

# Irrelevant sensory stimuli interfere with working memory storage: Evidence from a computational model of prefrontal neurons

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**Abstract** The encoding of irrelevant stimuli into the memory store has previously been suggested as a mechanism of interference in working memory (e.g., Lange & Oberauer, *Memory*, 13, 333–339, 2005; Nairne, *Memory & Cognition*, 18, 251–269, 1990). Recently, Bancroft and Servos (*Experimental Brain Research*, 208, 529–532, 2011) used a tactile working memory task to provide experimental evidence that irrelevant stimuli were, in fact, encoded into working memory. In the present study, we replicated Bancroft and Servos’s experimental findings using a biologically based computational model of prefrontal neurons, providing a neurocomputational model of overwriting in working memory. Furthermore, our modeling results show that inhibition acts to protect the contents of working memory, and they suggest a need for further experimental research into the capacity of vibrotactile working memory.

**Keywords** Attention · Computational model · Prefrontal cortex · Short-term memory · Working memory · Single-unit physiology

Vibrotactile working memory has recently been the subject of substantial research interest (e.g., Auksztulewicz, Spitzer, Goltz, & Blankenburg, 2011; Bancroft, Hockley, & Servos, 2012; Bancroft & Servos, 2011; Bancroft, Servos, & Hockley, 2011; Hannula et al., 2010; Savolainen et al., 2011; Spitzer &

Blankenburg, 2011; Spitzer & Blankenburg, 2012; Spitzer, Wacker, & Blankenburg, 2010) and has considerable promise as a model system for psychological, neuroscientific, and computational research (Bancroft, Hockley, & Servos, 2011). In vibrotactile working memory tasks, subjects are presented with a vibration to the hand, usually to the dominant index finger (the target stimulus), followed by an unfilled delay period, followed by a second stimulus (the probe stimulus). The subjects are instructed to decide whether the target and probe are of the same vibrational frequency or of different frequencies, or, alternately, whether the probe is of a higher or lower frequency than the target. At the neural level, vibrotactile stimuli have been shown to possess a simple neural code: Neural firing rates are increasing or decreasing monotonic (often linear) functions of stimulus frequency (Romo & Salinas, 2003). The set of neural regions involved in vibrotactile working memory tasks is also well defined. Primary somatosensory cortex (SI) is involved in stimulus processing (Luna, Hernández, Brody, & Romo, 2005), secondary somatosensory cortex (SII) is involved in stimulus processing and possibly decision making (Romo, Hernández, Zainos, Lemus, & Brody, 2002), and prefrontal cortex (PFC) is involved in information storage and decision making (Brody, Hernández, Zainos, & Romo, 2003; Hernández, Zainos, & Romo, 2002; Romo, Hernández, & Zainos, 2004; Romo, Brody, Hernández, & Lemus, 1999). Premotor cortex is also thought to be involved (Romo & Salinas, 2003). Neurons in all three of these regions use the simple neural code defined above.

Behaviorally, vibrotactile working memory displays many properties similar to those of other domains of working memory. Harris, Harris, and Diamond (2001) noted that presenting a brief “interference” or “distractor” stimulus during the delay period reduced overall performance, similar to the effects of interference in other domains of working

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memory (e.g., Mercer & McKeown, 2010). More recently, Bancroft and Servos (2011) and Bancroft, Servos, et al. (2011) provided experimental evidence that interference stimuli are actually encoded into working memory, interfering with the previously stored target stimulus.

Feature overwriting has previously been suggested as the mechanism of interference in working memory (cf. Lange & Oberauer, 2005; Nairne, 1990; Neath, 2000; Oberauer & Kliegl, 2006). Overwriting theories generally assume that stimuli are stored in short-term memory in a set of “feature detectors.” A new stimulus may interfere with the stored representation(s) of prior stimuli by competing for and overwriting the contents of feature detectors. Lange and Oberauer identified two relevant forms of overwriting theory: feature deletion, in which a new stimulus overwrites some of the feature detectors containing the representations of previous stimuli (as in Nairne, 1990), and feature adoption, in which some of the features of a new stimulus are incorporated into the representation of a previously stored stimulus (as in Neath, 2000).

Vibrotactile memory tasks differ from many other working memory tasks in that only one stimulus feature is salient: vibrational frequency. (We refer to this as *scalar* or *unidimensional working memory*; others have used the term *parametric working memory*.) In contrast, stimuli such as words and pictures can have many salient features. Despite this difference, we can treat overwriting in vibrotactile memory as a specific case of the general overwriting theories previously developed. Stimuli stored in vibrotactile memory are still stored in a set of feature detectors, and interference effects are still produced by the competition of different stimuli for detectors. However, although there are many detectors (prefrontal neurons), they all represent the same stimulus feature, frequency. When a distractor stimulus is encoded into memory, it may overwrite the previously stored representation to some degree by modifying the firing rates of PFC neurons. It is not entirely clear which version of overwriting theory best describes overwriting in vibrotactile working memory. While it seems unlikely that the storage of a distractor stimulus would completely delete the stored representation of previous stimuli (as the large number of PFC neurons encoding stimulus frequency provides a degree of redundancy), it is possible that the storage of a distractor shifts the firing rates of some or all PFC neurons such that they actually encode a stimulus frequency that is an average of the previously stored and new stimulus frequencies, similar to the feature adoption account described above. It is also possible that both the target item and the distractor are discretely stored in memory (e.g., if some PFC neurons encode the target stimulus while different PFC neurons encode the distractor) and that interference effects are due to the inability to differentiate between the representations of the distractor and target during the decision-making process. Common to both of these

cases, however, is this: Interference is produced when irrelevant stimuli are encoded into vibrotactile working memory. The unidimensionality and straightforward neural coding of vibrotactile working memory makes it a good neural model system in which to study overwriting.

