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Neural Mechanisms of Interference and Storage in Vibrotactile Working Memory

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THESIS

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Abstract

Vibrotactile working memory has attracted increasing attention in recent years. Substantial research into the neural correlates has been conducted, especially using single-cell paradigms in non-human primates (Romo & Salinas, 2003). The vibrotactile working memory system uses a relatively simple neural code for the representation of stimuli, making it possible to determine when stimulus information is present in the various cortical areas thought to be involved. In humans, vibrotactile working memory displays properties (such as overwriting mechanisms of interference) that make it an ideal system for testing general theories of working memory. In the present study, we demonstrate that vibrotactile working memory has a capacity larger than one item, a critical trait of other working memory tasks. Further, we demonstrate the existence of overwriting and non-overwriting mechanisms of interference, providing strong evidence in support of feature overwriting theories, and also providing a neural mechanism for overwriting.

Acknowledgements

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Introduction

In recent years, somatosensory working memory has received increasing attention from researchers. The neural systems involved are well-characterized at the cellular level, making it an ideal model system for understanding working memory as a whole and testing the predictions of working memory theories. Notably, however, the large majority of research into somatosensory working memory has been carried out using animal models. The present thesis has three aims: First, to extend findings from animal research to humans; second, to resolve a number of questions that cannot be easily answered using single-cell paradigms; and third, to use findings from somatosensory working memory to clarify important outstanding issues in working memory theory. The prospect of identifying a new form of working memory is especially exciting, given recent findings that link working memory to many important cognitive traits, such as reading ability, mathematical skill, and general intelligence (see Kane & Engle, 2002 for a review; also Kane & Engle, 2003). Further, deficits in working memory are implicated in a number of disease processes, such as schizophrenia (Goldman-Rakic, 1994), dementia (Morris, 1994), and focal brain damage (Malouin, Belleville, Richards, Desrosiers, & Doyon, 2004). Identifying a new form of working memory gives us another tool for assessing overall cognitive and neural function. This is especially exciting given the non-verbal nature of vibrotactile stimuli, as many pathological conditions affect language abilities at a relatively early stage (Murdoch, Chenery, Wilks, & Boyle, 1987).

Experimental paradigms

While research into working memory has been carried out in both animals and humans, and using single-cell recording, event-related potentials (ERP), magnetoencephalography (MEG), functional magnetic resonance imaging (fMRI), and behavioural paradigms, almost all

such research has used the same vibrotactile delayed match-to-sample paradigm. Vibrotactile stimuli are vibrations presented to the hand (most commonly to the index finger). The delayed match-to-sample paradigm is commonly used in working memory research. Subjects are presented with a stimulus (the target), a delay period, and a second stimulus (the probe). Subjects are then asked to make some comparison between the target and probe stimuli (most commonly whether they are the same or different). This involves three processes: Encoding of stimuli, maintenance of stored representations, and the comparison between stored representations and the probe stimulus. There are substantial disagreements as to how these processes are instantiated at the neural level; we will examine competing accounts of working memory in a later section.

Neural mechanisms underlying vibrotactile working memory

The majority of published research on vibrotactile working memory has been carried out using single-cell recording in macaques. While there is less human research literature, findings in macaques appear to be generally consistent with those in humans. There is strong evidence that there are four anatomically and functionally distinct cortical regions involved in the processing and storage of stimulus frequency information in vibrotactile working memory: Primary somatosensory cortex (SI), secondary somatosensory cortex (SII), prefrontal cortex (PFC), and medial premotor cortex (MPC) (Romo & Salinas 2003). We are primarily interested in SII and PFC, as SI is thought not to be involved in stimulus storage (Haegens et al., 2010; Spitzer et al., 2010), and MPC is thought to be involved in preparing motor responses to decisions made in PFC and SII.

Single-cell recordings from SI have demonstrated that neuron firing rates are monotonic functions of stimulus frequency, and that the neurometric sensitivities to frequency of individual

neurons are very similar to the overall psychometric sensitivities of monkeys (Hernández et al. 2000). While periodicity also varies as a function of task parameters, it does not appear to covary with performance, suggesting that firing rate is the primary method of transmitting information (Salinas et al. 2000).

Secondary somatosensory cortex appears to play two roles in the vibrotactile working memory system: Stimulus processing, and decision-making. Secondary somatosensory cortex demonstrates activity related to stimulus presentation, with activity persisting into the delay period for several hundred milliseconds after stimulus offset (Romo, Hernández, Zainos, Brody, & Salinas 2002). Similar to neurons in SI, neurons in SII have firing rates that are functions of stimulus frequency (Salinas et al. 2000). Periodicity is largely absent in the firing patterns of SII neurons, suggesting that mean firing rate is the mechanism of information transmission (Salinas et al. 2000).

Upon presentation of a probe stimulus, neurons in SII present an intriguing pattern of behaviour (Romo, Hernández, Zainos, Lemus, & Brody 2002). Within the first 200ms of stimulus presentation, firing rates are functions of the probe stimulus frequency. After 200ms, the firing rate does not appear to be a function of target frequency, but rather reflects a comparison between the frequencies of the target and probe stimuli, with one subset of neurons having a higher firing rate if the target stimulus has a higher frequency than the probe, and another subset having the converse pattern. While activity in SII neurons during this period is correlated with behavioural responses, it is not entirely clear where SII falls within the decision-making hierarchy. While comparison-based activity in SII neurons precedes similar activity in primary motor cortex, it occurs later than comparison activity in MPC, which in turn occurs later than comparison activity in PFC (Romo et al., 1999, 2002). It is possible that decision-making

occurs in PFC, which then drives activity in SII. It has been demonstrated that PFC can drive activity in the inferior temporal cortex in a similar fashion during a visual working memory task (Tomita et al. 1999).

