



# The cognitive neuroscience of visual short-term memory

Bradley R Postle

Our understanding of the neural bases of visual short-term memory (STM), the ability to mentally retain information over short periods of time, is being reshaped by two important developments: the application of methods from statistical machine learning, often a variant of multivariate pattern analysis (MVPA), to functional magnetic resonance imaging (fMRI) and electroencephalographic (EEG) data sets; and advances in our understanding of the physiology and functions of neuronal oscillations. One consequence is that many commonly observed physiological ‘signatures’ that have previously been interpreted as directly related to the retention of information in visual STM may require reinterpretation as more general, state-related changes that can accompany cognitive-task performance. Another is important refinements of theoretical models of visual STM.

## Addresses

University of Wisconsin-Madison, Psychology and Psychiatry,  
1202 W. Johnson St., Madison, WI 53706, United States

Corresponding author: Postle, Bradley R ([postle@wisc.edu](mailto:postle@wisc.edu))

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## Signal intensity-based versus multivariate analyses of fMRI data

### Reconsidering the link between delay-period activity and ‘storage’

For decades, a governing assumption in STM research has been that the short-term retention of visual information is supported by regions that show elevated levels of activity during the delay period of STM tasks. Thus, for example, debates over the role of the prefrontal cortex (PFC) in STM and the related construct of working memory were framed in terms of whether or not its delay-period activity showed load-sensitivity — systematic variation of signal intensity as a function of memory set size [1–4]. Similarly, patterns of load-sensitive variation of activity in the intraparietal sulcus

have been used to test and refine theoretical models about mechanisms underlying capacity limits in visual STM e.g., 5,6]. With the advent of MVPA, however, this signal-intensity assumption has been called into question.

A fundamental difference between MVPA and univariate signal intensity-based analyses is that the former does not entail thresholding the dataset before analysis, but, rather, analyzes the pattern produced by all elements in the sampled space. The analytic advantages to this approach are marked gains in sensitivity and specificity e.g., 7]. In the domain of visual STM, this was first demonstrated with the successful decoding of delay-period stimulus identity from early visual cortex, including V1, despite the absence of above-baseline delay-period activity [8,9]. Subsequently, it was demonstrated that although the short-term retention of specific directions of motion was decodable from medial and lateral occipital regions (despite the absence of elevated delay-period activity), this information was not decodable from regions of intraparietal sulcus and frontal cortex (including PFC) that nonetheless evinced robust elevated delay-period activity [10\*]. Further, in these posterior areas the strength of MVPA decoding, a proxy for the fidelity of neural representation, declined with increasing memory load. Importantly, these changes in MVPA decoding predicted load-related declines in behavioral estimates of the precision of visual STM [11\*\*] (Figure 1). Relatedly, an fMRI study using a forward encoding-model approach [12\*] has demonstrated that interindividual differences in the dispersion (i.e., ‘sharpness’) of multivariate channel tuning functions in areas V1 and V2v predicts recall precision of STM for orientations [13\*\*]. Thus, studies [11\*\*] and [13\*\*] indicate an important link between the fidelity of the distributed neural representation and the fidelity of the mental representation that it is assumed to support.

### The localization of visual STM, and insight into mechanism

It is not the case that intraparietal sulcus and frontal cortex are inherently ‘undecodable’ (see Box 1), nor that they are never recruited for the short-term retention of information. A determinant of whether a network will be engaged in the short-term retention of a particular kind of information is whether it is engaged in the perception or other processing of that information in situations that do not explicitly require STM. Thus, for example, when the

**Box 1 Population coding in PFC**

PFC shows increases in activity during difficult versus easy conditions of many types of task, not just STM (for which load is an operationalization of difficulty) [14\*]. With regard to STM, MVPA of neuronal activity recorded from monkeys provides hints of what functions may be supported by the elevated activity measured in humans with fMRI. In two studies, MVPA revealed a delay-period transition from an initial representation of properties specific to a stimulus, to one of either the item's status as a 'Go' or 'No-go' cue [15\*\*], or the trial's status as a 'Match' or 'Nonmatch' trial [16\*]. In a test of STM for the color of varying numbers of objects, PFC represented the passage of time across the delay period and the location of to-be-remembered stimuli, but not the colors themselves [17\*\*] (cf [18\*\*]). Consistent with these unit-level findings, MVPA of human fMRI of STM has shown PFC to encode such factors as stimulus category, attentional context, and match-nonmatch status of a trial (e.g., [10\*,19\*\*,20\*\*]). Thus, in addition to its well-established role in the top-down control of neural processing (e.g., [14\*,20\*\*]), another function of PFC may be the processing of information that, although not explicitly being tested, is nonetheless unfolding, and of possible relevance to the organism [17\*\*,21,22].