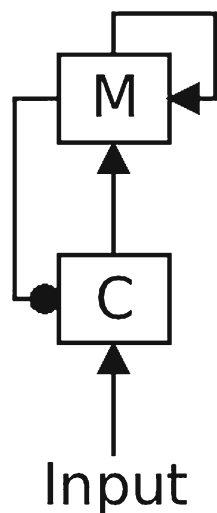
The simple neural code found in the neurons encoding vibrotactile stimuli has allowed the development of a number of computational models of vibrotactile working memory performance. The majority of these models are biologically based models of frontal cortex (Deco & Rolls, 2006; Machens, Romo, & Brody, 2005; Miller, Brody, Romo, & Wang, 2003; Miller & Wang, 2006; Singh & Eliasmith, 2006; see also Verguts, 2007, for a connectionist model). While these models commonly use detailed spiking-neuron models, some of the models (including those of Machens et al., 2005, and Miller & Wang, 2006) can also be instantiated as simple firing-rate models of neuron populations. The behavior of such a model is easily analyzed. We have opted to adapt Miller and Wang’s model, as it is a rate model that can be implemented simply and transparently.

In the present study, we applied the model to the findings of Bancroft and Servos (2011). Bancroft and Servos modified the standard vibrotactile working memory paradigm by presenting an irrelevant “distractor” stimulus during the delay period, in an attempt to interfere with the storage of the target stimulus. Previously, Harris et al. (2001) found that presenting a distractor stimulus during the delay period reduced overall performance on vibrotactile working memory tasks. However, it was unclear whether this was due to direct interference with the mechanisms underlying working memory storage or to other factors (e.g., attentional processes). Bancroft, Servos, et al. (2011) and Bancroft and Servos (2011) extended Harris et al.’s work by setting the frequency of the distractor stimulus as a function of the target stimulus frequency. Critically, in the different-probe condition (in which the target and probe were of different frequencies), the frequency of the distractor could lie between those of the target and probe (referred to as a “toward-shift” distractor; e.g., target = 20 Hz, distractor = 22 Hz, probe = 24 Hz) or be farther from the probe frequency than from the target frequency (an “away-shift” distractor; e.g., target = 20 Hz, distractor = 18 Hz, probe = 24 Hz). This experimental design allowed Bancroft and Servos to test their hypothesis that the interference due to a distractor is due to the distractor being encoded into working memory, rather than to some other process (e.g., attention). If the distractor were encoded into memory and included in the comparison process, we would expect better performance in the away-shift than in the toward-shift condition. Why would this be? If the probe is being compared with some combination of the target and distractor, a combination of a target and a toward-shift distractor (from above: target = 20 Hz, distractor = 22 Hz, probe = 24 Hz) will be perceived as having a

frequency closer to that of the probe than will a combination of a target and an away-shift distractor (from above: target = 20 Hz, distractor = 18 Hz, probe = 24 Hz). As such, subjects will be more likely to make incorrect “same” responses in the toward-shift than in the away-shift condition—consistent with Bancroft and Servos’s findings.

## Model

The present model is an adaptation of Miller and Wang’s (2006) model that has been streamlined for transparency of operation and ease of use when modeling experimental results; as such, the present model has only two free parameters. It uses a rate code, consistent with experimental examinations of the coding of vibrotactile stimuli in working memory tasks (see Romo & Salinas, 2003, for a review). The basic neural circuit is illustrated in Fig. 1. Populations of “comparison” (C) neurons have excitatory projections to populations of “memory” (M) neurons, which in turn have excitatory connections to themselves and inhibitory projections to C neurons. Inputs are delivered to the C layer, which in turn passes them to the M layer. The amplitudes of inputs to the C layer are either positive or negative monotonic functions of stimulus frequency, with equal numbers of each. The excitatory self-connections in the M layer allow neurons to maintain their firing rates in the absence of external input, while the inhibitory connections drive activity in the C layer to zero. Therefore, upon presentation of the target stimulus, the stimulus is stored in the M layer, while the C layer receives inhibitory input equal to the magnitude of the stored input. When the probe stimulus is presented, the C neurons



**Fig. 1** Basic circuit construction. Arrows indicate excitatory connections, and circles indicate inhibitory connections

receive excitatory input corresponding to the magnitude (frequency) of the probe stimulus and inhibitory input corresponding to the magnitude (frequency) of the target stimulus. As such, C neurons will calculate some function of  $f_2 - f_1$ , consistent with experimental findings (Jun et al., 2010; Romo & Salinas, 2003).