Implications for working memory theory

Perhaps the most interesting byproduct of research into somatosensory working memory has been the implications for various theories of working memory. While working memory has been a well-established topic of study for decades, with a number of attempts to construct a comprehensive theory of working memory (e.g., Baddeley & Hitch, 1974), no commonly-accepted theory yet exists. Research into somatosensory working memory has produced results that pose substantial (and potentially intractable) challenges to leading attempts to build a general theory of working memory. Problems with current theories fall into three broad categories: Theories that do not have the ability to represent somatosensory information, theories that do have the ability to represent somatosensory information, but which make predictions that are inconsistent with the experimental literature, and theories that do have the ability to represent somatosensory information (or can easily be modified to do so), but which do so in such a vague or ambiguous manner as to make no useful predictions.

Baddeley's multiple-components model of working memory has been (and still is) influential, in no small part due to its longevity (Baddeley & Hitch, 1974; Repovs & Baddeley, 2006). However, the multiple-components model has no ability to handle somatosensory stimuli. The model contains components to handle auditory stimuli (the phonological loop) and visual stimuli (the visuospatial sketchpad), a component that controls the processing and handling of information (the central executive) and a recently-added component that is capable of binding together information from the other components, as well as from episodic memory

(the episodic buffer) (Baddeley, 2000). Notably, however, none of these components are capable of handling somatosensory stimuli. While it is theoretically possible that subjects are somehow recoding vibrotactile stimuli so they can be represented in other subsystems (for example, by a verbal code), human neuroimaging data (Haegens et al., 2010; Spitzer et al., 2010) has failed to find activation in visual, auditory, or language cortex consistent with the recoding of vibrotactile stimuli. While we could add more subsystems to the multiple-components model to allow the representation of vibrotactile stimuli, this seems like an inelegant approach. Further, there is little in the present model to suggest how we would instantiate the new component with respect to interaction with other components. Further, if we continue to add components to explain every working memory phenomena the present version of the model cannot explain, the model will rapidly lose the simplicity and parsimony that made it influential in the first place.

Cowan's (1999, 2005) embedded-processes model also has difficulties explaining vibrotactile working memory. The embedded-processes model identifies working memory with an activated subset of long-term memory (Cowan 1999, 2005; Morrison, 2005). This does not appear to account for vibrotactile working memory. First, it is unclear whether vibrotactile stimuli are (or can be) stored in long-term memory, especially considering the short durations of stimuli used in vibrotactile tasks (often shorter than 1000ms). Secondly, and perhaps more damningly, hippocampal activity has not been identified in either of the two extant fMRI studies of vibrotactile working memory in humans (Preuschhof et al., 2006; Sörös et al., 2007). If vibrotactile working memory depends on long-term memory, we would expect hippocampal activation to vary with performance. Further, neuropsychological patients with severe medial temporal lobe damage often display intact short-term memory (Corkin, 2002). The embedded-

processes model appears to have little ability to explain vibrotactile working memory, and it does not appear to be easily modifiable to do so.

More recently, Postle (2006) has taken a different approach to working memory and argued that it is an emergent function of pre-existing systems in the brain, rather than a discrete and separate system. In short, Postle's model is a sensory-maintenance model, where information is stored in sensory cortex and maintained by attentional systems. This is a parsimonious suggestion, as sensory cortex is already capable of processing the stimuli that are stored in working memory, and attentional systems are already capable of modulating activity in sensory cortex in response to both sensory and cognitive cues. Further, the model is based around what we know about the neural underpinnings of working memory, rather than how we believe the cognitive processes involved function. However, in the case of vibrotactile working memory, Postle's model is not congruent with either single-cell research in primates or with human neuroimaging research. Substantial work by Romo and colleagues (see Romo & Salinas, 2003 for a review) has demonstrated that activity does not persist in primary or somatosensory cortex throughout the delay period of vibrotactile working memory tasks, but rather that information is stored in prefrontal regions. In a human ERP study, Spitzer et al. (2010) found no delay-period activity in SI or SII, but did note that prefrontal activity varied as a function of stimulus frequency. Similarly, in a human MEG study, Haegens et al. (2010) found that task performance was significantly correlated with delay-period PFC activity, but not SII activity. While Postle's model is elegant and parsimonious, it is inconsistent with the literature on vibrotactile working memory.

There are, of course, other models of working memory. (e.g., O'Reilly, Braver, and Cohen, 1999) The three we have selected, however, are some of the most influential: The

multiple-components model is often considered to be the closest we have come to a "standard" model of working memory (Nairne, 2002), the embedded-processes model unifies long-term and working memory, and Postle's sensory-maintenance model is parsimonious and is heavily informed by the neuroscience literature. However, as vibrotactile working memory does not easily fit into any of these models, it might be argued that vibrotactile working memory is not actually a form of working memory. On the surface, this might appear a reasonable rebuttal. The stimuli used in typical working memory tasks, (such as word span or digit span) are more complex than vibrotactile stimuli, which can be described along one dimension (stimulus frequency). However, vibrotactile discrimination is a challenging task, independently of the mnemonic aspects of the task. When the discrimination process is difficult, it places more demand on the mnemonic process, as relatively small losses of information may lead to the failure of the discrimination process. Hannula et al. (2010) demonstrated that even ongoing, baseline activity in primary somatosensory cortex can interfere with vibrotactile working memory. As such, attentional processes must be engaged to protect the contents of memory. It would then appear that vibrotactile working memory has similar attentional demands to other working memory tasks.

The present study is comprised of three experiments and a computational simulation. Experiments 1 and 2 examine mechanisms of interference in vibrotactile working memory. Experiment 3 and Simulation 1 examine the capacity of the vibrotactile working memory system.

