" or produce a burst of semantically and/or phonetically related responses, and then "switch" to a new cluster (3–5). Through an evolutionary foraging lens, these strategies have been viewed as local "exploitation" of patches of words in semantic space, producing related items until that patch has been depleted, interspersed with strategically timed global "exploration" to find new patches (6). Moreover, better verbal fluency test performance has been associated with greater adherence to the Marginal Value Theorem (MVT) of optimal foraging theory (7). Specifically, people who produced more responses tended to leave local patches to explore new ones closer to the optimal point, when their current interitem response time approached their overall average response time (6). Bridging these fields of behavioral ecology and experimental psychology inspires novel research questions, including how cognitive search mechanisms vary in the presence of psychopathology (8–10).

However, there is debate as to whether search for related items in memory is better explained by foraging processes with strategically timed switches or by undirected random walk models without strategic switches. Past studies have found random walk models of memory search to produce results similar to human behavior in a range of word-based tasks. Some of these models simply generate the next word based on a local step from the previous word, as in an uncontrolled "naïve random walk" model of creative search on a semantic network (11). Other random walk models incorporate occasional more distant switches or jumps in addition to the local steps; for instance, a model for solving Remote Associates Tests used a random walk with probabilistic switches back to cue words (12). Notably, these switches or jumps are themselves randomly generated (e.g., occurring with

Significance

Efficient storage and retrieval of information from memory are critical for adaptive behavior. There is debate as to whether humans search their memories using i) foraging strategies similar to how animals explore and exploit patches of resources such as food when searching in physical space or ii) nonstrategic random walk processes. We used neuroimaging to measure brain activity while participants performed time-limited semantic and phonetic word retrieval search tasks. Hippocampal and cerebellar activation was greater while switching (exploring) to new word groupings than while clustering (exploiting) within patches of related words, and this activity increased leading up to decisions to switch. Findings provide neural evidence of strategically timed switches during memory search, suggesting continuity between foraging in space and mind.

some fixed probability defined by the model). These types of random walk models have also been tested using category fluency test data. One study demonstrated that including some amount of random switching in a random walk model of category fluency improved its ability to reach parts of representational space more quickly (13). Other studies have found that a random walk model both with and without randomly occurring jumps could produce apparent clustering and switching behavior in category fluency search (14, 15).

In contrast to the random walk models of memory search with or without randomly occurring switches, the strategic foraging model (6) can be thought of as local random walks (or instances of spreading activation; ref. 16) that are punctuated at strategically determined (nonrandom) points by global jumps or switches to more distant parts of the semantic space. Specifically, the foraging model proposes that behavioral switches between semantic clusters occur when a cognitive process which monitors search success detects a relevant decline in performance, triggering the searcher to seek new resource clusters after the previous one has been depleted (i.e., aligning with the MVT; ref. 7). Abbott and colleagues (15) argued against this strategic foraging framework, as their random walk models with and without randomly occurring jumps produced verbal fluency output that broadly aligned with predictions of the MVT, such that simulated participants who left patches earlier or later than specified by their average response time produced fewer responses overall. However, the conclusions of Abbott et al. have been challenged by 1) the argument that the free associations data composing the chosen semantic network had embedded representations which closely align with verbal fluency search mechanisms (17), as well as by 2) direct model comparisons holding constant the semantic representations, which demonstrated a sizable advantage for the foraging model over the random walk model without strategic jumps (ref. 18; see also refs. 19–21 regarding the representation on which the search operates).

Taken together, at issue is whether strategic cognitive mechanisms such as foraging behavior that evolved to search efficiently for resources in external spatial environments have been repurposed for similar searches in internal informational environments (22). The present study used functional MRI (fMRI) during memory search to test whether patterns of brain activation align with strategically timed switches or with random walk processes without strategic switches. We characterized phases of local (clustering) and global (switching) memory search in overt (spoken) verbal fluency response sequences in several ways, including using computational metrics of semantic and phonetic similarity and participants' post hoc evaluations of the relatedness of their successive responses. We initially analyzed category and letter fluency data responses separately, as these tasks have been shown to have distinct mechanisms (e.g., free-associative processes in category fluency versus potentially greater executive functioning demands and intentional suppression of semantic activations in letter fluency; ref. 23). We further analyzed category and letter fluency responses together in the same model as the tasks also have shared processes (e.g., self-monitoring; refs. 23–25). This enabled us to test whether aspects of semantic and phonetic search could be controlled by the same higher-level strategic search process, specifically one which monitors success in searching locally for the next relevant item and decides when to switch to global exploration when success drops.

We first tested whether neural activation in any brain region differed while participants were switching compared to clustering. If the strategic foraging model (6) best fit the data, we expected differences in brain activity during behaviorally defined switching compared to clustering, as these are posited to be distinct cognitive events of exploring for a new patch versus exploiting a local patch.

In contrast, if a simple random walk model without switches (14, 15) best fit the data, we would expect no neural differences between these event types, as each item retrieval would correspond to the same kind of step on a network or in a space.

Second, if we found distinct neural activity while participants were switching compared to clustering, we planned follow-up models to test whether significant switch-related activation could be fully accounted for by longer search times (i.e., interitem response times, or IRTs; see refs. 26 and 27) or longer steps (i.e., greater computational semantic or phonetic distance between responses). While we expected IRT and linguistic distance to strongly relate to switching (in fact these metrics are often used to define switches; refs. 4 and 6), finding activation even after controlling for these continuous variables associated with steps on a random walk would further support the presence of distinct switches in memory search. This result could indicate either foraging-like decisions to switch to new patches in memory at strategic points or nonstrategic random walk processes with randomly occurring switches or jumps.

Third and finally, to distinguish between strategic foraging and random walks with randomly timed switches, we tested for the presence of neural activity which ramped up during local within-cluster search leading up to switch events and then reset to a lower level for the next search (28). We posit that this type of activation would provide further evidence for strategically generated switches guided by a neural process which monitors the success of resource accumulation (verbal fluency item retrieval). This prediction was motivated by the cognitive control literature, in which performance monitoring typically entails the presence of a representation of past events and signals that indicate that additional effort is needed in cases of suboptimal performance (29–32). In the case of cognitive foraging, we hypothesized that increasing neural activation during each within-patch search could represent increases in working memory load and/or signals indicating a failure to generate the next unique similar response with the expected speed and ease, which ultimately triggers a switch to a new patch (33–37).

If search for related items in memory is based in strategic foraging mechanisms involving active monitoring of response generation, which brain regions may be critical for signaling decisions to explore and exploit? Based on previous research, our hypothesized regions included the cingulate cortex, hippocampus, and posterior cerebellum.

Neural correlates of cognitive foraging have rarely been examined in the context of memory search but are frequently studied in risky decision-making and reward research, often pointing to a crucial role of the cingulate cortex. Studies in nonhuman primates have found that increased neuronal spiking activity in the anterior and posterior cingulate predicts reward-based motor selection and exploration away from the current search strategy (28, 38), as well as evaluation of rewards not received after a decision has been made (39). Reward-based decision-making fMRI studies in humans have also found that the dorsal anterior cingulate cortex plays an important role in foraging, though whether this region tracks monitoring of the cost and value of foraging (40, 41) or choice difficulty (42, 43) is debated.

The hippocampus is another candidate region that may be involved in memory search foraging given its well-established functions in memory consolidation, retrieval, spatial navigation via cognitive maps (44, 45), and more recently semantic memory (46). Hippocampal activation has been reported during verbal fluency test performance compared to control conditions (47–51), and it may specifically aid in memory search foraging via monitoring and signaling memory-based prediction errors (52) and

recruiting autobiographical and episodic memory to assist semantic retrieval (53).

An often-overlooked brain region that may also subserve coordination during memory search foraging is the cerebellum. Posterior cerebellar activation is commonly associated with verbal fluency test performance (47, 54, 55) but is rarely discussed in depth despite evidence of its association with fluid cognitive and linguistic functions beyond motor control (56, 57). The cerebellum is theorized to serve as a regulator of precise timing systems (58) as well as a computational predictor of future states by forming and updating internal models via error learning (59) and detecting deviations from expected sequences (60). Accordingly, the cerebellum's role during memory search could be to monitor the retrieval of responses and signal to cortical and subcortical regions when the expected outcome is violated (i.e., when one runs out of related words to say), triggering the switch to a new patch.

Of note, in two small fMRI studies examining neural correlates of verbal fluency strategy usage, regions including the inferior frontal gyrus, cerebellar Crus I (54), and posterior parietal cortex (61), among several others, showed greater activation when participants indicated that they were switching compared to clustering. However, the brief (15 to 30 s), nonverbalized, and constrained (in some cases forced switching and clustering) nature of these tasks precluded a comprehensive understanding of the neural correlates of more natural cognitive search processes.