A decision as to whether the target or probe stimulus is of a higher frequency (or, alternatively, whether the target and probe are of the same or of different frequencies) can be made by reading out the firing rates from C populations upon presentation of the probe stimulus. If  $f_2 > f_1$ , then  $C_{\text{pos}}$  neurons (populations of neurons receiving inputs that are positive monotonic functions of stimulus frequency) will have firing rates significantly above zero. If  $f_2 < f_1$ ,  $C_{\text{neg}}$  neurons will have firing rates above zero. Alternatively, in the case in which we are testing the same versus different frequencies, we would analyze the average firing rate of all C neurons: If the stimuli are of different frequencies, the average firing rate will be significantly above zero. If they are of the same frequency, the average firing rate will approach zero. As previously stated, we simulate four populations of C/M neurons in this model: one C–M pair receiving positive monotonic inputs, and one C–M pair receiving negative monotonic inputs. We have also designed a decision (D) neuron population to simplify the readout of C neuron activity. (This population does not deliberately conform to any particular experimentally observed pattern of neuronal activity, but rather is aimed at simplifying the decision-making process.) A schematic of our model, as instantiated in this article, is displayed in Fig. 2.

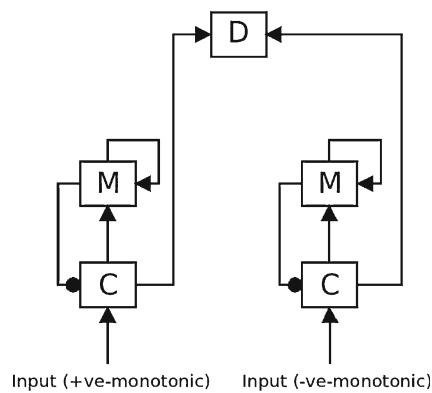
To model prefrontal neurons, we have adopted Miller and Wang’s (2006) rate equations. The firing rates of the C and M populations are represented in two equations:

$$\frac{d}{dt}r_c = \left(\frac{1}{\tau}\right)(-r_c - w_{m \rightarrow c}r_m + I(t)), \quad (1)$$

$$\frac{d}{dt}r_m = \left(\frac{1}{\tau}\right)(-r_m + w_{c \rightarrow m}r_c + w_{m \rightarrow m}r_m), \quad (2)$$

where  $w$  is the connection weight between two populations,  $r$  is the firing rate of a given population,  $I$  is the external input to a given population, and  $\tau$  is the time constant. Neuronal firing rates were restricted to the range  $[0, 100]$ . Note that when the weight of the connection from the M neurons to themselves is set to 1, Eq. 2 reduces to

$$\frac{d}{dt}r_m = \left(\frac{1}{\tau}\right)(w_{c \rightarrow m}r_c), \quad (3)$$



**Fig. 2** Complete model, as used in Simulations 1 and 2. Arrows indicate excitatory connections, and circles indicate inhibitory connections

simplifying the operation of the network. The bounds for the connection weights from C to M neurons and from M to C neurons were determined analytically by Miller and Wang:

$$\tau/(2T) \ll w_{CM}w_{MC} < 0.25. \quad (4)$$

For ease of analysis, we have used symmetrical weights, so that  $w_{CM} = -w_{MC}$ .

To decide whether a probe was of the same frequency as a stored target or a different frequency, we compared the sum of activity of the C neurons during the presentation of the probe stimulus against some decision threshold. As stated above, we designed a “decision” (D) neuron to sum the activity of C neurons. Initially, and while  $t < t_{\text{probe onset}}$ ,  $r_d$  was set to zero. Once the probe was presented, the D-population firing rate changed as follows:

$$\frac{d}{dt}r_d = \left(\frac{1}{\tau}\right) \sum_i w_{c_i \rightarrow d} r_{c_i}. \quad (5)$$

Note that this population was not designed to conform to any pattern of activity observed in experimental work, but rather was a convenient mathematical fiction. (There are a number of ways to implement the decision-making process in the present model. We have chosen to implement decision neurons to simplify the simulation process.) The connection weights from C to D neurons were all set to be equal. Upon the offset of the probe stimulus, we compared the firing rates of the decision neuron to our decision threshold ( $\theta$ ). If the rate equaled or exceeded the threshold, subjects would make a “different” response; otherwise, they would make a “same” response. The threshold was allowed to vary as a free parameter.

Substantial “noise” occurs in the neural systems underlying vibrotactile working memory: Irrelevant sensory input, background neural activity, attentional modulation, and other processes have the potential to introduce inaccuracy into vibrotactile working memory tasks. By the time that the signal produced by a vibrotactile stimulus reaches the PFC

neurons that are simulated in our model, it has passed through the peripheral nervous system, spinal cord, brain stem, thalamus, primary somatosensory cortex, and secondary somatosensory cortex, any of which can add noise and distortion to the signal. Describing all of these processes is beyond the scope of this article; however, we must account for noise in the sensory signal. As one of our goals in constructing this model was to allow straightforward analysis of model operation, as well as easy fitting of the model to experimental results, we have opted to account for noise by constructing our inputs to the system by drawing from a normal distribution with a mean equal to the frequency of the stimulus being presented, and the standard deviation ( $\sigma$ ) as our second free parameter. The fixed parameters for all simulations are presented in Table 1, and a summary of our model (following Nordlie, Gewaltig, & Plesser’s, 2009, suggested tabular format) is presented in Table 2.