Experiment 1

If vibrotactile working memory is, in fact, a form of working memory, we would expect vibrotactile working memory to display effects found on other working memory tasks. For example, Harris, Harris, and Diamond (2001) found that a distractor stimulus presented between

the target and probe reduces performance on a vibrotactile working memory task, an effect found in other domains of working memory (e.g., Mercer & McKeown, 2010). What is unclear is the mechanism or mechanisms of interference. One account of interference in working memory suggests that processing (or inhibiting the processing of) a stimulus, while simultaneously maintaining a previously-stored item in memory places an increased demand on shared cognitive resources (e.g., attention) (Brown, 1997; Kane & Engle, 2000). As such, stored representations are likely to degrade or be lost. Alternately, feature overwriting accounts of interference (e.g., Nairne, 1990, Oberauer, 2009) suggest that stimuli are stored in a finite set of "feature detectors". When a distractor is presented, it competes with stored items for some of those feature detectors, and therefore may overwrite part of the stored representations.

Vibrotactile working memory is an ideal system in which to test these theories. While the feature detectors hypothesized in overwriting theory are treated in an abstract fashion, vibrotactile working memory gives us a neural analogue to feature detectors. The neural code used to represent stored stimuli is quite simple - neurons in PFC have firing rates that are monotonic functions of stimulus frequency. Many of these neurons have non-linear tuning curves, making them an ideal biological analogue to the abstract feature detectors suggested in overwriting theory.

In the present experiment, we present distractor stimuli during the delay period between the target and probe. Critically, we vary the frequency of the distractor as a function of target frequency. As such, on trials where the probe is a different frequency from the target, our distractor stimulus can be either shifted towards the probe frequency (for example, a target frequency of 18 Hz, a distractor frequency of 20 Hz, and a probe frequency of 22 Hz), or shifted away from the probe frequency (for example, a target frequency of 18 Hz, a distractor frequency

of 16 Hz, and a probe frequency of 22 Hz). If the distractor is overwriting the stored

representation of the target stimulus, the distractor frequency information should be present in

memory, and when subjects make their probe/target comparison, they will actually compare the

probe against some combination of target and distractor. As such, we would expect subjects to

make more "different" responses when the distractor is shifted away than towards, and/or more

"same" responses when the distractor is shifted towards than away.

<div align="center">Methods</div>

Participants

Eighteen subjects participated in the study for a payment of $11. All subjects self-identified as

being right-handed. Four subjects were excluded from analysis after reporting an inability to

make frequency discriminations and/or performing below chance.

Apparatus and Procedure

Subjects were presented with vibrotactile stimuli to the right index finger using a

magnetomechanical device similar to that used by Graham et al. (2001). The device was

constructed by placing a speaker cone within a plastic housing and gluing a nylon screw to the

top of the cone such that the surface of the screw was flush with the top surface of the housing.

The device was driven by wave files of a pure tone delivered to the speaker. Subjects received a

1,000-ms target stimulus, followed by a 900-ms delay, a 250-ms distractor stimulus, a 350-ms

delay and a 1,000-ms probe stimulus. Subjects were instructed to compare the frequency of the

target and probe stimuli and to ignore the distractor stimulus. All target and probe stimuli were

14, 18, 22 or 26 Hz. There were two test conditions: same (with target frequency and probe

frequency the same) and different (with the probe frequency either ±4 Hz compared to the target

frequency).

Distractor stimulus frequencies were either the same as the target stimulus (a 0 Hz shift), ±2 Hz, or ±4 Hz.

Critically, in different-test trials, the frequency shift could be towards or away from the probe stimulus. For example, if the target stimulus was 18 Hz and the probe was 22 Hz, a distractor stimulus with a 4-Hz shift could be 14 Hz (away from the probe) or 22 Hz (towards the probe). This gives a total of eight conditions: same test, 0 Hz interference shift; same test, 2 Hz interference shift; same test, 4 Hz interference shift; different test, 0 Hz interference shift; different test, 2 Hz interference shift towards probe; different test, 2 Hz interference shift away from probe; different test, 4 Hz interference shift towards probe; and different test, 4 Hz interference shift away from probe. There were a total of 240 same-test trials (80 per interference condition) and 240 different-test trials (48 per interference condition).

Subjects were instructed to compare the first and last stimuli, and to ignore the distractor stimulus. Subjects were instructed to press the 's' key if they believed the target and probe were the same frequency, and the 'd' key if they were different frequencies.

Results and Discussion

Proportions of correct responses are presented in Table 1. Performance was significantly better in the same-test condition than the different-test, $t(13) = 4.858, p < .001$. The magnitude of distractor frequency shift did not have an effect on performance in the same-test condition, $F(2, 39) = .033, p = .968$. In the different-test condition, proportion of correct responses was averaged across away- and towards-shift interference conditions. A 2X2 repeated-measures ANOVA was then performed on hit rates with direction of frequency shift (away from vs. towards the probe frequency) and magnitude of frequency shift (2 vs. 4 Hz) as factors and correct responses as the dependent variable. A significant main effect of direction was found, $F(1, 13) = 22.918, p < .$

001, with performance significantly better in the away-shift condition than the towards-shift condition. The magnitude of frequency shift and the interaction did not reach significance. As predicted by feature overwriting theory, the direction of the distractor stimulus frequency shift had a significant effect on performance. While subjects were instructed to compare the probe stimulus to the target stimulus, the results suggest that decision-making was partially based on the frequency of the distractor stimulus.