Overall, we hypothesized that results would provide support for strategic foraging during verbal fluency test performance, evidenced by brain activation differences between switching and clustering and a switch-related neural monitoring process. Specifically, we predicted that regions including the anterior cingulate cortex, hippocampus, and posterior cerebellum (e.g., lobule VI, Crus I–II) would show switch-related activation not fully accounted for by

search time and linguistic distance between responses, as well as within-cluster ramping activation leading up to switch events.

Results

Verbal Fluency Test Performance and Strategies. Participants produced an average of 44 correct responses in 3-min category fluency tests and 34 correct responses in 3-min letter fluency tests. Fig. 1 depicts examples of the cluster and switch designation methods for selected participants. Concordance between similarity-based and participant-designated clusters and switches was approximately 60% overall (*SI Appendix*). Responses to the open-ended search strategies questionnaire were summarized and grouped into themes (*SI Appendix,* Table S8). When asked to describe their task strategies, most participants spontaneously reported using strategies akin to clustering and switching. Additionally, some participants reported remembering personal life experiences, employing visual imagery tactics (e.g., picturing a map), and imagining they were walking around or searching a physical space (e.g., the zoo, their refrigerator). Participants reported working to jump to new categories slightly more than smoothly moving from one item to the next ($M = 6.25$, $SD = 1.64$, on a 1 = smoothly moving to 10 = effortful jumping scale).

fMRI Clustering and Switching Models. Preliminary event-related analyses comparing verbal fluency conditions to the spoken control condition showed widespread activation across temporal, frontal, cerebellar, parietal, occipital, and subcortical areas (see *SI Appendix,* Figs. S15–S20 and Table S9 for further detail and comparisons between category and letter fluency). Here, we focus on the general linear models comparing switch- and cluster-related activation.
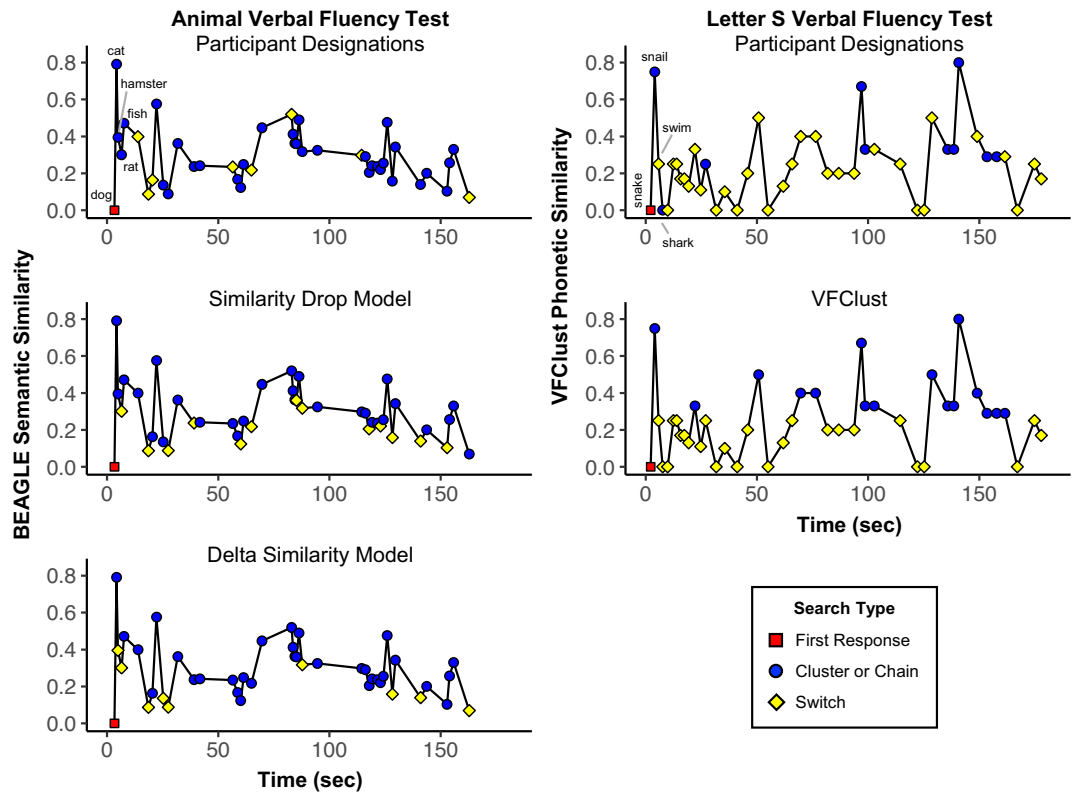

Fig. 1. Verbal fluency responses produced by two selected participants over 3-min task periods. Separate plots illustrate different methods of designating switch- and cluster-related responses.

First, we describe results from the participant-designated models, in which responses were coded as cluster-related or switch-related based on participants' post hoc evaluations of when they think they switched between groupings of related responses. The Switch–Cluster contrast for the category fluency model revealed significant activation in the bilateral anterior hippocampus extending into the right amygdala (Fig. 2 and Table 1); no significant activation emerged in the letter fluency model or in the Cluster–Switch contrasts for either. In the combined participant-designated category and letter fluency model, the Switch–Cluster contrast showed significant activation peaking in the bilateral hippocampus and amygdala (including the parahippocampal gyrus), right insula, and left inferior frontal gyrus, among others. The Cluster–Switch contrast in this same model showed significant activation peaking in the left precuneus ($k_E = 101$, $t = 4.41$, MNI = $-4, -56, 24$). Follow-up analyses confirmed that search type (switching versus clustering) did not significantly interact with verbal fluency test type in the combined category and letter fluency model (*SI Appendix*).

Next, we describe results from the similarity-based models, in which responses were coded as cluster-related or switch-related based on thresholds of semantic or phonetic similarity between consecutive responses (using similarity drop, delta similarity, and VFClust models). The Switch–Cluster contrast in the category fluency delta similarity model showed activation in the cerebellar-specific SUIT analysis in the left posterior cerebellum (peak voxels in Crus I–II and lobule VI–Crus I; Fig. 2), whereas no significant switch- or cluster-specific activation emerged in the category fluency similarity drop model. In the letter fluency VFClust model, the Switch–Chain ("chain" is the VFClust term for cluster) contrast showed significant activation peaking in the left superior medial gyrus, left precuneus/middle cingulate cortex, posterior cerebellum (bilateral Crus I–II, lobule VIIIa vermis), and the right anterior cingulate cortex. None of the
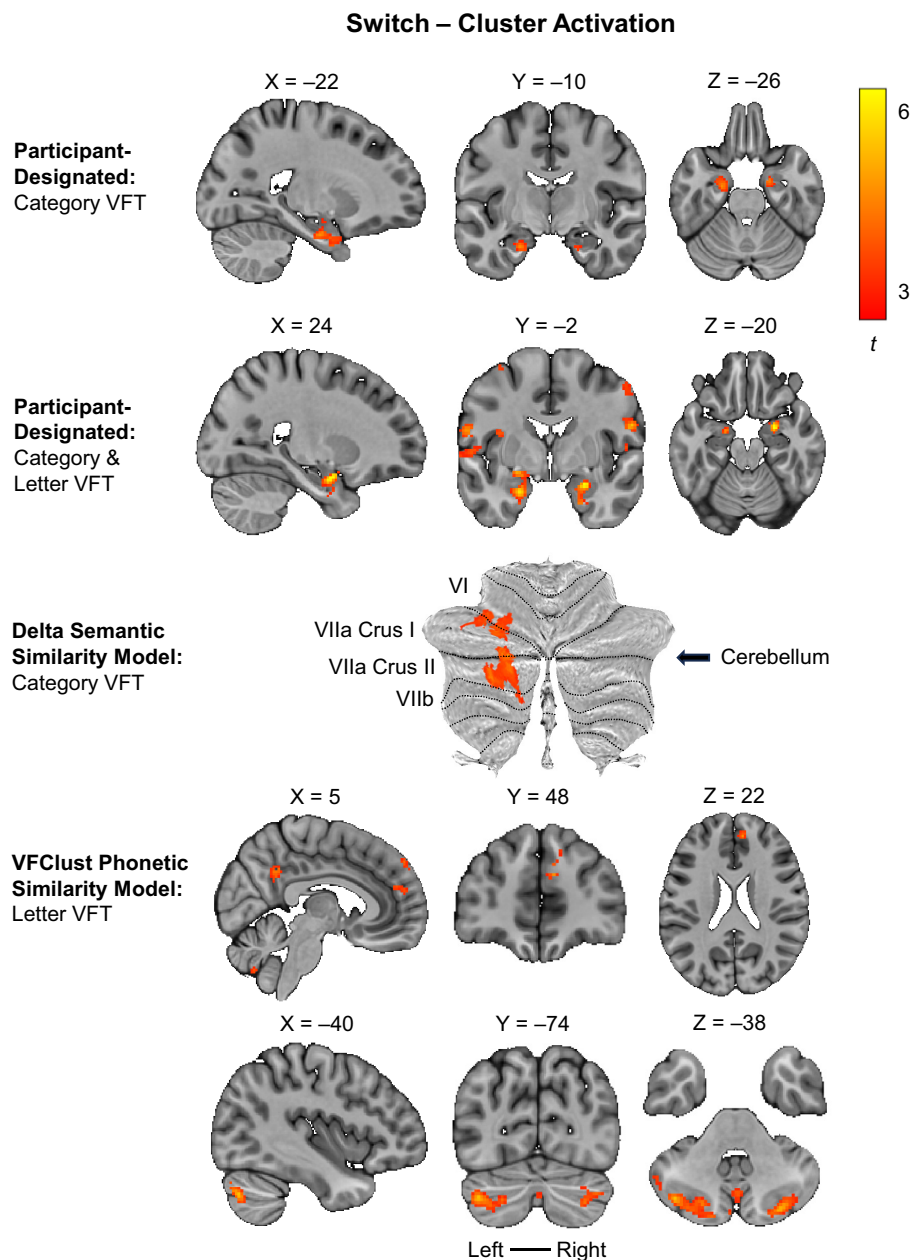