### Simulation 1

As we wished to confirm the intrusion of the distractor stimulus into working memory, we simulated an experiment in which a distractor was presented (Simulation 1A) and compared the results with those of an experiment in which no distractor was presented (Simulation 1B). (In other words, the latter model was identical to a standard vibrotactile memory paradigm.) Simulation 1B tested the assumption that the interference effects found by Bancroft and Servos (2011) and by Bancroft, Servos, et al. (2011) were not due to the encoding of the distractor stimulus, but rather to an unidentified process (possibly attentional) that was not accounted for in the model. Essentially, it was a control simulation, to ensure that a good fit by Simulation 1A was actually due to the effects of the distractor. We fit the experimental findings of Bancroft and Servos by varying the free parameters over a parameter space ( $\sigma = [0.5, 5]$ , step size = 0.5;  $\theta = [0, 20]$ , step size = 0.1) and selecting the free parameters that minimized the sum of squared differences between the simulated and experimental results. The initial rates for all populations of neurons were set to zero. We simulated 1,000 trials in each experimental condition, at

**Table 1** Fixed parameters for all models

Parameter	Value
Time constant ( $\tau$ )	10
Maximum neuronal firing rate	100
Connection weight (input to C neurons)	0.5
Connection weight (C to M neurons)	0.4
Connection weight (M to C neurons)	−0.4
Connection weight (C to D neurons)	0.01

**Table 2** Adapted version of Miller and Wang's (2006) model

A: Model Summary			
Populations	Three: C, M, and D		
Connectivity	Fixed connections from C to M, M to C, and C to D		
Neuron model	Population rate model		
Input	Linear function of stimulus frequency		
Measurements	Firing rate of D population		
B: Populations			
Name	Elements	Size	
C	Rate model	Two subpopulations	
M	Rate model	Two subpopulations	
D	Rate model	One subpopulation	
C: Connectivity			
Name	Source	Target	Pattern
CM	C	M	Excitatory
MC	M	C	Inhibitory
CD	C	D	Excitatory
Input	N/A	C	Excitatory
D: Neuron and Synapse Model			
Type	Rate model		
Dynamics	$dr_i/dt = (1/\tau)(-r_i + \sum w_{ji}r_j + \text{input})$		
E: Input			
Linear function of stimulus frequency	$0.5 * f_{\text{stimulus}}$		
F: Measurements			
Firing rate of D population			

each point in the parameter space. The results of the simulation using the parameters with the best fit are reported in Table 3, along with Bancroft and Servos's experimental results.

## Results and discussion

Both Simulations 1A and 1B were equally capable of explaining a substantial amount of the variance in Bancroft and Servos's (2011) experimental findings, with  $R^2$ s of .931 and .930, respectively. Similarly, 1A and 1B displayed similar degrees of error, with  $SS$ s of .013 and .010, respectively. While no difference between these models appeared at first glance, 1B failed to replicate the interference effect found in Bancroft and Servos's experimental data (.01 vs. .09, respectively, for the simulation and empirical results). In contrast, 1A did produce an effect. Qualitatively, 1A did appear to do a better job of modeling the experimental findings on interference, consistent with the suggestion that distractors are encoded into vibrotactile working memory. Notably, however, Simulation 1A's interference effect was substantially larger than the effect found in the experimental data (.15 vs. .09, respectively). We addressed this issue in a second simulation.

## Simulation 2

While the results of the first simulation suggested that the distractor is encoded into working memory, Simulation 1A overestimated the interference effects displayed in Bancroft and Servos's (2011) experimental data. Why might this be? Transcranial magnetic stimulation (TMS) studies have suggested that inhibition of irrelevant sensory stimuli during the delay period is critical to maintaining information in vibrotactile working memory, but also that endogenous inhibitory processes are less than fully effective (Hannula et al., 2010; Savolainen et al., 2011). Given that Bancroft and Servos's subjects were instructed to ignore the distractor, the distractor stimulus may have received substantial inhibition, reducing the degree to which it was encoded in memory. In Simulation 2, we varied the proportions of trials in which the distractor was encoded by the model. On some trials, the model encoded the distractor (similar to Simulation 1A), while on others, no distractor was encoded (similar to Simulation 1B). We allowed the proportion of trials on which the distractor was encoded ( $k$ ) to vary over the range (0, 1], with a step size of .1. As in our earlier simulations,  $\theta$  varied over the range [0, 20], with a step size of 0.1. We did not allow  $\sigma$  to vary as a free parameter. However, as Simulations 1A and 1B had found different fits for  $\sigma$  (4.5

**Table 3** Simulated results and free parameters for Simulations 1A, 1B, and 2

Probe Condition	Distractor Frequency Difference (Hz)	Empirical (Proportion of Correct Responses)	Simulation 1A (Proportion of Correct Responses)	Simulation 1B (Proportion of Correct Responses)	Simulation 2 (Proportion of Correct Responses)
Same/0 Hz distractor shift	0	.70	.70	.71	.68
Same/2 Hz distractor shift	2	.71	.66	.70	.70
Same/4 Hz distractor shift	4	.71	.66	.70	.70
Different/0	0	.43	.44	.45	.45
Different/2 Hz (away)	2 (away)	.52	.49	.44	.48
Different/4 Hz (away)	4 (away)	.50	.54	.45	.52
Different/2 Hz (toward)	2 (toward)	.43	.39	.44	.44
Different/4 Hz (toward)	4 (toward)	.41	.35	.43	.39
Mean overwriting effect		.09	.15	.01	.09
SS			.0131	.0098	.0036
$r^2$			.931	.930	.975
$\sigma$			4.5 (free)	3.5	3.5
$\theta$			1.0	1.6	1.2
Distractor duration			250 ms (fixed)	none	250 ms/none (distractor encoded on 50% of trials)

and 3.5, respectively), we performed ad hoc simulations of those values (as well as  $\sigma = 4.0$ ) and found that  $\sigma = 3.5$  provided the best fit to the data. We therefore held  $\sigma$  as a fixed parameter with value 3.5. We simulated 1,000 trials per experimental condition for each point in the parameter space.