When subjects are presented with a vibrotactile stimulus, frequency information is encoded in the firing rates of neurons in contralateral SI, followed by bilateral SII (Romo & Salinas, 2003; Haegens et al., 2010). Information is then encoded and maintained in the firing rates of prefrontal neurons during the delay period (Romo et al., 1999; Spitzer et al., 2010). Prefrontal neurons appear to have frequency preferences: When recording from neurons in the inferior convexity, Romo et al. (1999) found 50% to be monotonically increasing and 44 per cent to be monotonically decreasing as a function of vibrotactile frequency. Feature overwriting accounts of interference suggest that information in short-term memory is maintained by a set of feature detectors and that interfering stimuli are also stored in these units, overwriting previous representations (Oberauer, 2009; Mercer and McKeown, 2010). The neurons that Romo et al. (1999) identified in prefrontal cortex as encoding vibrotactile frequency can be considered as analogous to feature units. Notably, this is different from more traditional overwriting theories, in that all feature units in vibrotactile working memory represent a single feature—vibrational frequency, and therefore incoming stimuli compete for all feature detectors, rather than a subset.

Experiment 2

Experiment 1 added an interfering distractor stimulus to the standard delayed match-to-sample paradigm and demonstrated that the distractor stimulus was (at least partially) encoded in

memory. Notably, however, the distractor stimulus was presented such that there was a 350ms gap between distractor offset and probe onset. As information tends to persist in SII for approximately 400ms after stimulus onset (Romo & Salinas, 2003), it is possible that the distractor information is not overwriting the stored representation of the target, but rather is being combined with target information during the decision-making process. The present study aims to clarify this issue by varying distractor timing such that we can compare effects when neural activity due to distractors overlaps with that due to the probe, against effects when the distractor does not overlap with the probe.

Method

Participants

Thirty-three undergraduate students from Wilfrid Laurier University participated for course credit. All subjects self-identified as right-handed. Two subjects were excluded from analysis due to performance below chance.

Apparatus and Procedure

Subjects were presented with vibrational stimuli to the right index finger using a magnetomechanical device similar to those used by Graham et al. (2001). The device was constructed by gluing a nylon screw to a speaker cone, and placing the cone within a plastic housing such that the surface of the screw was flush with the top surface of the housing. The device was driven by WAV files delivered to the speaker, using an IBM-compatible PC running SuperLab 2.0 (San Pedro, CA: Cedrus). To mask any residual sound from the device, subjects were presented with white noise through headphones, and volume was adjusted until subjects reported they did not hear any residual sound.

Subjects engaged in a brief (40 trials) delayed match-to-sample practice session before beginning the experiment. Subjects were presented with two 1000ms stimuli, separated by an unfilled 1500ms delay period. Target and probe stimuli were either the same or different and separated by a 4 Hz frequency difference. Subjects were instructed to make a "same" response (by pressing the 's' key) if they believed the probe was the same frequency as the target, and a "different" response (by pressing the 'd' key) if they believed the probe was a different frequency from the target. Subjects were provided with visual feedback during the practice session.

During the actual experiment, all target stimuli (denoted f1) were 18 or 22 Hz. Probe stimuli (denoted f2) were either the same frequency as the target, or were +/- 4 Hz. Distractor stimuli were all equal to f1 +/- 3 Hz. Target and probe stimuli were all 1000ms. The delay period was 1500ms. The distractor stimulus was 250ms, with an onset of either 250ms into the delay period (the early condition), 625ms (the middle condition), or 1000ms (the late condition). Subjects received 168 same-probe trials and 168 different-probe trials, for a total of 336 trials. Subjects were instructed to press the 's' key to make a "same" response, and the 'd' key to make a "different" response. There was a 500ms delay between subject response and the beginning of the next trial. Subjects received a break approximately halfway through the experiment.

Results and Discussion

Mean correct responses are reported in Table 2. A 2 (test type, same vs. different) X 3 (distractor timing, early vs. middle vs. late) repeated-measures ANOVA was performed on correct responses. A significant main effect of test type was found, $F(1, 30) = 24.931$, $MSe = .059$, $p < .001$, $eta2 = .454$, with higher performance on same trials than on different trials. While the main effect of timing did not reach significance, $(F < 1)$, the interaction did, $F(2, 60) = 4.789$,

MSe = .007, *p* = .012, *eta2* = .138. Paired-sample *t*-tests were used to break down the interaction, and found a significantly better performance for the same/middle than the same/late condition (*t*(30) = 2.999, *p* = .005), but marginally worse performance for different/middle than different/early, *t*(30) = 2.011, *p* = .053. These results can be interpreted as an overall increase in the number of "same" responses, and subjects made significantly more "same" responses on middle-distractor trials than on early trials, *t*(30) = 3.206, *p* = .003. Subjects also made marginally more same responses on late-distractor than early-distractor trials, *t*(30) = 1.799, *p* = . 082.

A 3 (distractor timing, early vs. middle vs. late) X 2 (distractor frequency shift, towards probe vs. away) repeated-measures ANOVA was performed on correct responses to different-probe trials in order to test for overwriting effects. An overwriting effect would appear as significantly more correct "different" responses to away-shift than towards-shift distractors on different-probe trials. There was a significant main effect of frequency shift direction, *F*(1, 30) = 20.028, *MSe* = .006, *p* < .001, partial *eta2* = .400, confirming the existence of an overwriting effect. The main effect of timing approached significance, *F*(2, 58) = 2.213, *MSe* = .010, *p* = . 118, partial *eta2* = .069, suggesting performance was not equal at all distractor timings. The interaction did not reach significance, *F*(2, 58) = .688, *p* = .507. Planned paired-sample *t*-tests were performed to compare different-towards and different-away performance in order to determine the existence of an overwriting effect. A significant overwriting effect was present with both early (*t*(30) = 3.325, *p* = .002) and late (*t*(30) = 3.184, *p* = .003) distractors, but not with middle distractors (*t*(30) = 1.341, *p* = .190).

