

# A shared representation of order between encoding and recognition in visual short-term memory

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## ABSTRACT

Many complex tasks require people to bind individual events into a sequence that can be held in short term memory (STM). For this purpose information about the order of the individual events in the sequence needs to be maintained in an active and accessible form in STM over a period of few seconds. Here we investigated how the temporal order information is shared between the presentation and response phases of an STM task. We trained a classification algorithm on the fMRI activity patterns from the presentation phase of the STM task to predict the order of the items during the subsequent recognition phase. While voxels in a number of brain regions represented positional information during either presentation and recognition phases, only voxels in the lateral prefrontal cortex (PFC) and the anterior temporal lobe (ATL) represented position consistently across task phases. A shared positional code in the ATL might reflect verbal recoding of visual sequences to facilitate the maintenance of order information over several seconds.

## Introduction

One of the most important features of human short term memory (STM) is the ability to bind individual events into a sequence. A host of complex behaviours including language processing, vocabulary acquisition, and chunk formation are thought to rely on sequence encoding in STM (see Hurlstone et al. (2014), for a review). Information about the order of the individual stimuli in the sequence needs to be held in an active and accessible form in STM over a period of few seconds (Botvinick and Watanabe, 2007; Baddeley, 2003). Research has shown that the position of a stimulus in a sequence is encoded in STM separately and independently of its identity (Henson and Burgess, 1997; Henson et al., 1996; Page and Norris, 2009, Fig. 1A). From hereon we refer to such neural representation of an item's position in the sequence as *positional code*. Fig. 1C gives an example of a simple positional code showing the responses of position-sensitive neurons from monkey Supplementary motor area, as observed by Berdyeva and Olson (2010).

The neural implementation of the positional code has been extensively studied in animal neurophysiology. Neurons selective for each position in a sequence have been observed in monkey dorsolateral prefrontal cortex (Averbeck and Lee, 2007; Inoue and Mikami, 2006; Ninokura et al., 2004; Barone and Joseph, 1989), Supplementary and Presupplementary motor area (Nakajima et al., 2009; Berdyeva and Olson, 2010; Isoda and Tanji, 2004), and medial premotor cortex (Crowe et al., 2014; Merchant et al., 2013). Other research on animal neurophysiology and human neuroima-

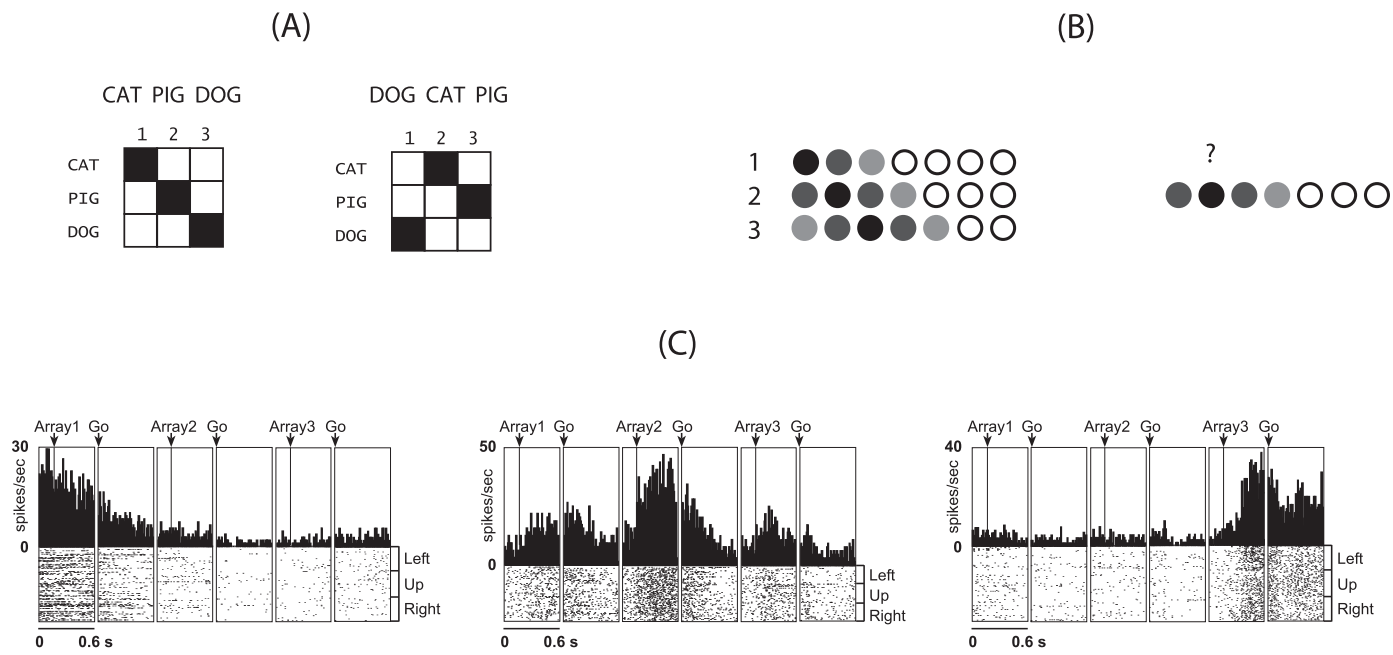
ging has suggested that the hippocampus encodes the position of items in a sequence (Heusser et al., 2016; Rangel et al., 2014; Hsieh et al., 2014; DuBrow and Davachi, 2014; Ginther et al., 2011), with some authors proposing the existence of 'time cells' tracking the temporal information during sequence processing (MacDonald et al., 2011; MacDonald et al., 2013).