## Results and discussion

The results from the simulation are presented in Table 3. Simulation 2 displays less error ( $SS = .0036$ ) and explains a greater proportion of the variance in the experimental data ( $R^2 = .975$ ) than did Simulation 1A or 1B ( $SS = .0131$  and  $.0098$ ,  $R^2$ 's = .931 and .930, respectively). Most importantly, Simulation 2 replicated the magnitude of the overwriting effect found in Bancroft and Servos's (2011) experimental data (.09 vs. .09, respectively). Intriguingly, the best fit for the distractor encoding parameter ( $k$ ) was 0.5, suggesting that the distractor receives substantial inhibition and is not encoded on a full half of the trials. The results of Simulation 2 suggest that interference in vibrotactile working memory tasks can occur when irrelevant sensory stimuli are encoded into memory. Furthermore, consistent with recent TMS studies (Hannula et al., 2010; Savolainen et al., 2011), it appears that the processing of distractors is inhibited.

The results of Simulations 1 and 2 strongly suggest two things: first, that the contents of vibrotactile working memory are vulnerable to (potentially high levels of) interference, even from stimuli of relatively short duration; second, that subjects attempt to inhibit irrelevant sensory stimuli

during the delay period, but that the inhibitory process is not entirely effective. How can we reconcile these findings with previous experimental reports of a multistimulus capacity for vibrotactile working memory (Bancroft et al., 2012; Spitzer & Blankenburg, 2011)? We explored the issue of memory capacity in Simulation 3.

## Simulation 3

Most domains of working memory have been shown to be capable of storing multiple items or stimuli (Cowan, 2005). Our ability to compare results in vibrotactile working memory research to results using other working memory tasks would be substantially stronger if vibrotactile working memory also had a multi-item capacity. The findings of research into vibrotactile memory capacity have been mixed. Research by Harris et al. (2001), Hannula et al. (2010), Bancroft and Servos (2011), and Bancroft, Servos, et al. (2011) has found that items stored in vibrotactile working memory are vulnerable to interference from irrelevant sensory stimuli, and Simulations 1 and 2 showed that these effects are produced by the intrusion of distractors into memory. Notably, distractors intrude into and overwrite the contents of memory even though (a) the subjects in the Bancroft and Servos (2011) and Bancroft, Servos, et al. (2011) studies were instructed to ignore the distractor, and (b) the distractor had one quarter the duration of the previously stored target stimulus, suggesting that the contents of vibrotactile working memory are potentially very vulnerable

to interference. However, recent articles by Spitzer and Blankenburg (2011) and Bancroft et al. (2012) have suggested that vibrotactile working memory can store more than one stimulus.

Spitzer and Blankenburg (2011) recently provided evidence suggestive of a multi-item capacity: Subjects were presented with two vibrotactile stimuli to different fingers and retained both stimuli for a brief period, until they were given a visual cue to retain one of the stimuli for the full delay period and to cease maintaining the other stimulus. Notably, however, subjects only retained the stimuli for a brief period before receiving the retention cue, and the stimuli were presented to different fingers rather than the same finger. In contrast, other domains of working memory (e.g., auditory or verbal) have capacities larger than one, even when stimuli are presented to the same receptive field. It should also be noted that research by Harris et al. (2001) found a degree of somatotopy in vibrotactile working memory storage, as the effects of distractors were reduced when distractors were not presented to the same digit to which the target and probe stimuli were presented.

Bancroft et al. (2012) modified the standard vibrotactile memory paradigm by presenting subjects with two consecutive target stimuli (of different frequencies and equal durations) on each trial, followed by a probe stimulus that matched one of the two targets, did not match either target but was closer in frequency to one target or the other, or did not match either target and had a frequency that was equal in distance from both targets. Their subjects were instructed to report whether the probe stimulus matched either of the target stimuli. Bancroft et al. found the overall performance to be moderately above chance (55% correct responses), as well as finding above-chance performance for tests of both target items, and they argued that this was evidence that both target items were stored in memory.

This study was not conclusive, however: Due to the experimental design, an argument could be made that only one of the items was stored in memory. In the Bancroft et al. (2012) design, subjects were presented with two consecutive target stimuli of different frequencies, with the stimulus frequencies differing by 8 Hz. The subjects were then presented with a probe stimulus and asked to report whether the probe was of the same frequency as one of the target stimuli or of a different frequency from both. Five experimental conditions were used: ST1, in which the probe stimulus was of the same frequency as the first target stimulus; ST2, in which the probe stimulus was of the same frequency as the second target stimulus; DB, in which the stimulus frequency was between the frequencies of the target stimuli (and therefore different from each by 4 Hz); DT1, in which the stimulus frequency was separated from the first target stimulus by 4 Hz and from the second by 12 Hz; and DT2, in which the stimulus frequency was separated from the first

target stimulus by 12 Hz and from the second by 4 Hz. For example, if the first target had a frequency of 16 Hz and the second target had a frequency of 24 Hz, an ST1 probe stimulus would be 16 Hz, an ST2 probe would be 24 Hz, a DB probe would be 20 Hz, a DT1 probe would be 12 Hz, and a DT2 probe would be 28 Hz.