A net overwriting effect was present for early and late distractors, consistent with the distractor overwriting the stored target representation, rather than the distractor being

incorporated into the decision-making process. Intriguingly, distractor timing had an effect on overall performance, with middle distractors producing significantly better performance on same-probe trials, and slightly worse performance on different-probe trials. This pattern of results can actually be treated as an increase in the number of same responses, (although this increase was not significant), independent of trial type, as more same responses to same probes will give better performance, and more same responses to different probes will give worse performance. Further, subjects did not present a significant overwriting effect with middle distractors. It was established in Experiment 1 that subjects have a bias towards making same responses. Vibrotactile frequency discrimination is a challenging task, independent of the memory aspects of the present task (Sinclair & Burton, 1996). For subjects to make a "different" response, they must be able to discriminate between the stored representation of the target, and the probe stimulus. If they cannot, either due to a weak stored representation of the target, or due to the psychophysical difficulty of the task, they will make a "same" response.

In this case, the increased number of "same" responses to trials containing a middle distractor could be due to a degraded memory trace. Given the lack of a significant overwriting effect, middle distractors appear able to interfere with performance in the absence of overwriting. Given the limited research into vibrotactile interference, the mechanism of interference is unclear, but attentional processes are likely to be involved. It is well-established that stimulus processing/encoding and working memory maintenance are separate processes that share some common neural resources (Cohen et al., 1997), and there is evidence that maintenance can affect stimulus encoding (Rypma & D'Esposito, 1999; Rypma et al., 1999). If simultaneous maintenance and encoding of vibrotactile stimuli cannot be performed effectively in parallel, we

would expect degradation of stored traces (and reduced performance), as well as reduced encoding of the incoming stimulus (in this case, a reduced overwriting effect).

It follows that the effects of simultaneous stimulus processing and encoding would be most pronounced on middle distractors. Middle distractors are processed more thoroughly than early or late distractors, as early distractors overlap with activity in SII that is persisting from the processing of the target stimulus (reducing the degree to which the distractor is processed), and persisting activity in SII from late distractors overlaps with activity from the probe stimulus (also reducing the degree to which the distractor is processed). Further, given the overlap of target/early distractor neural activity, subjects may not engage maintenance processes until distractor offset, preventing deleterious effects due to attentional requirements. In the case of late distractors, encoding processes are engaged at the same time as maintenance processes, but neural activity due to late distractors overlaps with the probe, giving a shorter period of encoding/maintenance overlap than for middle distractors.

It may also be possible that attentional resources are required for the inhibition of middle distractors. Evidence in favour of this explanation comes from Hannula et al. (2010), who applied TMS to the middle frontal gyrus (MFG), a region involved in inhibiting activity in primary somatosensory cortex. Increasing activity in MFG during the delay period increased behavioural performance, suggesting that baseline activity in sensory cortex (even in the absence of a stimulus) can interfere with performance. Further, Sörös et al. (2007) used fMRI to compare neural activity on vibrotactile working memory tasks with and without a distractor during the delay period, and found increased activity in attention-related regions (including MFG). However, it is not clear why the middle distractor would be inhibited, but not the late distractor.

The existence of a non-overwriting method of interference could be tested using methods already in the literature. Romo et al. have provided measures of how many neurons in a given population contain information about a target stimulus (see Romo & Salinas 2003 for a review). It would appear relatively straightforward to apply these methods to determining how many PFC neurons are encoding stimulus information after distractor presentation, and whether there is a net loss of total stimulus information. Further, a recent ERP study found that stimulus frequency can be determined based on modulation of frontal activity in the beta band, suggesting that it may be possible to develop a similar measure in humans (Spitzer et al., 2010). Human neuroimaging methods are also well-suited for testing attentional load. Increased attentional cost for middle distractors may present as increased activity in frontal and parietal regions known to be involved in attention (Sörös et al., 2007; Haegens et al., 2010) and working memory encoding (Rypma & D'Esposito, 1999).

In the present study, we demonstrate that feature overwriting in vibrotactile memory is due to interference with a stored trace, rather than interference with the decision-making process. Further, we demonstrate an aspect of interference that does not involve overwriting stored representations. The precise mechanism of this effect is unknown, but may very well involve attentional processes.

Experiment 3

Experiments 1 and 2 suggest that stored stimuli may be susceptible to high levels of interference. This suggests that the capacity of vibrotactile working memory may be limited to one item - a property that would significantly diminish our ability to compare vibrotactile working memory to other working memory systems, most of which are able to store multiple items (e.g., Miller's (1956) "magic number seven-plus-or-minus-two"). The present study

extends the standard delayed match-to-sample paradigm to use two target stimuli. Subjects are presented with a test set of two separate stimuli, with a vibrotactile frequency difference of 8 Hz, and a test stimuli/probe frequency difference of 4 Hz. Experiment 1 demonstrated that subjects are able to perform significantly above chance on a delayed match-to-sample task with a 4 Hz difference between the target and the probe. PFC neurons with non-linear tuning curves may allow the large frequency difference between target items to reduce interference, and allow storage of separate representations of the stimuli. Synchronous firing of neurons encoding a given item may also reduce interference between stored representations. It has been suggested that increasing gamma-band activity (often found to be correlated with working memory load) is representative of ensembles of prefrontal neurons encoding items in working memory (Howard et al., 2003; Jokisch & Jensen, 2007).

If subjects are able to perform above chance on tests for memory for both the first and second targets, it suggests that they are able to encode more than one item in memory, strengthening the relationship between vibrotactile working memory and working memory in other domains.

Method

Subjects

Twelve undergraduate students at Wilfrid Laurier University participated for course credit. All subjects self-identified as right-handed.