short-term retention of abstract visuospatial patterns [23\*] or dynamically morphing flow-field stimuli [24] is tested, MVPA reveals delay-period stimulus representation in intraparietal sulcus, in addition to occipital regions; the same is true for face, house, and human-body stimuli in ventral occipitotemporal regions (e.g., [20\*\*]). When the to-be-remembered stimulus affords oculomotor planning, its identity can also be decoded from oculomotor-control regions of intraparietal sulcus and of frontal cortex [25\*\*]. Indeed, [25\*\*] demonstrated that an MVPA classifier trained on only one condition — attention to a location, planning a saccade to a location, or STM for a location — can decode the other two. This could only be possible if similar patterns of neural activity, implying similar mechanisms, underlie the behaviors that have traditionally been categorized as 'attention' versus 'intention' versus 'retention'.

Patterns of localization can also reflect how the brain supports the strategic recoding of information from the format presented at study into one best suited for the impending memory-guided action. One study first presented subjects with a sample object, then, early in the delay, indicated whether memory for fine-grained perceptual details or for category membership would be tested. For the former, MVPA found evidence for delay-period stimulus representation in inferior occipitotemporal cortex, but not PFC; for the latter, the converse was true [19\*\*]. Combining MVPA with univariate and functional connectivity analyses has revealed a role for frontal cortex and intraparietal sulcus in implementing such strategic shifts of mental coding in visual STM [20\*\*]. MVPA can also track the evolution of mental coding in the absence of instructions, demonstrating,

**Box 2 Network-level dynamics in STM**

Under conditions for which a stable mental code is assumed (e.g., no instructions to strategically recode [19\*\*,26]), MVPA typically reveals a stable set of regions to represent memoranda across the duration of a delay-period. However, the activity patterns within these regions can be dynamic. For example, with auditory STM, the frequency-specific pattern of elevated stimulus-evoked activity transitions to become a pattern of negative activity during the delay period [30]. For visual STM, a classifier trained on a time point early in the trial will often perform progressively worse as it is slid forward across the remainder of the delay period, the converse being true for a classifier trained on a late-in-the-delay time point and slid backwards (Figure 1b). This suggests a temporal evolution of the neural code underlying the short-term retention of a subjectively 'stable' mental representation [11\*\*,31\*]. It remains to be determined whether these observations from fMRI relate in a meaningful way to the finding of dynamic coding in populations of neurons in monkeys performing tasks requiring sustained attention to an object [32,33].

for example, that the verbal recoding of visually presented information also entails the recruitment of a semantic code [26].

Neural data also provide important constraints on models of capacity limitations of visual STM [27\*,28\*]. One influential model holds inferior intraparietal sulcus to be important for individuating objects that are to be encoded into visual STM, whereas superior intraparietal sulcus and an area of lateral occipital cortex are responsible for identifying these objects [6]. Recently, however, although the univariate analyses of data from a follow-up experiment [29\*\*] did reproduce many of the findings from the earlier study, MVPA of the same data failed to support a model of segregated circuits performing these two operations. Instead, the study of Naughtin *et al.* [29\*\*] produced two novel findings. First, the contrasts intended to operationalize individuation versus identification recruited primarily overlapping regions, thereby calling into question the dissociability of these two hypothesized mechanisms. Second, many regions outside of the intraparietal sulcus regions emphasized by [6] were also sensitive to these contrasts, suggesting that broadly distributed systems underlie the control of visual STM (Box 2).

**Signal intensity-based versus multivariate analyses of EEG data****Event-related potential (ERP) correlates of STM**

Another neural effect that has influenced models of visual STM capacity limitation is the contralateral delay activity (CDA), an ERP component that scales monotonically with STM load, but asymptotes at the psychophysically estimated capacity of an individual [34]. The CDA is widely interpreted as an index of the short-term retention of information (e.g., [35]), such that, for example, the presence of a CDA during visual

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