Fig. 2. Significant fMRI activation during verbal fluency test (VFT) performance from Switch–Cluster contrasts. Separate rows illustrate results from models which differ by method of cluster and switch designation.

Table 1. Switch–Cluster fMRI activation across different switch and cluster designation methods

VFT type	Switch designation	Analysis	MNI coordinates	Cluster size	t	Peak region	Side
Category	Participant	Whole brain	24 –2 –22	90	5.52	Amygdala, hippocampus	R
			–22 –10 –26	138	4.64	Hippocampus	L
		SUIT	–	–	–	–	–
	Delta similarity model	Whole brain	–	–	–	–	–
		SUIT	–20 –72 –35	156	5.07	Cerebellar lobule VIIa Crus I, Crus II	L
			–32 –72 –23	77	4.37	Cerebellar lobule VIIa Crus I, lobule VI	L
Letter	VFClust	Whole brain	–8 44 52	97	6.37	Superior medial gyrus	L
			–2 –48 36	198	5.92	Precuneus, middle cingulate cortex	L
			–2 56 36	235	5.79	Superior medial gyrus	L
			–40 –74 –38	540	5.28	Cerebellar lobule VIIa Crus I	L
			30 –80 –38	253	5.07	Cerebellar lobule VIIa Crus I	R
			8 48 22	80	4.66	Anterior cingulate cortex	R
			2 –70 –38	88	4.06	Cerebellar vermis lobule VIIIa	–
		SUIT	–28 –78 –43	573	5.64	Cerebellar lobule VIIa Crus II	L
			22 –86 –43	308	5.32	Cerebellar lobule VIIa Crus II	R
Category and Letter	Participant	Whole brain	24 –2 –20	148	6.69	Amygdala, hippocampus	R
			36 –12 20	189	5.98	Insula	R
			–52 –10 18	779	5.78	Postcentral gyrus	L
			–22 –2 –26	256	5.68	Amygdala, parahippocampal gyrus	L
			–54 12 –2	135	5.04	Inferior frontal gyrus (p. opercularis)	L
			–42 –8 58	82	4.63	Precentral gyrus	L
			–60 –38 14	108	4.57	Superior temporal gyrus	L
			12 –68 34	84	4.52	Precuneus, cuneus	R
			46 –10 42	146	4.47	Precentral gyrus	R
		SUIT	2 –30 –29	195	6.13	Brain stem	R

Note: VFT = verbal fluency test.

similarity model-based analyses showed significant Cluster–Switch activation.

fMRI Models Including Interitem Response Time and Linguistic Distance. Models including interitem response time (IRT), semantic distance, and phonetic distance showed widespread activation loading on these regressors (*SI Appendix,* Figs. S21–S24 and Tables S10 and S11). Of note, in the cerebellar-specific analyses, semantic distance was associated with activation peaking in bilateral lobule VI and right Crus I–II, whereas phonetic distance was associated with more posterior cerebellar activation peaking in right Crus II and vermis lobule VIIIa (*SI Appendix,* Fig. S25).

To test whether switch-related activation could be fully explained by continuous processes such as longer search times and greater linguistic distance, we added regressors of IRT and semantic and/or phonetic distance to the switching versus clustering models described above. Activation in the Switch–Cluster and Cluster–Switch contrasts in these models accounting for IRT and distance largely remained significant in regions identified in the original models (*SI Appendix,* Figs. S26–S30 and Tables S12 and S13), indicating that switch-related activity corresponded to more than

just instances of greater IRT or linguistic distance. A few differences were as follows. In the follow-up category fluency participant-designated switch model, Switch–Cluster activation remained significant in the left parahippocampal gyrus but not in the right hippocampal region. In the follow-up category fluency delta similarity model, Switch–Cluster posterior cerebellar activation (peaking in lobule VI and Crus I) reached significance in the whole brain analysis in addition to the cerebellar-specific SUIT analysis. Finally, in the follow-up letter fluency VFClust model, Switch–Chain activation was no longer significant in the anterior cingulate cortex.

fMRI Switching Ramp Models. In analyses modeling neural activation linearly ramping up during cluster events and resetting at switch events, the category fluency participant-designated switch model showed significant activation in the left parahippocampal gyrus (Fig. 3 and Table 2). The model which collapsed across category and letter fluency participant designations showed significant ramping activation in the left inferior frontal gyrus, bilateral hippocampus and parahippocampal gyrus, right cerebellar lobule VI, left superior temporal gyrus, and brain stem. The letter
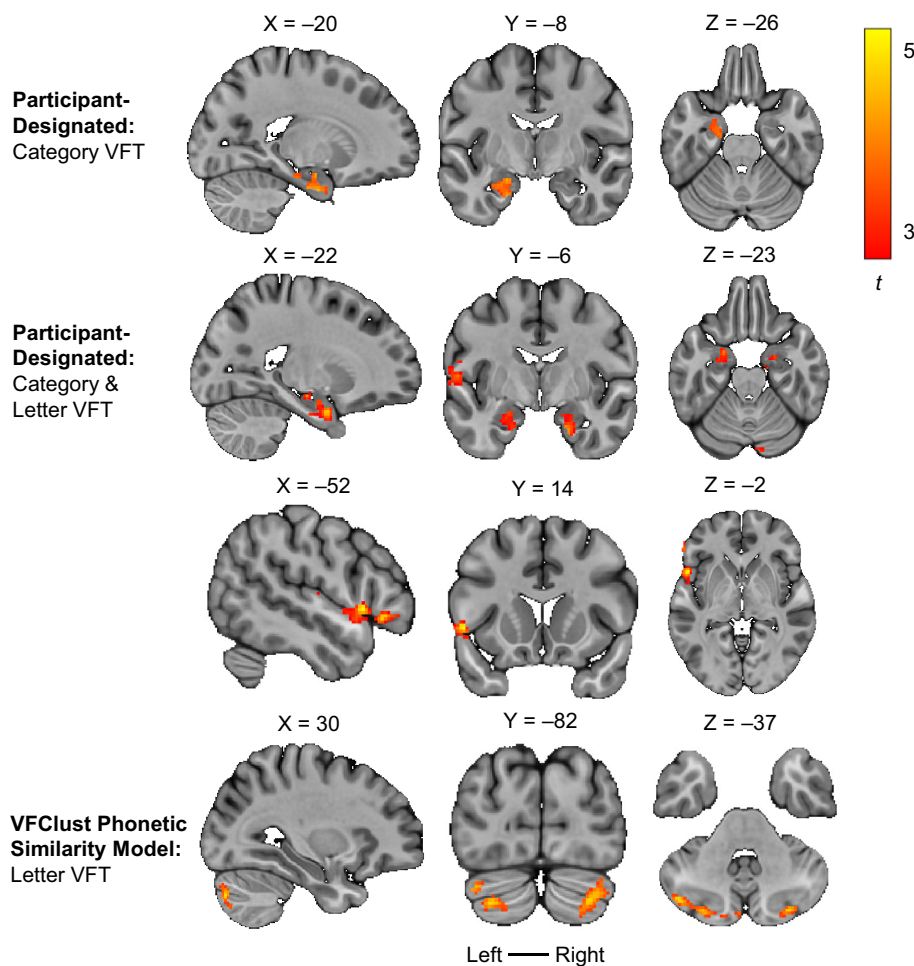
Activation Ramping up to Switches

Fig. 3. Significant fMRI activation during verbal fluency test (VFT) performance which loaded onto parametrically modulated regressors (PMRs) that increased linearly during cluster events and reset at switch events. Separate rows illustrate results from models which differ by method of cluster and switch designation.

fluency VFClust model showed ramping activation in bilateral posterior cerebellar Crus I–II, lobule VI, and the brain stem. Remaining switch designation models did not show significant ramping activation.