Apparatus and Procedure

Subjects were presented with vibrational stimuli to the right index finger using a magnetomechanical device similar to those used by Graham et al. (2001) and Bancroft and Servos (2011). The device was constructed by gluing a nylon screw to a speaker cone, and

placing the cone within a plastic housing such that the surface of the screw was flush with the top surface of the housing. The device was driven by WAV files delivered to the speaker, using an IBM-compatible PC running SuperLab 2.0 (San Pedro, CA: Cedrus). To mask any residual sound from the device, subjects were presented with white noise through headphones, and volume was adjusted until subjects reported they did not hear any residual sound.

Subjects engaged in a brief (48 trials) delayed match-to-sample practice session before beginning the experiment. Subjects were presented with two 1000ms stimuli, separated by an unfilled 1500ms delay period. Target and probe stimuli were either the same or different and separated by a 4 Hz frequency difference. Subjects were instructed to make a "same" response (by pressing the 's' key) if they believed the probe was the same frequency as the target, and a "different" response (by pressing the 'd' key) if they believed the probe was a different frequency from the target. Subjects were provided with visual feedback during the practice session.

During the actual experiment, subjects were presented with three 1000ms stimuli: Target 1 (referred to as T1), target 2 (T2), and the probe (P). Stimuli were separated by an unfilled 600ms delay periods. The target items were always of different frequencies, separated by 8 Hz. The probe stimulus was either the same as one of the target items, or different from both of the target items. In the different-probe condition, the frequency of the probe was either 4 Hz away from one of the targets (and therefore 12 Hz away from the other), or in between the frequencies of the two targets (and therefore 4 Hz away from each target). This gives us five test conditions in total: Probe same as target 1 (the ST1 condition); probe same as target 2 (the ST2 condition); probe different from T1 and T2 with a frequency between T1 and T2 (the Different-Between (DB) condition); probe different from T1 and T2 with a frequency closest to T1 (the DT1

condition); and probe different from T1 and T2 with a frequency closest to T2 (the DT2 condition). For example, given a target set T1 = 18 Hz and T2 = 26 Hz, an ST1 probe would be 18 Hz, an ST2 probe would be 26 Hz, a DT1 probe would be 14 Hz, a DT2 probe would be 30 Hz, and a DB probe would be 22 Hz.

Subjects were presented with 332 trials: 160 same- and 162 different-probe trials. (Due to software error, two same-probe trials were not presented.) There were equal numbers of same-probe trials where the probe matched T1 and T2 (80 per condition), and equal numbers of DB, DT1, and DT2 trials (54 per condition).

Subjects were instructed to make a "same" response (by pressing the 's' key on the keyboard) if the probe matched either of the target stimuli. They were instructed to make a "different" response (by pressing the 'd' key) if the probe did not match either of the target stimuli. The experiment was subject-paced, and subjects were given a break approximately halfway through the experiment.

Results and Discussion

The mean proportion of correct responses for the five test conditions are presented in Table 3. Results were averaged across all conditions, and a one-sample t-test found that performance was significantly better than chance, $t(11) = 5.694$, $p < .001$, demonstrating that subjects can reliably store multiple items in vibrotactile working memory.

A 2 (test type, same vs. different) X 2 (item position, first item (T1) vs. second item (T2)) repeated-measures ANOVA was performed on the proportion of correct responses (e.g., same responses to same probes, and different responses to different probes). There was a marginally significant main effect of test type, $F(1, 11) = 4,359$, $MSe = .046$, $p = .061$, partial $eta2 = .284$, indicating better performance for same trials than different trials. Although there was no effect

of item position, $F(1, 11) = .634$, $MSe = .003$, $p = .443$, partial $eta2 = .055$, the interaction was

significant, $F(1, 11) = 13.645$, $MSe = .005$, $p = .004$, $eta2 = .554$. Paired-sample t-tests were

performed to interpret the interaction. Whereas performance was significantly better on ST2

than DT2 trials ($t(11) = 2.924$, $p = .014$), there was no significant difference between ST1 and

DT1 trials, $t(11) = .924$, $p = .375$. In addition, although performance on DT1 trials was

significantly better than DT2 trials, ($t(11) = 3.712$, $p = .003$), performance was marginally worse

on ST1 trials than ST2 trials, $t(11) = 2.162$, $p = .054$.

The pattern of results found in the interaction (DT1 > DT2, but ST1 < ST2) can be

treated as a change in the number of "same" responses, without a change in overall

discrimination. Subjects made significantly more same responses to T2 probes than to T1

probes, $t(11) = 3.694$, $p = .004$, with no differences in overall performance, $t(11) = .797$, $p = $.

443. This pattern of results is indicative of worse memory for T2 items than T1 items. In

vibrotactile working memory, subjects make "same" responses when the perceived frequency

difference between the stored representation and the probe stimulus does not reach the threshold

for making a "different" response. If the stored representation is weakened or degraded, subjects

are less likely to make "different" responses, and therefore the number of "same" responses

increases (Exp. 1). While this does not have a net negative effect on performance, (as increased

"same" responses gives an increase in performance for same probes, and a decrease for different

probes), it does indicate weaker memory for T2 items than T1 items. This may be due to

attentional processes: It is well-established that encoding and maintenance are separate

processes, but ones that share neural resources (Cohen et al., 1997; Rypma & D'Esposito, 2000).

Further, load effects have been observed in cortical regions involved in encoding (Rypma,

Prabhakaran, Desmond, Glover, & Gabrieli, 1999; Rypma & D'Esposito, 1999, 2000; Tuladhar

et al., 2007), and maintenance-related regions display reduced activity during encoding (Woodward et al. 2006), suggesting that T2 items are encoded less efficiently than T1 items due to competition between maintenance processes and encoding processes. Feature overwriting is also likely to play a role. Feature overwriting theory argues that items stored in working memory will compete for a limited set of feature detectors. In the case of vibrotactile working memory, we know that stimuli compete for most of the feature detectors (PFC neurons) available. Stored stimuli may have an advantage over new stimuli in the competition process (possibly through reduced efficiency of encoding, as described above).