It could be argued that above-chance accuracy could be produced when only one stimulus was encoded per trial. For example, if only the first stimulus were encoded, subjects would display above-chance performance on DT2 trials, as the probe would differ from the target by 12 Hz. First-item-only encoding would also likely result in chance or below-chance performance on ST2 trials. If only the second stimulus were encoded, the converse would be true: Subjects would perform above chance on DT1 trials, and at or below chance on ST1 trials. However, if subjects did not encode only the first or only the second target on each trial, but rather the stimulus that they encoded varied from trial to trial, it would be possible for the subjects' overall performance to be above chance while they only encoded a single stimulus on each trial.

While the research of Bancroft et al. (2012) and Spitzer and Blankenburg (2011) is suggestive of a multi-item capacity for vibrotactile working memory, this small number of studies is insufficient to conclusively demonstrate a multi-item capacity. Furthermore, both studies had certain issues that raised the question of whether subjects could reliably and consistently store more than one stimulus in memory. As vibrotactile working memory is gaining in popularity as a model system for testing hypotheses about working memory in general, it will be important to confirm that vibrotactile working memory can store more than one item, as most domains of working memory are also considered to have multi-item capacities (Cowan, 2005).

To test for multistimulus capacity, we simulated four potential explanations of Bancroft et al.'s (2012) experiment: one in which only the first stimulus was encoded into memory, one in which only the second stimulus was encoded into memory, one in which one randomly selected stimulus was encoded into memory, and one in which both stimuli were encoded into memory. In the dual-item case, the two stimuli would be presented sequentially. In this case, when storing two stimuli in memory, their representations would overlap with each other. While this was identical to the method used in Simulation 1A, it differed in that it was beneficial to have both stimuli encoded into memory, as memory for either stimulus could be tested. In contrast, in Simulation 1A, it was maladaptive to encode the distractor into memory, as it would interfere with memory for the target stimulus. Essentially, we were testing the same neural mechanisms of encoding and maintenance in both simulations, but varying the experimental task. The question of interference would then become critical: If vibrotactile

working memory is capable of storing representations of more than one stimulus without catastrophic interference, we would expect the dual-stimulus simulation to provide the best fit to their experimental data. Alternatively, if the degree of interference was such that it prevented subjects from storing a representation of more than one stimulus in memory, we would expect the dual-stimulus simulation to be no better than one or more of the single-item simulations.

As in Simulation 1, two parameters were allowed to vary freely: The threshold parameter  $\theta$  varied within the range [0, 20], with a step size of 0.1, and the parameter  $\sigma$  varied within the range [0.5, 10], with a step size of 0.5. All of the stimuli were 1,000 ms in duration, and all delay periods were 600 ms in duration. One thousand trials were simulated in each condition for each point in the parameter space.

Results and discussion

The results of the simulations above are presented in Table 4, along with Bancroft et al.’s (2012) experimental findings. The dual-item case and the random-item case fit the experimental data equally well, with approximately equal degrees of error ( $SS = .011$  and  $.012$ , respectively) and of variance explained ( $R^2 = .906$  and  $.908$ , respectively). These cases performed substantially better than the first- or second-item models, which produced greater errors ( $SS = .080$  and  $.025$ , respectively) and smaller proportions of variance explained ( $R^2 = .210$  and  $.832$ , respectively).

In the present simulation, we aimed to determine whether previous research (e.g., Bancroft et al., 2012) could be interpreted as conclusive evidence that vibrotactile working memory has a multistimulus capacity. The results of the simulations suggested that Bancroft et al.’s (2012) results are not conclusive evidence for multistimulus capacity, but rather that a single-stimulus capacity is equally plausible. The dual-item and random-item simulations accounted for virtually equal amounts of error ( $SS = .011$  and  $.012$ ,

respectively) and variance explained ( $R^2 = .906$  and  $.908$ , respectively). As such, there is no reason to accept the dual-item interpretation of Bancroft et al.’s (2012) data over the single-item interpretation, and it appears that interference between the stored representations of stimuli may be the limiting factor. Given that the stimuli were presented to different receptive fields and were only retained for a short duration in Spitzer and Blankenburg’s (2011) study, we cannot say that we have unequivocal (or even strong) evidence for a multistimulus capacity in vibrotactile working memory.

How can a model in which only one randomly selected target stimulus is encoded produce above-chance memory for both the first and second target stimuli? Consider the following thought experiment: Imagine that only the first target were encoded. The frequency of an ST1 probe would differ from that of the target by 0 Hz; an ST2 probe, by 8 Hz; DT1 and DB probes, by 4 Hz; and a DT2 probe, by 12 Hz. If we set the decision-making threshold between 8 and 12 Hz, probes that differed from the target by 8 Hz or less (i.e., ST1, ST2, DT1, and DB probes) would be reported as “same,” and DT2 probes would be reported as “different.” As such, we would get good performance on ST1, ST2, and DT2 probes, and poor performance on DT1 and DB probes. If only the second target were encoded, performance would still be good on ST1 and ST2 probes and poor on DB probes. However, the pattern of performance on DT1 and DT2 probes would reverse, with good performance on DT1 probes and poor performance on DT2 probes.