Discussion

This study provides neural evidence suggesting a strategic foraging process during human memory search for semantically and phonetically related words. We modeled category and letter VFT responses as distinct actions of exploration (switching) between and exploitation (clustering) within "patches" of related responses and found differences in brain activation between these search actions. Anterior hippocampal activation was greater during participant-designated switching compared to clustering, and posterior cerebellar activation was greater during similarity model-based switching compared to clustering. Greater switch-related activation using phonetic similarity-based designations was also detected in the superior medial gyrus, precuneus, and the cingulate cortex. Moreover, switch-related neural activity was not explained solely by a continuous change in linguistic distance or response time (i.e., likely not aligning with a simple random walk model with local steps and no switching). Finally, both hippocampal and cerebellar activation was shown to increase during within-patch

search and then reset once a switch occurred, suggesting a potential cognitive foraging monitoring process (i.e., likely not aligning with a random walk model with random switches; refs. 13 and 15). The present fMRI findings, in conjunction with participants' qualitative descriptions of engaging in effortful decisions to switch when running out of related items, suggest that individuals may use strategic monitoring and switching processes during memory search, potentially in combination with local random walk processes, akin to how animals forage for resources in physical space (2, 6, 22).

Participants' descriptions of strategies they used to generate verbal fluency responses aligned with those found in prior research (62), including a mixture of visual, semantic, and random strategies. Some of these strategies are consistent with producing items in local clusters (e.g., by locations or types). Participants' descriptions of switching when running out of items and reports of effortful jumping to new word groupings are consistent with (though not conclusive of) strategic switching upon patch depletion. Unsworth and colleagues (62) reached a similar conclusion, interpreting their study findings to mean that participants engaging in verbal fluency tests were likely dynamically alternating between using passive or random retrieval and more directed and effortful retrieval throughout the task. Further studies should examine such subjective assessments of search strategies recorded in real time during task performance.

Table 2. fMRI activation ramping up to switch events across different switch and cluster designation methods

VFT type	Switch designation	Analysis type	MNI coordinates	Cluster size	t	Peak region	Side
Category	Participant	Whole brain	–20 –6 –30	174	4.44	Parahippocampal gyrus	L
		SUIT	–	–	–	–	–
Letter	VFClust	Whole brain	–44 –74 –40	347	5.18	Cerebellar lobule VIIa Crus I	L
			34 –84 –32	140	4.7	Cerebellar lobule VIIa Crus I	R
		SUIT	–28 –78 –45	163	5.73	Cerebellar VIIa Crus II	L
			30 –80 –47	262	5.05	Cerebellar VIIa Crus II	R
			–10 –30 –21	47	4.79	Brain stem	L
			14 –68 –15	51	4.66	Cerebellar lobule VI	R
			–34 –68 –25	44	4.23	Cerebellar lobule VIIa Crus I	L
Category and Letter	Participant	Whole brain	–52 14 –2	201	5.41	Temporal pole, inferior frontal gyrus (p. opercularis, p. triangularis)	L
			–18 –18 –16	171	5.24	Hippocampus	L
			14 –72 –16	140	5.11	Cerebellar lobule VI	R
			16 –14 –30	118	4.78	Parahippocampal gyrus	R
			–58 –6 8	181	4.36	Rolandic operculum, superior temporal gyrus	L
		SUIT	12 –24 –19	132	5.66	Brain stem	R
			–12 –28 –21	104	4.45	Brain stem	L

Note: VFT = verbal fluency test.

Hippocampal Regions. The switch-related and ramping hippocampal activation we observed may be driven by multiple possible mechanisms which are not mutually exclusive. The hippocampus is theorized to play a central role in prospection (63); hippocampal activity may reflect recall of past events to make projections about the future in the service of guiding ongoing behavior (64). Consistent with this notion, individuals with hippocampal damage retain general knowledge about the future but are unable to make predictions about specific future events involving themselves (63). The hippocampus may therefore be recruited during verbal fluency test performance to guide retrieval of future fluency responses by using information about recently retrieved items and recently visited patches in semantic memory.

The switch-related activation could also reflect an effortful generative process, such that the hippocampus engages when word generation reaches a threshold level of difficulty indicating that a switch to a new cluster in memory is needed. An approximately linear increase in hippocampal activity prior to a switch, as we found here, could reflect difficulty level in terms of greater working memory load, because each response (particularly within a patch of related responses) must be remembered to avoid repeating items. In support of this idea, recent work in humans has found such a parametric increase in hippocampal activity with larger working memory load (33). The ramping activity may also reflect increasing prediction errors (52), or mismatch between the expected successful outcome and the actual increasingly difficult time retrieving a correct response (e.g., due to not finding a nearby item or finding a repeated response).

As an alternative to or in conjunction with monitoring of effort or difficulty driving switching, the detected hippocampal activation may relate to probing autobiographical episodic memory during search (53). Almost half of the participants spontaneously reported recalling personal life experiences to generate responses when asked about their search strategies. Greater anterior hippocampal activation found at switching than clustering may suggest an increased effort to access episodic memory when running out of items within a patch (50). Relatedly, both the switch-related activation and the within-patch ramping activity in hippocampal regions could be associated with signaling event boundaries in episodic memory (with theorized mechanisms involving sharp-wave ripples), as hippocampal engagement has been reported when individuals transition to a new spatial location, movement, action, or goal (65–67). Future studies explicitly asking about autobiographical recall during different phases of search would contribute to the more specific mapping of these strategies onto patterns of neural activity.

Finally, our hippocampal findings can be interpreted alongside the semantic cognition literature. The Controlled Semantic Cognition (CSC) model posits a system including components of semantic representation and control (68). The parahippocampal gyrus is one "hub" of the hub-and-spoke model between a distributed, modality-specific semantic network and semantic control activation. Thus, we found activation in a hub of the CSC model of semantic cognition, which is where one would expect to find greater activation related to control processes that drive strategic semantic retrieval. Our results are consistent with these prior studies, but further work is required to discriminate among these candidate mechanisms of hippocampal involvement in switching during memory search.

Cerebellum. A growing body of evidence suggests that the cerebellum's well-established roles in precise timing, error correction, and constructing predictive models extend beyond the motor domain and into cognitive, linguistic, and affective

domains (58, 59, 69–74). Studies have revealed a distinct functional topography of the cerebellum. Broadly, anterior regions are more associated with sensorimotor functioning, and posterior regions are more associated with cognitive functioning (57, 75), likely through distinct closed-loop circuits (76). Consistent with this past research, in this study, the more purely motor-based spoken control condition was associated with anterior cerebellar activation (lobule V-VI; *SI Appendix,* Fig. S16), whereas the more cognitively involved processes during verbal fluency tests were associated with posterior cerebellar activation (lobule VI, Crus I–II).

The present study found that greater posterior cerebellar activation related to longer IRTs, greater semantic and phonetic distance, switching (even while accounting for IRT and distance), and ramping activity leading up to switches. Several potential mechanisms could explain the cerebellum's role in memory foraging, some of which overlap with previously studied functions of the hippocampus and cingulate cortex. We posit that exploration and exploitation within cognitive foraging involves an ongoing process of monitoring search success. The cerebellum may heavily contribute to this monitoring process, as this complex brain region is theorized to act as a comparator of current and predicted states via construction of internal models and error signaling, ultimately promoting the coordination of motor and cognitive actions (59, 60, 73, 74). This may be instantiated within memory foraging as cerebellar generation of an ongoing set of predictions about producing the next related verbal fluency response alongside increasing error signals that retrieval is becoming more difficult, ultimately catalyzing a switch to explore a new patch. Present lobule VI activation results in particular may be indicative of increasing working memory load (36), which is a critical component of verbal fluency-based search to avoid response repetition.