Alternately, inhibitory processes may reduce encoding of the second target item. Hannula et al. (2010) found that increasing top-down inhibition of somatosensory cortex (by applying excitatory TMS to the middle frontal gyrus, a region known to inhibit activity in primary somatosensory cortex) during vibrotactile maintenance increased performance. Sörös et al. (2007) also found increased activity in the middle frontal gyrus when a distractor was presented during the delay period, relative to trials with an unfilled delay. Such a mechanism may operate automatically, and interfere with encoding of subsequent items.

We performed a second set of analyses to confirm that both items were stored in memory. We performed paired-sample t-tests to compare the DB condition to the DT1 and DT2 conditions. Performance was significantly lower in the DB condition than both the DT1 ($t(11) =$ 8.353, $p < .001$) and DT2 ($t(11) = 4.956, p < .001$) conditions. This result suggests that both target items are being stored in memory. The PFC and SII neurons involved in comparing the target and probe stimuli do so essentially by computing the difference in firing rates between the stored target and the incoming probe (Romo, Hernández, Zainos, Lemus, & Brody, 2002). As some PFC neurons are storing the T1 representation, and some neurons are storing the T2

representation, some of the comparison neurons will calculate the difference between the probe and T1, and some will calculate the difference between the probe and T2. As such, the output from the comparison process will effectively be a comparison between the probe and both T1 and T2. If the computed difference between probe and target(s) meets some criterion, then subjects will make a "different" response; if not, a "same response". In the case where the probe frequency is between those of T1 and T2, (for example, T1 = 22 Hz, T2 = 30 Hz, Probe = 26 Hz) it will be computed as more similar to the contents of memory than when the probe is outside the test set frequencies (for example, T1 = 22 Hz, T2 = 30 Hz, Probe = 34 or 18 Hz), giving us reduced performance on DB trials.

Alternately, it is possible that only one item is being stored in memory. Even if only one item is stored, subjects will still be able to perform well on different-frequency probes to the non-stored item, as there will be a 12 Hz gap between the stored item and the probe. While this appears to be a weaker explanation for our data (as there will be an 8 Hz gap between the stored item and same-frequency probes to the non-stored stimulus, and we would therefore expect poor performance on same-frequency probe trials), we cannot rule it out based on our data alone. Simulation 1 is designed to compare these alternatives.

The present experiment suggests that subjects are able to store more than one item in vibrotactile working memory. This is a critical aspect in which vibrotactile WM is comparable to other domains of working memory. The ability to maintain multiple items in memory, (as well as add items to the memory store without loss of previously-encoded items), indicates that VWM is a working memory system, rather than being an especially long-lived form of sensory memory. Further, weaker memory for the second item in the test set suggests competition or interference between encoding and maintenance processes - a pattern of results found in other

studies of working memory (e.g., Rypma & D'Esposito, 1999). The present experiment strengthens the argument that VWM is an appropriate model system for testing theories of working memory.

<center>**Simulation**</center>

The results of Experiment 3 can be interpreted both as evidence for a single-item and multi-item capacity of vibrotactile working memory. We will use Kinchla and Smyzer's (1967; also see Marley, 1971) diffusion model of perceptual memory to differentiate between these competing accounts. This model has been shown to be effective at predicting performance on delayed match-to-sample tasks. Mathematically, the model is relatively simple. A value x, (representing the initial memory trace) is stored. In our case, x represents stimulus frequency. During the delay period (with length d), a random walk is performed on x. The random walk represents degradation of the stored representation, or an increase in noise. At each time step t, there is a 50% chance that the value of x will increase by the step size s, and a 50% chance that it will decrease by the step size s. At the end of the delay period, therefore, a memory trace m is calculated by adding the results of the random walk to the original value x. We can summarize this in a single equation:

$$m = x + s(p - n)$$

where p is the number of time steps where a positive step was taken, and n is the number of time steps where a negative step was taken. When a probe stimulus r is presented, the magnitude y of the perceived difference between the probe and the stored trace corresponding to the target is calculated simply by taking the absolute value of the difference between r and m:

$$y = |m - r|$$

If the value y is larger than the subjects' response criterion c, they will make a "different" response. Otherwise, they will make a "same" response.

For the purposes of the present simulation, we will compare four separate models: A two-item model (where both items are stored in memory), a random-item model (where one randomly-selected item is stored in memory), a first-item model (where only the first item is stored in memory), and a second-item model (where only the second item is stored in memory).

Method

All simulations were written in the Python programming language (version 2.6.5). The simulation was structured to replicate the design of Experiment 3, with five test conditions: Same as target 1 (ST1), same as target 2 (ST2), different from both, with a frequency between T1 and T2 (DB), different from both, with a frequency 4 Hz away from T1 (DT1), and different from both, with a frequency 4 Hz away from T2 (DT2).

Values for fixed parameters are presented in Table 4. The values of the stored items were set to be equal to the experimental frequencies used in Exp. 3. As we assumed equal sensitivity across the frequency range used in Exp. 3, we simplified the simulation by setting x_1 to 18 Hz and x_2 to 26 Hz. The duration of the delay periods were set to the duration from stimulus offset and probe onset (2200 ms for T1, and 600 ms for T2). We used a time step of 5 ms.