If we look at the patterns of performance in these two single-stimulus cases (Table 5), we can see how the encoding of a randomly selected item could yield the results found by Bancroft et al. (2012). In both cases, subjects would perform well on ST1 and ST2 probes and poorly on DB probes. Subjects would also perform well on DT1 and DT2 probes in one case, and poorly in the other. These results are consistent with Bancroft et al.’s experimental results, which found good performance for ST1 and ST2 probes, moderate performance for DT1 and DT2 probes, and poor performance for DB probes. In fact, the results are consistent with our computational simulations of the first-item only, second-item only, and random-item cases. Of course, we must remember that input from sensory cortex can be noisy,

**Table 4** Simulation results from Simulation 3

	Experimental Results	Encoding Model			
		First-Item	Second-Item	Random-Item	Dual-Item
ST1	.64	.67	.56	.64	.61
ST2	.70	.53	.72	.64	.66
DB	.33	.41	.33	.27	.26
DT1	.59	.39	.61	.53	.57
DT2	.50	.58	.37	.54	.56
SS	N/A	.080	.025	.012	.011
$R^2$	N/A	.210	.832	.908	.906
$\theta$	N/A	1.7	1.5	1.2	0.4
$\sigma$	N/A	9.0	6.5	4.0	4.5

**Table 5** Hypothetical performance by single-item models with a threshold between 8 and 12 Hz

	First-Item	Second-Item	Random-Item
ST1	Good	Good	Good
ST2	Good	Good	Good
DB	Poor	Poor	Poor
DT1	Poor	Good	Moderate
DT2	Good	Poor	Moderate



introducing another degree of error: If the decision threshold is close enough to the actual frequency differences, sometimes subjects will correctly identify ST2 probes, sometimes they will incorrectly report DT or DB probes as being the same frequency as the target, and so forth. This accounts for the error in our simulations.

Why would subjects encode a random item, rather than a more consistent pattern of encoding? The answer likely lies in the competition between the attempt to encode both target stimuli and the protection of the contents of memory through the inhibition of stimuli. Bancroft et al.'s (2012) task required subjects to retain both target stimuli in memory, unlike Bancroft and Servos's (2011) and Bancroft, Servos, et al. (2011) interference tasks. Furthermore, the second target stimulus in Bancroft et al.'s (2012) task was of the same duration as the first stimulus, potentially producing a greater degree of overwriting than the relatively short distractors used by Bancroft and Servos (2011) and Bancroft, Servos, et al. (2011). As such, it is possible that subjects may have alternated between inhibition of the second target (in order to protect the contents of memory) and encoding of the second target (thereby entirely overwriting the contents of memory).

In the present study, we used the first computational simulations of vibrotactile working memory capacity to test whether this memory store is capable of storing representations of more than one stimulus. Establishing a multi-item capacity for vibrotactile working memory will be critical for drawing comparisons between vibrotactile working memory and other domains of working memory, given that most such domains are known to have a multi-item capacity (Cowan, 2005). The results of our simulations suggest that we lack conclusive evidence that subjects can store more than one vibrotactile stimulus in the same sensory receptive field.

This does not contradict the findings of Spitzer and Blankenburg (2011), who reported that subjects were able to temporarily retain stimuli presented to different receptive fields (e.g., different index fingers). It appears that the spatial distribution of stimuli may play a role in vibrotactile working memory capacity. Indeed, Harris et al. (2001) found that subjects performed best when the target and probe were presented to the same digit, and that the effects of an irrelevant distractor stimulus were ameliorated when the distractor was presented to a different digit than the target and probe. However, most domains of working memory are able to store multiple items or stimuli, even when they are presented to the same sensory receptive field.

This question has interesting implications for the theoretical interpretation of vibrotactile working memory experiments. Vibrotactile working memory has many of the same traits as other working memory systems: for example, the involvement of attentional systems (Hannula et al., 2010; Neuvonen et al., 2008; Savolainen et al., 2011; Sörös et al., 2007); vulnerability to interference from irrelevant stimuli

(Bancroft & Servos, 2011; Bancroft, Servos, et al., 2011; Harris et al., 2001), and the involvement of prefrontal cortex (Jun et al., 2010; Preuschhof, Heekeren, Taskin, Schubert, & Villringer, 2006; Romo & Salinas, 2003; Sörös et al., 2007). Furthermore, the simple coding of stimuli in the neural systems underlying vibrotactile working memory makes it an appealing model system for investigating working memory, and recent work by Spitzer and Blankenburg (2011; see also Spitzer et al., 2010) has also demonstrated the potential of vibrotactile working memory as a model system. While a multi-item capacity is a common trait of working memory systems, the present study has demonstrated that we currently lack conclusive evidence that vibrotactile working memory is capable of storing representations of multiple stimuli in the same sensory field. At the same time, evidence does exist that vibrotactile working memory is capable of storing multiple stimuli when they are presented to different sensory fields.

How does this affect our ability to compare vibrotactile working memory to other domains of working memory? This question remains open. Indeed, the relationship between "traditional" working memory tasks (e.g., verbal working memory) and scalar memory tasks (also known as *unidimensional* or *parametric* memory) remains open. Scalar memory tasks (including vibrotactile working memory) have recently received substantial research interest. Research by Lemus, Hernández, and Romo (2009a, b) has demonstrated that the neural codes and cortical organization underlying auditory working memory for pitch (a form of scalar memory) are similar to those underlying vibrotactile working memory. These neural codes are simpler than those often proposed for more complex stimuli.