The cerebellum has also been implicated in autobiographical recall (77–79), which almost half of the present participants spontaneously described using as a search strategy. An activation likelihood estimation meta-analysis (78) found cerebellar Crus I to be reliably activated during retrieval from episodic memory. Moreover, the same study found that Crus I exhibited functional connectivity with areas including the hippocampus and parahippocampal gyri at rest and during task-based autobiographical memory retrieval in an independent sample. Interconnected functions of the cerebellum and hippocampus have also been found in rodent studies; in mouse models, impairing cerebellar functioning has led to disruptions in hippocampal-dependent foraging behavior and spatial working memory performance (80, 81). Therefore, while we found switch-related activation in the hippocampus or the cerebellum depending on how switching and clustering were operationalized, it is possible that these analyses revealed activation in different nodes of the same network.

Finally, it was interesting that semantic distance was associated with more anterior regions of the posterior cerebellum (e.g., lobule VI), and phonetic distance was associated with more posterior regions (e.g., Crus II). Future studies could test whether these findings replicate and help to further distinguish between candidate mechanisms of cerebellar contributions to memory foraging.

Cingulate Cortex. Robust evidence in the reward-based decision-making literature suggests a prominent role of the anterior and posterior cingulate in encoding foraging cost, value, and/or choice difficulty, and in driving switching or decisions to forage (28, 38, 40, 41, 43). Unexpectedly, cingulate cortex activation in the present study was not strongly implicated in verbal fluency switch-related processes. Activation in the anterior cingulate cortex was associated with letter fluency switching using phonetic similarity-based designations yet was not significant after accounting for IRT and phonetic distance. This may indicate that anterior cingulate cortex activation was related to switching signals, but that such signals were strongly associated with the between-patch distance or search time. It is also possible that cingulate activity more strongly relates to monitoring processes during foraging contexts with more salient risks such as gambling tasks, in contrast to the lower-risk context of memory search tasks.

Additional Brain Regions and Networks. A study using a compound remote associates task found that inferior frontal gyrus (IFG) and middle temporal gyrus (MTG) activation was correlated with search space extension (i.e., greater semantic distance between prime and solution words) (82). This finding aligns with ours, as we found that left IFG and MTG activation was associated with greater semantic distance and longer IRTs between fluency responses overall (*SI Appendix,* Tables S10 and S11 and Figs. S21–S23). Additionally, in the combined category and letter fluency participant-designated switching models, the left IFG showed within-patch ramping activation (Table 2 and Fig. 3), as well as switch-related activation while accounting for IRT and distance (*SI Appendix,* Table S12). The left MTG also showed switch-related activation while accounting for IRT and distance in the VFClust letter fluency model. These findings, alongside previous studies (83–86), illustrate the importance of the IFG and MTG in creative lexical search, controlled semantic retrieval, and strategic memory foraging.

Semantic cognition and memory retrieval are known to recruit an interconnected network of brain regions. A recent functional connectivity study (87) found that higher connectivity between the default mode and executive control networks uniquely predicted greater switching but not clustering between different meanings of a cue word in a polysemous verbal fluency test. This prior study also estimated participants' semantic memory structure using data from a relatedness judgment task (instructing participants to rate the semantic associations of word pairs from 0 to 100) and found that more efficient semantic networks related to greater switching. These findings demonstrate how interactions between controlled and spontaneous associative neural processes may promote creative linguistic search and provide valuable information for future investigations of semantic network characteristics that may enhance cognitive foraging behavior.

Limitations and Future Directions. This study had limitations that inform several future directions. The precise timing of each switch—whether it comes immediately after saying the last item in a cluster, or after a longer pause while the participant continues searching for another item in that cluster before giving up and exploring—likely varies within and across individuals and is not clearly distinguishable based on verbalized response onsets alone. To further isolate the switch process, future studies could have participants press a button when they have left a local patch and have started global search for a new patch (54). This could provide insight into switch timing but also may introduce distraction that disrupts the natural flow of cognitive search.

Another limitation relates to the determination of the similarity-based threshold at which one cluster ends and the next begins in the computational switch models. Specifically regarding semantic similarity thresholds, the similarity drop model (6) is useful in capturing local minima of relative similarity in a stream of responses, but is limited by its inability to designate immediately consecutive switch events when two or more items are dissimilar from each other and from the preceding and following

items. Consequently, the delta similarity model was created to attempt to address this problem. It is not clear that the delta similarity model performed better than the similarity drop model at capturing actual switch points, given its slightly lower match rate with participant-designated responses and its greater overlap of generated cluster and switch IRT distributions (*SI Appendix*). Yet the delta similarity model, and not the similarity drop model, revealed distinct switch-related neural activity. The delta similarity model could be tested further with different similarity thresholds (88) and training corpora (as well as semantic spaces from large language models) to evaluate its utility in characterizing semantic memory search processes.

This study used a variety of clustering and switching designation methods (e.g., participant report, computational similarity models), which generated some differing neural results. Because there is not yet a gold standard for when (or whether) switches occur during memory search, we analyzed and presented all of these plausible approaches, without necessarily expecting strong concordance between them. Additionally, the current similarity-based clustering and switching designation methods were distinct for category and letter fluency and did not account for instances in which participants may use combined semantic and phonetic information in their search (e.g., one participant said "sun, stars, Saturn" during the letter fluency test, apparently also using semantic cues; see ref. 89). Future studies could test novel methods for more comprehensively designating and predicting switches by combining sources of information such as semantic and phonetic similarity values (including participant-based ratings; ref. 87), participant reports of switches, and response times.

While we found evidence for both ramping and switching signals within the hippocampus and cerebellum, fMRI results are by nature correlational. Therefore, future work should evaluate whether these signals are causally driving switches using neuropsychological or neurostimulation methods. Lastly, participant responses absent in the text corpus used to train the BEAGLE semantic similarity model were replaced with approximations, in some cases resulting in a loss of cultural specificity (e.g., "tonkatsu" was replaced with "pork cutlet"). This highlights a broader issue that automated linguistic analysis must be scrutinized for cultural biases introduced via the selected text corpus and the way semantic similarity is defined (90).

Conclusions

Previous research has shown that when people search through memory during word retrieval tasks, they exhibit behavioral signatures of alternating between local exploitation of patches of related words and global exploration to find new patches (6), aligning with the Marginal Value Theorem of optimal foraging theory (7). In the present fMRI study using verbal fluency tests, hippocampal and posterior cerebellar regions showed greater activation while participants were switching between (exploring) compared to clustering within (exploiting) patches of similar words. Furthermore, these regions showed activity that increased during within-patch search leading up to switches, which may index a cognitive monitoring process. Present findings in conjunction with those of past studies offer support for the theory that people exhibit strategic foraging behavior during memory search (22). Future studies could build upon this work by directly comparing fMRI models of strategic and random switching and by incorporating deliberate nonrandom (i.e., strategic) switches into other models of memory search that have previously used probabilistic switches and jumps (12, 15). This work would further our understanding of the mechanisms of human memory search which promote adaptive behavior.

Methods

Methods are summarized below; see *SI Appendix* for further detail.

Participants and Procedures. Participants were recruited via flyers in the Bloomington, Indiana community. Inclusion criteria were being right-handed, 18 to 40 y old, and a native speaker of English. Exclusion criteria were a history of serious medical or neurological problems, self-reported psychiatric diagnosis, use of psychiatric medication, and MRI contraindications. Thirty participants were included (age M = 22 y old; 17 women; 13 men). Participants completed a demographics and history questionnaire and underwent structural and functional MRI; they were paid for their time. All participants provided informed consent and agreed to study procedures approved by the Indiana University Human Subjects Institutional Review Board.

Verbal Fluency Tests. Four fMRI runs each consisted of one 3-min category fluency test (participants were instructed to list different animals, cities, foods, or occupations), one 1-min control speaking condition (instruction to repeat the word "nothing" at one's own pace), one 3-min letter fluency test (instruction to list different words beginning with A, F, M, or S), 5-s stop sign periods, and 20-s fixation periods (*SI Appendix*, Fig. S1). The order of verbal fluency test types alternated between runs, and the order of domains was randomized per participant. White text or a stop sign image on a black background remained on the screen for the duration of each event. A FOMRI III™+ Optoacoustics microphone filtered out scanner noise and isolated participant speech. Experimenters audio recorded participants' verbal responses and transcribed them in real time. After scanning, participants completed a questionnaire about their strategy usage during the tasks. Response onsets were transcribed manually offline. IRTs were calculated as the duration between response onsets.