In the current paper we investigate how the positional code is represented in human STM. By contrast, previous human neuroimaging studies have focussed on the representations elicited by learned sequences (Ross et al., 2009; Albouy et al., 2008; Schendan et al., 2003; Hsieh and Ranganath, 2015; Hsieh et al., 2014), which can be assumed to be represented very differently from those maintained in STM. Similarly, in many studies the task has not required participants to actively retain the order of the stimuli in memory (Heusser et al., 2016; DuBrow and Davachi, 2014, 2016; Amiez and Petrides, 2007; Hsieh and Ranganath, 2015; Hsieh et al., 2014). No previous imaging studies have reported multivariate analyses of an order STM task. Furthermore, previous studies have not addressed the fact that several unrelated cognitive processes, such as memory load, sensory adaptation, and reward expectation, also change in a consistent manner as the sequence unfolds. Therefore it becomes difficult to ascertain whether their results are actually indicative of order memory or a collinear change in some other variable such as memory load (for a detailed treatment of this issue see Kalm and Norris (2016)).

Here we used an STM task where participants had to remember and subsequently recognise a short sequence of images. In order to recall

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**Fig. 1.** Sequence representation and positional code. (A) Representation of two sequences as mappings between item codes and temporal position codes. (B) Left: representation of the temporal position of three first items in a 7-item sequence. The variance around positional code is represented in terms of the darkness of the circle. Right: the item at position 2 is retrieved by reinstating each positional code which then cues the associated item. (C) Examples of temporal position selective neurons from Berdyeva and Olson (2010). From left to right: Pre-supplementary motor area neuron selective for 1st position, Supplementary eye field neuron selective for 2nd position, and Supplementary motor area neuron selective for the 3rd position in the serial object task.

items in the correct order participants had to retrieve the positional code instantiated during the presentation phase of the STM task (Fig. 1B). We investigated whether any brain regions shared this positional code between the presentation and response phases of the task. For this purpose, we trained a classification algorithm to use the fMRI activity patterns of individual items to predict the positions of those items when they appeared in different sequences. Such an analysis abstracts over item identity (such as a specific image) but is sensitive to the representations that consistently code for an item's position within a sequence. Importantly, we used activity patterns from the presentation phase of the STM task to predict the position of the items during the subsequent recognition phase. This allows us to identify brain regions where the positional code is shared between encoding and response phases. Representations shared by encoding and recognition should reflect a common memory representation of order and not other sequential processes such as memory load or sensory adaptation. In sum, we consider our study to be the first controlled fMRI experiment to study the order representations in STM.

Our results revealed that although several brain regions showed sensitivity to order within a single phase, only the voxels in the lateral prefrontal cortex (PFC) and the anterior temporal lobe (ATL) represented item position consistently across task phases. This suggests that while many brain areas, including sensory and motor cortices, are sensitive to temporal position, those representations might not be used to guide behaviour and could instead reflect perceptual or load-related aspects of the task. Our findings suggest that voxels in the PFC and ATL are not only sensitive to sequentially presented stimuli (Amiez and Petrides, 2007) or sequentially executed actions (Averbeck and Lee, 2007) but encode temporal position information across task phases in a manner which could be used to guide behaviour.

## Methods

### Participants

In total, 13 right-handed volunteers (6 female, 20–33 years old) gave informed, written consent for participation in the study after its

nature had been explained to them. Subjects reported no history of psychiatric or neurological disorders and no current use of any psychoactive medications. Two participants were later excluded from the study because of excessive motion artefacts in the collected fMRI data (see *Physiological noise removal* for the exclusion criteria). The study was approved by the Cambridge Local Research Ethics Committee (LREC) (Cambridge, UK).

### Task

We used an immediate serial recognition task where participants had to remember sequences of one, two or three pictures of houses or faces in the order they were presented (Fig. 2). On each trial participants were presented with a visual fixation cross to indicate the start of the presentation of the sequence. During the presentation phase, pictures of houses or faces were presented individually (each item for 3.5 s so as to obtain two scans per item) followed by a brief delay (2 s). This was followed by an order recognition phase, where a replay of the initial sequence was displayed. At the end of this phase participants had to indicate whether the items in the sequence were presented in the same order as in the original sequence (Fig. 2). In order to ensure that participants paid constant attention during recognition we changed the replayed sequence on 8 trials out of 96. Items which did not appear in their original presented positions during those trials were not included in the later fMRI data analysis. On 1/3 of the trials the recognition phase (replay of the sequence) was omitted. The recognition phase was followed by a cue+indicating that there would be a delay of between 6 and 16 s before the next trial. The inclusion of the recognition phase in the trial was randomised across the experiment.

We used short 3-item sequences to ensure that the entire sequence could be accurately retained in STM. If we had used longer sequences then the representation of any given sequence would necessarily vary from trial to trial depending on the nature of the errors, and no consistent pattern of neural activity could be detected. Furthermore, we wanted to estimate separate regressors for individual items in the sequence during both the presentation and recognition phases of the

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