However, as in many other working memory tasks, attentional and inhibitory processes are involved in vibrotactile working memory. Research has shown that inhibition helps to protect the contents of vibrotactile working memory (Bancroft, Servos, et al., 2011; Hannula et al., 2010; Savolainen et al., 2011), and imaging research has pointed to a role for attention in selecting task-relevant stimuli (Haegens, Luther, & Jensen, 2012; Sörös et al., 2007). These properties of vibrotactile working memory are consistent with proposed roles for attentional processes in working memory in general (e.g., Engle, 2002; Engle & Kane, 2003; Kane, Bleckly, Conway, & Engle, 2001). While the information being stored in vibrotactile working memory (and, by extension, the capacity thereof) differs from that in other domains of working memory, the mechanisms involved in encoding and maintaining that information appear to be similar. As such, vibrotactile working memory is likely to remain useful for studying working memory in general. We also point out that the results of the present study do not contradict a multi-item capacity for vibrotactile memory. Rather, they show that the experimental data presently available are insufficient to conclusively decide this issue, one

way or the other. The capacity of vibrotactile working memory remains an important and open question.

## General discussion

The results of our computational simulations are consistent with the notion that interference in vibrotactile working memory can be due to the encoding of irrelevant sensory information. The variable-encoding overwriting simulation (Simulation 2) produced less error and explained more variance in the empirical data than did the full-duration overwriting simulation (Simulation 1A) or the nonoverwriting model (Simulation 1B). Furthermore, Simulation 2 accurately replicated the magnitude of the interference effect reported by Bancroft and Servos (2011). This suggests that subjects are, in fact, encoding distractors, even though they are instructed not to do so—a finding with some intriguing implications. However, the results of Simulation 2 also suggest that subjects do attempt to inhibit the processing of irrelevant sensory stimuli, as was suggested by the work of Hannula et al. (2010). The results of Simulation 3 suggest that, contrary to recent experimental reports, the combination of inhibition of stimuli and overwriting of the contents of memory may very well limit the effective capacity of vibrotactile working memory to one stimulus.

It has previously been suggested that interference in working memory can occur when irrelevant stimuli are encoded into memory (Lange & Oberauer, 2005; Nairne, 1990; Neath, 2000; Oberauer, 2009; Oberauer & Kliegl, 2006; Oberauer & Lange, 2008). The implications of the present study are compatible with earlier research into overwriting. A question left unanswered by the present study, however, is which account of overwriting is most compatible with the interference effects found in experimental and computational studies of vibrotactile working memory. Answering this question may require a more complicated modeling paradigm or experimental research using the methods of Spitzer, Wacker, and Blankenburg (2010) or Romo and colleagues (see Romo & Salinas, 2003, for a review). The present study integrates previous behavioral and neuroscientific research and provides the first computational demonstration that interference in working memory occurs when irrelevant stimuli are encoded.

A recent TMS study suggested that inhibition of activity in somatosensory cortex during the delay period improves performance or response times on vibrotactile working memory tasks, and also reduces the effects of distractors (Hannula et al., 2010). More recently, a magnetoencephalography study provided corroborating evidence (Haegens, Luther, & Jensen, 2012). It seems reasonable to suggest (as we did in Simulation 2) that endogenous inhibitory processes that

are ongoing during the delay period would reduce the degree to which a distractor is processed.

Finally, the present study provides testable predictions about the contents of the memory store. Spitzer, Wacker, and Blankenburg (2010; see also Spitzer & Blankenburg, 2011) devised methods for extracting the frequency of stimuli stored in vibrotactile working memory by examining modulations of prefrontal beta-band electroencephalography activity. If distractors are, in fact, stored in vibrotactile working memory, we would expect to find evidence for their storage using the methods of Spitzer et al. Single-cell recordings from prefrontal neurons also offer the potential to confirm the encoding of distractors.

The results of our simulations are consistent with the argument that interfering distractor stimuli are encoded into vibrotactile working memory, affecting task performance. In making this argument, we have provided a concise neurocomputational model of interference in vibrotactile working memory, and have provided results consistent with a previous hypothesis. It should be noted, however, that recent analyses of single-cell recordings from primate behavioral studies have found complex time- and stimulus-frequency-dependent patterns of activity in prefrontal neurons (Jun et al., 2010). The model used in the present article does not reproduce those patterns of activity, and it is possible that a rate-based model will be insufficient to reproduce aspects of neuronal activity in the cortical systems underlying vibrotactile working memory. However, as was pointed out by Jun et al., no extant models of vibrotactile working memory fully grasp the complexities of prefrontal firing patterns, and, in fact, as yet there is no consensus on how the stimulus comparison and decision-making processes are implemented on a neural level (cf. the models of, e.g., Machens et al., 2005, and Miller & Wang, 2006). Nevertheless, while the Miller and Wang model is able to account for a number of results from the experimental literature, modeling efforts using more biologically detailed models may very well be necessary to account for all of the properties of neural and behavioral data in the empirical literature.

In the present article, we have demonstrated that a simplified neurocomputational model of prefrontal cortex using only two free parameters is capable of simulating complex patterns of behavioral results and explaining the vast majority of variance in experimental data. Additionally, the model is capable of explaining a variety of interference effects in behavioral experiments in humans. Our present results open up a number of interesting questions: For example, can vibrotactile working memory reliably store multiple stimuli when they are presented to the same sensory field? What is the precise mechanism of overwriting in vibrotactile memory? And could subjects improve their ability to inhibit irrelevant stimuli with practice? Further computational and experimental research will be necessary to answer these questions.

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