Semantic and Phonetic Similarity. Semantic representations for category verbal fluency responses were constructed using the Bound Encoding of the Aggregate Language Environment (BEAGLE) distributional semantics model (91), which is based in well-established principles of human associative memory (92). BEAGLE was trained on an extensive natural language corpus of fiction and nonfiction books across multiple genres (93). The cosine of the angle between multidimensional semantic memory vectors for two consecutive words was computed as a measure of their semantic similarity, with higher cosines corresponding to greater similarity (e.g., "cat" and "dog" would have a higher cosine than "cat" and "zebra"), with values ranging from 0 to 1. Context-based cosine similarity matrices were generated for all unique participant responses from each of the four category domains, and each item in participants' response streams was assigned the similarity value between that item and the following item. Semantic distances between consecutive responses were calculated as 1−similarity.

VFClust version 0.1.1 (94) with Python 2.7 was used to measure phonetic similarity of letter fluency responses. VFClust uses a modified version of the CMU Pronouncing Dictionary (version *cmudict.0.7a*) to translate words into compact phonetic representations and an automated representation generator for words not in the dictionary. All words were assigned representations. Then phonetic similarity was calculated for responses within each of the four letter domains using the edit distance method, which assigns similarity values equal to 1 minus the Levenshtein distance between two adjacent responses, normalized to the length of the longer response. Phonetic similarity scores ranged from 0 to 1, with higher values representing greater similarity (e.g., "anchor" and "Anchorage" are more phonetically similar than "anchor" and "accordion"). Phonetic distances between consecutive responses were calculated as 1−phonetic similarity.

Verbal Fluency Switch and Cluster Designations. Several methods were used to estimate when participants were switching and clustering during the verbal fluency tests based on their sequence of verbalized responses. The first switching designation method for both category and letter fluency responses used participants' subjective report. After fMRI, participants were shown a spreadsheet containing the temporally ordered list of responses they produced for each category and letter domain as transcribed by the experimenter. Participants were asked to place an X next to each response that they thought, in their own view, started a group of related responses. For analysis, responses marked with an X were designated as switch events and unmarked

responses were designated as cluster events. The next two switching designation methods for category fluency responses used BEAGLE semantic similarity values. The similarity drop model (6) designates responses that correspond to relative drops in similarity compared to adjacent responses as switches and the remaining responses as clusters. A delta similarity model was also developed for this study; transitions between search states occur when there is a sufficient decrease in similarity between successive items (indicating a transition from clustering to switching) or a sufficient increase in similarity (indicating a transition from switching to clustering). The final switching designation method for letter fluency responses used VFClust phonetic similarity values. VFClust uses empirically derived thresholds specific to each letter cue to classify successive responses with phonetic representations that meet or exceed the similarity threshold as falling within a phonetic "chain" (equivalent to our use of the term "cluster" or "patch") and responses that fall below the threshold as switches.

MRI Acquisition, Processing, and Analysis. Whole brain T1-weighted anatomical scans and four 8.5-min functional scans (repetition time: 2,000 ms) were collected on a Siemens 3T MRI system (Magnetom, Prisma Fit) with a 64-channel coil. fMRI data were processed using Statistical Parametric Mapping (SPM) version 12 (Wellcome Imaging Department, University College, London, UK). Functional images were slice time corrected, realigned, and co-registered to their corresponding anatomical image. Scans were warped to the Montreal Neurological Institute (MNI152) brain template for whole brain analysis. Cerebellar-specific analyses were also conducted using the Spatially Unbiased Infratentorial Template (SUIT; ref. 95) toolbox v3.4, including isolation and segmentation of the anatomical image cerebellum and brainstem followed by Dartel SUIT normalization of the functional images.[*] All functional images were resampled to $2 \times 2 \times 2$ mm^3 isovoxels and spatially smoothed with a 6mm full-width half-maximum Gaussian kernel.

fMRI analyses were performed in SPM12 using the general linear model. PMRs were z-scored. The canonical hemodynamic response function (HRF) was convolved with task-related regressors in first-level analyses. Motion parameters, high motion volumes (based on framewise displacement; ref. 96), and average z-scored ventricle signal (likely speech/breathing-related; refs. 97 and 98) were modeled but not convolved with the HRF. Second-level one-sample t-tests were conducted. Preliminary analyses examined activation related to generation of category and letter verbal fluency responses compared to control responses and to one another. 3dFWHMx and 3dClustSim in AFNI (99) were used to estimate activation significance thresholds of voxel-wise $P < 0.001$, cluster-corrected $P < 0.05$, $k_E = 78$ (whole brain) or $k_E = 34$ (cerebellar SUIT). Significant activation was visualized on an MNI standard template and cerebellar SUIT flatmap (100).

In the first stage of testing for neural evidence of a strategic foraging search process, models were constructed to compare activation associated with switching and clustering using the various designation methods. The onset of the switch or cluster event was designated as the onset of the verbal response preceding it to capture the neural activity associated with the search process, under the premise that once a participant verbalizes a response, they have begun another local or global search to find their next item. Separate models included cluster and switch events as designated by participant report (for category fluency, letter fluency,

and combined category and letter fluency responses), BEAGLE semantic similarity (similarity drop and delta similarity for category fluency responses), and VFClust phonetic similarity (for letter fluency responses).

Second, models were constructed to examine activation related to search time and linguistic distance. One model included PMRs of IRT on category and letter fluency response events. A second model included PMRs of semantic distance on category fluency response events and phonetic distance on letter fluency response events. Next, a set of models was constructed for each switch type as described above[†] with the addition of IRT and semantic and/or phonetic distance as PMRs on cluster and switch events to ascertain whether activation related to switching could be fully accounted for by search time or linguistic distance, rather than as a distinct switch-related effect.

Third, models were constructed to test whether neural activation increases in a ramping pattern during within-cluster search and resets at a switch. Ramps were modeled as PMRs on the main effect of category or letter fluency response for each switch designation method; positive loadings were examined. The bottom of the ramp started at the first event after a switch event, and the regressor heights linearly increased at each cluster event until reaching a fixed arbitrary maximum threshold of 1 at the following switch event (*SI Appendix*, Fig. S3).

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[*]Six participants were excluded from SUIT analyses due to insufficient cerebellar coverage during fMRI acquisition, leaving final sample sizes of $N = 30$ for whole brain analyses and $n = 24$ for cerebellar-specific analyses.

[†]The participant-designated letter fluency cluster and switch model was not included in this set of follow-up analyses because a high switch-to-cluster ratio resulted in parametrically modulated regressors not being uniquely specified for several participants.

1. P. M. Todd, T. T. Hills, T. W. Robbins, Eds., *Cognitive Search: Evolution, Algorithms, and the Brain* (MIT Press, 2012).
2. T. T. Hills, N. B. Lundin, M. Luthra, P. M. Todd, "Seeking inner knowledge: Foraging in semantic space" in *The Drive for Knowledge: The Science of Human Information Seeking*, I. Cogliati Dezza, E. Schulz, C. M. Wu, Eds. (Cambridge University Press, 2022), pp. 237–258.
3. W. A. Bousfield, C. H. W. Sedgewick, An analysis of sequences of restricted associative responses. *J. Gen. Psychol.* **30**, 149–165 (1944).
4. P. J. Gruenewald, G. R. Lockhead, The free recall of category examples. *J. Exp. Psychol. Hum. Learn.* **6**, 225–240 (1980).
5. A. K. Troyer, M. Moscovitch, G. Winocur, Clustering and switching as two components of verbal fluency: Evidence from younger and older healthy adults. *Neuropsychology* **11**, 138–146 (1997).
6. T. T. Hills, M. N. Jones, P. M. Todd, Optimal foraging in semantic memory. *Psychol. Rev.* **119**, 431–440 (2012).
7. E. L. Charnov, Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136 (1976).

8. N. B. Lundin *et al.*, Semantic search in psychosis: Modeling local exploitation and global exploration. *Schizophr Bull. Open* **1**, sgaa011 (2020).
9. L. J. Speers, D. K. Bilkey, Maladaptive explore/exploit trade-offs in schizophrenia. *Trends Neurosci.* **46**, 341–354 (2023).
10. C. Van den Driessche, F. Chevrier, A. Cleeremans, J. Sackur, Lower attentional skills predict increased exploratory foraging patterns. *Sci. Rep.* **9**, 10948 (2019).
11. Y. N. Kenett, J. T. Austerweil, "Examining search processes in low and high creative individuals with random walks" in *Proceedings of the 38th Annual Conference of the Cognitive Science Society*, A. Papafragou, D. Grodner, D. Mirman, J. C. Trueswell, Eds. (Cognitive Science Society, Philadelphia, PA, 2016), pp. 313–318.
12. D. D. Bourgin, J. T. Abbott, T. L. Griffiths, K. A. Smith, E. Vul, "Empirical evidence for Markov Chain Monte Carlo in memory search" in *Proceedings of the 36th Annual Meeting of the Cognitive Science Society*, P. Bello, M. Guarini, M. McShane, B. Scassellati, Eds. (Cognitive Science Society, Québec City, Canada, 2014), pp. 224–229.