Two free parameters (step size, s, and criterion, c) were estimated separately for each of the four models. Summed squares of differences between each model's predictions and the results of Exp. 3 were calculated for step sizes in the interval [0.05, 1], using a step size difference of 0.05 in each iteration, and performing 1,000 trials per experimental condition, per model. Step size was taken from the simulation that produced the smallest sum of squares. This step size was then used to estimate the criterion separately for each of the models. Criterion was

allowed to vary in the interval between the lowest and highest activation values in each data set. Summed squares of differences between each model's predictions and the results of Exp. 3 were calculated with 10,000 trials per experimental condition, per model. These criterion and step size values were inserted into the model and 10,000 trials per experimental condition, per model were performed.

<div align="center">Results</div>

Estimated free parameters, root mean squared differences, and model predictions are presented in Table 5. The root-mean-squared-difference between the two-item model and the data from Exp. 3 is substantially smaller than those of the three versions of the one-item models, suggesting that our Exp. 3 results are most consistent with both target items being stored in memory. In addition, the two-item model does a better job of qualitatively replicating certain patterns of results from Exp. 3. Empirically, subjects make significantly more "same" responses to T2 probes (.60) than to T1 probes (.53), without an overall difference in performance (.60 vs. .62, respectively). The two-item model replicates this pattern of results: More "same" responses are made to T2 probes (.60) than to T1 probes (.52), and without an overall difference in performance (.58 and .60, respectively). None of the one-item models replicate this pattern of results - in fact, all three predict more "same" responses on T1 trials than T2 trials, and better performance on T2 trials than T1 trials. The results of the simulation strongly suggest that subjects are able to encode and maintain multiple items in vibrotactile working memory.

<div align="center">**General Discussion**</div>

The present study makes multiple contributions to our understandings of working memory, neural organization, and the somatosensory system. Critically, vibrotactile working memory has been shown to have a capacity of more than one item, property of other working

memory systems (e.g. Miller, 1956; Cowan, 2005). Also, vibrotactile working memory is prone

interference mechanisms known to exist in other working memory systems (Nairne, 1990;

Oberauer, 2009). These findings strengthen the argument that vibrotactile working memory is,

in fact, working memory. This has two important consequences: First, that we can use findings

from vibrotactile working memory tasks to inform our understanding of working memory in

general. As laid out in the introduction, vibrotactile working memory poses significant problems

for leading theories of working memory, and the literature on vibrotactile working memory may

help us extend or replace those theories. Second, it suggests that vibrotactile tasks may provide a

new method of assessing cognitive function in clinical patients. Working memory is highly

correlated with measures of overall cognitive function, such as fluid intelligence. The non-

verbal, non-visual, and non-auditory nature of vibrotactile working memory tasks give them an

especially high utility when dealing with elderly or clinical populations, who may display a

variety of language or sensory deficits.

Our second major finding deals with the nature of interference in vibrotactile working

memory. It was previously established by Harris et al. (2001) that presenting a distracting

stimulus between target and probe had the effect of reducing performance on vibrotactile tasks.

This is consistent with findings from other domains of working memory, such as auditory

delayed match-to-sample tasks (e.g., Mercer & McKeown, 2010). Our results demonstrate

unequivocal evidence for feature overwriting: The distractor stimulus is both encoded into

memory and incorporated into the subsequent probe/target comparison process. Further, while

the feature detectors proposed by feature overwriting have often been treated in an abstract

fashion, the simple neural code used by PFC neurons involved in storing vibrotactile stimuli

allows us to treat those neurons as analogous to abstract feature detectors, giving us a potential neural basis for feature overwriting.

We have strengthened the relationship between vibrotactile working memory and other forms of working memory. We have also used vibrotactile working memory to provide support for the feature overwriting account of interference in working memory. Where, then, do we go from here? There are many unanswered questions around vibrotactile working memory in humans. What is the nature of the non-overwriting form of interference found in Exp. 3? How useful is vibrotactile working memory as a method for assessing cognitive function in clinical populations? What is the maximum capacity of the vibrotactile working memory system? It appears likely that future research into vibrotactile working memory will prove fruitful.

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Table 1: Mean proportion of correct responses for each test and distractor condition

	0 Hz	2 Hz	4 Hz
Same	.70	.71	.71
Different (towards)	.43	.52	.50
Different (away)		.43	.41

Table 2: Mean proportion of correct responses for each distractor onset condition

	Same	Different		Net overwriting effect
		Towards	Away	
Early	.68 (.02)	.52 (.02)	.58 (.02)	.06 (.02)
Middle	.74 (.02)	.50 (.03)	.53 (.03)	.03 (.02)
Late	.71 (.02)	.49 (.03)	.55 (.03)	.06 (.02)

Table 3: Mean proportion of correct responses for each test condition

	Correct Responses
Same as T1 (ST1)	.64 (.03)
Same as T2 (ST2)	.70 (.03)
Different, frequency between T1 and T2 (DB)	.33 (.03)
Different, frequency closest to T1 (DT1)	.59 (.04)
Different, frequency closest to T2 (DT2)	.50 (.05)

Table 4: Fixed parameters from Simulation 1

Step length	5 ms
Delay length (T1)	2200 ms
Delay length (T2)	600 ms
Frequency of T1	18 Hz
Frequency of T2	26 Hz

Table 5: Correct responses from Exp. 4 and results of simulations

	Correct Responses	Two-item model	Random-item model	First-item model	Second-item model
Same as T1 (ST1)	.64	.62	.72	.77	.79
Same as T2 (ST2)	.70	.68	.56	.55	.59
Different, frequency between T1 and T2 (DB)	.33	.30	.33	.32	.26
Different, frequency closest to T1 (DT1)	.59	.58	.28	.17	.21
Different, frequency closest to T2 (DT2)	.50	.48	.62	.59	.67
Criterion	N/A	19.0	34.4	42.1	34.0
Step size	N/A	.55	.95	.95	.90
Root mean square error	N/A	.055	.374	.471	.460
r^2	N/A	.999	.221	.157	.239