13. J. Goñi et al., Switcher-random-walks: A cognitive-inspired mechanism for network exploration. Int. J. Bifurcation Chaos 20, 913–922 (2010).

14. J. T. Abbott, J. L. Austerweil, T. L. Griffiths, "Human memory search as a random walk in a semantic network" in Advances in Neural Information Processing Systems (Curran Associates Inc., 2012).

15. J. T. Abbott, J. L. Austerweil, T. L. Griffiths, Random walks on semantic networks can resemble optimal foraging. Psychol. Rev. 122, 558–569 (2015).

16. C. S. Q. Siew, spreadr: An R package to simulate spreading activation in a network. Behav. Res. 51, 910–929 (2019).

17. M. N. Jones, T. T. Hills, P. M. Todd, Hidden processes in structural representations: A reply to Abbott, Austerweil, and Griffiths (2015). Psychol. Rev. 122, 570–574 (2015).

18. J. E. Avery, M. N. Jones, "Comparing models of semantic fluency: Do humans forage optimally, or walk randomly?" in Proceedings of the 40th Annual Meeting of the Cognitive Science Society, C. Kalish, M. A. Rau, X. Zhu, T. T. Rogers, Eds. (Cognitive Science Society, Madison, WI, 2018), pp. 118–123.

19. T. T. Hills, Y. N. Kenett, Is the mind a network? Maps, vehicles, and skyhooks in cognitive network science. Top. Cogn. Sci. 14, 189–208 (2022).

20. A. A. Kumar, M. Steyvers, D. A. Balota, A critical review of network-based and distributional approaches to semantic memory structure and processes. Top. Cogn. Sci. 14, 54–77 (2022).

21. M. Marko, I. Riečanský, The structure of semantic representation shapes controlled semantic retrieval. Memory 29, 538–546 (2021).

22. P. M. Todd, T. T. Hills, Foraging in mind. Curr. Dir. Psychol. Sci. 29, 309–315 (2020).

23. M. Marko et al., Assessment of automatic and controlled retrieval using verbal fluency tasks. Assessment 30, 2198–2211 (2023).

24. J. M. Biesbroek et al., Shared and distinct anatomical correlates of semantic and phonemic fluency revealed by lesion-symptom mapping in patients with ischemic stroke. Brain Struct. Funct. 221, 2123–2134 (2016).

25. C. S. M. Schmidt et al., Dissociating frontal and temporal correlates of phonological and semantic fluency in a large sample of left hemisphere stroke patients. Neuroimage Clin. 23, 101840 (2019).

26. J. Carp, K. Kim, S. F. Taylor, K. D. Fitzgerald, D. H. Weissman, Conditional differences in mean reaction time explain effects of response congruency, but not accuracy, on posterior medial frontal cortex activity. Front. Hum. Neurosci. 4, 231 (2010).

27. J. Grinband et al., The dorsal medial frontal cortex is sensitive to time on task, not response conflict or error likelihood. Neuroimage 57, 303–311 (2011).

28. K. Shima, J. Tanji, Role for cingulate motor area cells in voluntary movement selection based on reward. Science 282, 1335–1338 (1998).

29. W. H. Alexander, J. W. Brown, Medial prefrontal cortex as an action-outcome predictor. Nat. Neurosci. 14, 1338–1344 (2011).

30. W. H. Alexander, J. W. Brown, A general role for medial prefrontal cortex in event prediction. Front. Comput. Neurosci. 8, 69 (2014).

31. W. J. Gehring, B. Goss, M. G. H. Coles, D. E. Meyer, E. Donchin, A neural system for error detection and compensation. Psychol. Sci. 4, 385–390 (1993).

32. J. H. Woo, H. Azab, A. Jahn, B. Hayden, J. W. Brown, The PRO model accounts for the anterior cingulate cortex role in risky decision-making and monitoring. Cogn. Affect. Behav. Neurosci. 22, 952–968 (2022).

33. E. Boran et al., Persistent hippocampal neural firing and hippocampal-cortical coupling predict verbal working memory load. Sci. Adv. 5, eaav3687 (2019).

34. T. S. Braver et al., A parametric study of prefrontal cortex involvement in human working memory. Neuroimage 5, 49–62 (1997).

35. G. Bush, P. Luu, M. I. Posner, Cognitive and emotional influences in anterior cingulate cortex. Trends Cogn. Sci. 4, 215–222 (2000).

36. M. P. Kirschen, S. H. A. Chen, P. Schraedley-Desmond, J. E. Desmond, Load- and practice-dependent increases in cerebro-cerebellar activation in verbal working memory: An fMRI study. Neuroimage 24, 462–472 (2005).

37. M. L. Meyer, R. P. Spunt, E. T. Berkman, S. E. Taylor, M. D. Lieberman, Evidence for social working memory from a parametric functional MRI study. Proc. Natl. Acad. Sci. U.S.A. 109, 1883–1888 (2012).

38. D. L. Barack, S. W. C. Chang, M. L. Platt, Posterior cingulate neurons dynamically signal decisions to disengage during foraging. Neuron 96, 339–347.e5 (2017).

39. T. C. Blanchard, B. Y. Hayden, Neurons in dorsal anterior cingulate cortex signal postdecisional variables in a foraging task. J. Neurosci. 34, 646–655 (2014).

40. J. W. Brown, W. H. Alexander, Foraging value, risk avoidance, and multiple control signals: How the anterior cingulate cortex controls value-based decision-making. J. Cogn. Neurosci. 29, 1656–1673 (2017).

41. N. Kolling, T. E. J. Behrens, R. B. Mars, M. F. S. Rushworth, Neural mechanisms of foraging. Science 336, 95–98 (2012).

42. A. Shenhav, M. A. Straccia, M. M. Botvinick, J. D. Cohen, Dorsal anterior cingulate and ventromedial prefrontal cortex have inverse roles in both foraging and economic choice. Cogn. Affect. Behav. Neurosci. 16, 1127–1139 (2016).

43. A. Shenhav, M. A. Straccia, J. D. Cohen, M. M. Botvinick, Anterior cingulate engagement in a foraging context reflects choice difficulty, not foraging value. Nat. Neurosci. 17, 1249–1254 (2014).

44. H. Eichenbaum, T. Otto, N. J. Cohen, The hippocampus–what does it do? Behav. Neural. Biol. 57, 2–36 (1992).

45. E. A. Solomon, B. C. Lega, M. R. Sperling, M. J. Kahana, Hippocampal theta codes for distances in semantic and temporal spaces. Proc. Natl. Acad. Sci. U.S.A. 116, 24343–24352 (2019).

46. M. C. Duff, N. V. Covington, C. Hilverman, N. J. Cohen, Semantic memory and the hippocampus: Revisiting, reaffirming, and extending the reach of their critical relationship. Front. Hum. Neurosci. 13, 471 (2019).

47. C. T. Gauthier, M. Duyme, M. Zanca, C. Capron, Sex and performance level effects on brain activation during a verbal fluency task: A functional magnetic resonance imaging study. Cortex 45, 164–176 (2009).

48. R. Halari et al., Comparable fMRI activity with differential behavioural performance on mental rotation and overt verbal fluency tasks in healthy men and women. Exp. Brain Res. 169, 1–14 (2006).

49. M. Pihlajamäki et al., Verbal fluency activates the left medial temporal lobe: A functional magnetic resonance imaging study. Ann. Neurol. 47, 470–476 (2000).

50. S. Sheldon, M. P. McAndrews, J. Pruessner, M. Moscovitch, Dissociating patterns of anterior and posterior hippocampal activity and connectivity during distinct forms of category fluency. Neuropsychologia 90, 148–158 (2016).

51. C. Whitney et al., Task-dependent modulations of prefrontal and hippocampal activity during intrinsic word production. J. Cogn. Neurosci. 21, 697–712 (2009).

52. M. L. Mack, B. C. Love, A. R. Preston, Building concepts one episode at a time: The hippocampus and concept formation. Neurosci. Lett. 680, 31–38 (2018).

53. S. Sheldon, M. Moscovitch, The nature and time-course of medial temporal lobe contributions to semantic retrieval: An fMRI study on verbal fluency. Hippocampus 22, 1451–1466 (2012).

54. E. A. Hirshorn, S. L. Thompson-Schill, Role of the left inferior frontal gyrus in covert word retrieval: Neural correlates of switching during verbal fluency. Neuropsychologia 44, 2547–2557 (2006).

55. S. Wagner, A. Sebastian, K. Lieb, O. Tüscher, A. Tadić, A coordinate-based ALE functional MRI meta-analysis of brain activation during verbal fluency tasks in healthy control subjects. BMC Neurosci. 15, 19 (2014).

56. J. D. Schmahmann, J. C. Sherman, The cerebellar cognitive affective syndrome. Brain 121, 561–579 (1998).

57. C. J. Stoodley, E. M. Valera, J. D. Schmahmann, Functional topography of the cerebellum for motor and cognitive tasks: An fMRI study. Neuroimage 59, 1560–1570 (2012).

58. R. Ivry, Cerebellar timing systems. Int. Rev. Neurobiol. 41, 555–573 (1997).

59. M. Ito, Control of mental activities by internal models in the cerebellum. Nat Rev Neurosci 9, 304–313 (2008).

60. M. Molinari et al., Cerebellum and detection of sequences, from perception to cognition. Cerebellum 7, 611–615 (2008).

61. J. M. Gurd et al., Posterior parietal cortex is implicated in continuous switching between verbal fluency tasks: An fMRI study with clinical implications. Brain 125, 1024–1038 (2002).

62. N. Unsworth, G. A. Brewer, G. J. Spillers, Strategic search from long-term memory: An examination of semantic and autobiographical recall. Memory 22, 687–699 (2014).

63. R. L. Buckner, D. C. Carroll, Self-projection and the brain. Trends Cogn. Sci. 11, 49–57 (2007).

64. A. Jahn, D. E. Nee, J. W. Brown, The neural basis of predicting the outcomes of imagined actions. Front. Neurosci. 5, 128 (2011).

65. D. K. Bilkey, C. Jensen, Neural markers of event boundaries. Top. Cogn. Sci. 13, 128–141 (2021).

66. G. A. Radvansky, J. M. Zacks, Event boundaries in memory and cognition. Curr. Opin. Behav. Sci. 17, 133–140 (2017).

67. T. W. Ross, A. Easton, The hippocampal horizon: Constructing and segmenting experience for episodic memory. Neurosci. Biobehav. Rev. 132, 181–196 (2022).

68. M. A. Lambon Ralph, E. Jefferies, K. Patterson, T. T. Rogers, The neural and computational bases of semantic cognition. Nat. Rev. Neurosci. 18, 42–55 (2017).

69. D. Gatti, T. Vecchi, G. Mazzoni, Cerebellum and semantic memory: A TMS study using the DRM paradigm. Cortex 135, 78–91 (2021).

70. A. LeBel, S. Jain, A. G. Huth, Voxelwise encoding models show that cerebellar language representations are highly conceptual. J. Neurosci. 41, 10341–10355 (2021).

71. P. Mariën, M. Manto, Eds., The Linguistic Cerebellum (Academic Press, 2016).

72. H. Nakatani, Y. Nakamura, K. Okanoya, Respective involvement of the right cerebellar Crus I and II in syntactic and semantic processing for comprehension of language. Cerebellum 22, 739–755 (2023).

73. N. Ramnani, The primate cortico-cerebellar system: Anatomy and function. Nat. Rev. Neurosci. 7, 511–522 (2006).

74. P. L. Strick, R. P. Dum, J. A. Fiez, Cerebellum and nonmotor function. Annu. Rev. Neurosci. 32, 413–434 (2009).

75. R. L. Buckner, F. M. Krienen, A. Castellanos, J. C. Diaz, B. T. T. Yeo, The organization of the human cerebellum estimated by intrinsic functional connectivity. J. Neurophysiol. 106, 2322–2345 (2011).

76. F. A. Middleton, P. L. Strick, Cerebellar projections to the prefrontal cortex of the primate. J. Neurosci. 21, 700–712 (2001).

77. N. C. Andreasen et al., The cerebellum plays a role in conscious episodic memory retrieval. Hum. Brain Mapp 8, 226–234 (1999).

78. D. R. Addis, E. E. J. Moloney, L. J. Tippett, R. P. Roberts, S. Hach, Characterizing cerebellar activity during autobiographical memory retrieval: ALE and functional connectivity investigations. Neuropsychologia 90, 80–93 (2016).

79. E. Svoboda, M. C. McKinnon, B. Levine, The functional neuroanatomy of autobiographical memory: A meta-analysis. Neuropsychologia 44, 2189–2208 (2006).

80. Y. Liu et al., Causal evidence for a role of cerebellar lobulus simplex in prefrontal-hippocampal interaction in spatial working memory decision-making. Cerebellum 21, 762–775 (2022).

81. L. Zhang et al., The cerebellum promotes sequential foraging strategies and contributes to the directional modulation of hippocampal place cells. iScience 26, 106200 (2023).

82. M. Becker, T. Sommer, S. Kühn, Inferior frontal gyrus involvement during search and solution in verbal creative problem solving: A parametric fMRI study. Neuroimage 206, 116294 (2020).

83. D. Badre, A. D. Wagner, Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia 45, 2883–2901 (2007).

84. J. Davey et al., Automatic and controlled semantic retrieval: TMS reveals distinct contributions of posterior middle temporal gyrus and angular gyrus. J. Neurosci. 35, 15230–15239 (2015).

85. C. J. Price, The anatomy of language: A review of 100 fMRI studies published in 2009. Ann. N Y Acad. Sci. 1191, 62–88 (2010).

86. C. Whitney, M. Kirk, J. O'Sullivan, M. A. Lambon Ralph, E. Jefferies, The neural organization of semantic control: TMS evidence for a distributed network in left inferior frontal and posterior middle temporal gyrus. Cereb. Cortex. 21, 1066–1075 (2011).

87. M. Ovando-Tellez et al., An investigation of the cognitive and neural correlates of semantic memory search related to creative ability. Commun. Biol. 5, 604 (2022).

88. C. Barattieri di San Pietro, C. Luzzatti, E. Ferrari, G. De Girolamo, M. Marelli, Automated clustering and switching algorithms applied to semantic verbal fluency data in schizophrenia spectrum disorders. Lang. Cogn. Neurosci. 38, 950–965 (2023).

89. A. A. Kumar, N. B. Lundin, M. N. Jones, "Mouse-mole-vole: The inconspicuous benefit of phonology during retrieval from semantic memory" in Proceedings of the 44th Annual Conference of the Cognitive Science Society, J. Culbertson, A. Perfors, H. Rabagliati, V. Ramenzoni, Eds. (Cognitive Science Society, Toronto, Canada, 2022), pp. 651–657.

90. K. Hitczenko, V. A. Mittal, M. Goldrick, Understanding language abnormalities and associated clinical markers in psychosis: The promise of computational methods. *Schizophr Bull.* **47**, 344–362 (2021).

91. M. N. Jones, D. J. K. Mewhort, Representing word meaning and order information in a composite holographic lexicon. *Psychol. Rev.* **114**, 1–37 (2007).

92. B. B. Murdock, A theory for the storage and retrieval of item and associative information. *Psychol. Rev.* **89**, 609–626 (1982).

93. B. T. Johns, R. K. Jamieson, The influence of place and time on lexical behavior: A distributional analysis. *Behav. Res. Methods* **51**, 2438–2453 (2019).

94. J. O. Ryan, S. Pakhomov, S. Marino, C. Bernick, S. Banks, "Computerized analysis of a verbal fluency test" in *Proceedings of the 51st Annual Meeting of the Association for Computational Linguistics*, H. Schuetze, P. Fung, M. Poesio, Eds. (Association for Computational Linguistics, Sofia, Bulgaria, 2013), pp. 884–889.

95. J. Diedrichsen, A spatially unbiased atlas template of the human cerebellum. *Neuroimage* **33**, 127–138 (2006).

96. J. D. Power, K. A. Barnes, A. Z. Snyder, B. L. Schlaggar, S. E. Petersen, Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *Neuroimage* **59**, 2142–2154 (2012).

97. J. P. Farthing *et al.*, False activation in the brain ventricles related to task-correlated breathing in fMRI speech and motor paradigms. *MAGMA* **20**, 157–168 (2007).

98. R. M. Birn, K. Murphy, D. A. Handwerker, P. A. Bandettini, fMRI in the presence of task-correlated breathing variations. *Neuroimage* **47**, 1092–1104 (2009).

99. R. W. Cox, AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Comput. Biomed. Res.* **29**, 162–173 (1996).

100. J. Diedrichsen, E. Zotow, Surface-based display of volume-averaged cerebellar imaging data. *PLoS One* **10**, e0133402 (2015).

101. N. B. Lundin *et al.*, Data and code for "Neural evidence of switch processes during semantic and phonetic foraging in human memory." Open Science Framework. https://osf.io/mf5de. Deposited 23 September 2023.