Unexpected events disrupt visuomotor working memory and increase guessing

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Abstract

When an unexpected event, such as a car honking, occurs in daily life, it often disrupts our train of thought. In the lab, this effect was recently modeled with a task in which verbal working memory (WM) was disrupted by unexpected auditory events (Wessel et al., 2016). Here, we tested whether this effect extends to a different type of WM, viz. visuomotor. We found that unexpected auditory events similarly decremented visuomotor WM. Moreover, this effect persisted for many more trials than previously shown, and the effect occurred for two types of unexpected auditory event. Furthermore, we found that unexpected events decremented WM by decreasing the quantity, but not necessarily the quality, of the items stored. These studies show a statistically robust, and across-time enduring, impact of unexpected events on visuomotor WM. They also show an increase of guessing, consistent with a neuroscience-inspired theory that unexpected events ‘wipe out’ WM by stopping the ongoing maintenance of the trace.

Keywords: Inhibitory Control, Unexpected Events, Working Memory

Introduction

Daily life is littered with unexpected events – the jingling of a phone’s ringtone, the honking of a car horn, the screech of a passing crow – which are distracting. A recent study investigated such distraction using a laboratory task in which WM was interrupted by unexpected auditory events (Wessel, et al., 2016). On each trial, participants encoded a letter string, and were then presented with a standard tone (80%) or a novel birdsong (20%). The novel stimuli led to lower WM accuracy upon probe. While the typical view of the underlying mechanism might be that it is ‘caused’ by an attention shift, the same authors provided a deeper insight. The novel stimulus recruited the same brain network as outright stopping of action (Wessel & Aron, 2013; Wessel, et al., 2016), and the more it did so, the greater the WM disruption (Wessel, et al., 2016). It was proposed that verbal WM is maintained via thalamocortical drive, and that the novel stimulus recruits the subthalamic nucleus which suppresses basal ganglia output, resulting not only in an interrupt of motor activity but also of cognition (reviewed by Aron, Herz, Brown, Forstmann, & Zaghoul, in press). This account suggests intriguing links across several disparate areas of psychology, viz. attention, working memory, surprise, response inhibition, and distractibility (Banich, Mackiewicz Seghete, Depue, & Burgess, 2015; Horstmann, 2006; Leiva, Parmentier, Elchlepp, & Verbruggen, 2015). Here we set out to more thoroughly substantiate the behavioral effect.

In Experiment 1 we tested whether the impact of unexpected events on cognition also applies to visuomotor WM (i.e. the coordination of visual perception and planned movement (di Pellegrino & Wise, 1993; Goodale, 1998). Accordingly we designed a Corsi-like task (Corsi, 1972) in which participants encoded a sequence of boxes presented in different locations. They maintained this ‘sequence’ across the delay, when a sound occurred. As before, this was mostly standard stimuli, with infrequent novel birdsongs. They were then probed to recall the position of one of the boxes (Figure 1).

We established the basic effect that novels decremented visuomotor WM. We then tested (in Experiment 2) whether this effect was a generalizable feature of unexpected events. Along with the birdsong novels we included trials in which the standard tone was simply increased in duration (c.f. Naatanen, Pakarinen, Rinne, & Takegata, 2004).

In Experiment 3, we tested whether the ‘WM decrementing effect’ was truly due to the novelty of the tone, or instead attributable to different sensory elements of novels vs. standards. We now used a birdsong on every trial, with some of these remaining unexpected. We also probed *how* WM is impacted by unexpected events. As above, our theory is that visuomotor WM is maintained via cortico-basal-ganglia loops that are interrupted by the unexpected-events-driven subthalamic activation. This might predict a ‘wipe out’ of the WM itself (a reduction in ‘quantity’) which would lead to increased guessing at the probe, rather than a change in the ‘quality’ of the representation which would lead to a reduction in precision. Accordingly, we used a model-fitting procedure (Suchow, Brady, Fougine, & Alvarez, 2013) based on models of WM storage (Brady, Konkle, & Alvarez, 2011; Ma, Husain, & Bays, 2014; Zhang & Luck, 2008, 2011) to test for changes in guessing, precision or both.

Experiment 1

Method

Participants

Sixteen students (15 female; mean age 20.8 ± 2.1 years) from the University of California, San Diego (UCSD) participated for course credit. All were right-handed, and had normal or corrected-to-normal visual acuity. They signed written consent according to a local ethics committee (IRB #140033).

An earlier study of the effect of unexpected events on verbal WM showed a within-subject novel vs. standard effect size of Cohen’s $d = 0.78$ (Wessel, et al., 2016). From this we

estimated that 16 participants would give 90% power to detect a significant effect with alpha of 0.05, 1-tailed.

Apparatus and stimuli

Participants sat ~22 inches in front of a 19 inch iMac personal computer (Apple) supported by a chin rest. The study was run with MATLAB 2015b (Mathworks) and Psychtoolbox 3 (Brainard, 1997). The sounds were delivered through Sennheiser HD 280 Pro headphones. Responses were recorded using an Apple Mouse. Stimuli were turquoise (HEX #00EDFF) squares, measuring approximately 0.5 in x 0.5 in (subtended 1.3° x 1.3° of visual angle).

Procedure and design

Testing was divided into 1) determining WM span and 2) the main experiment.

The WM span procedure derived the correct span for each participant in order to have good sensitivity to detect WM decrements. Each trial began with a central fixation cross, and then a number of square stimuli (20 trials each of 3, 4, 5, and 6 squares) were shown in succession, with each presented for 500 ms in one of twelve different locations on the screen (no delay between presentation times). No locations were repeated within a trial. Then, the central fixation cross was again displayed for a delay of 1.4 to 2.9 s, jittered. This was followed by a tone, which in the case of the span test was always the standard tone, a 600 Hz sine wave for 200 ms, and then a delay of 300 ms. After the delay, a number would appear in the center of screen for 500 ms, indicating which square, based on the order, the participant needed to remember. Finally, a square would reappear, either in the exact same location as the target square, or in a slightly different location. Participants were given 3 s to respond by indicating whether the probe square was in the same location ('press 1') or a different location ('press 2') than the target square. We then calculated the number of individual squares remembered for each participant using Cowan's k : $K = (H - FA) * N$, where K is the number of items stored, H is

the hit rate, FA is the false alarm rate, and N is the number of items presented (Alvarez & Cavanagh, 2004; Cowan, 2001), which was then used as set size for the main experiment.

For the main experiment, each trial proceeded as in the span test, with two key differences (Figure 1). First, trials were divided into two conditions: standard and novel. In the standard condition (80% of trials), the tone in the delay period was the same 600 Hz sine wave as in the span test. However, in the novel condition (20% of trials), a unique birdsong segment was presented instead. Additionally, probe squares were no longer presented. Instead the mouse cursor reappeared in the center of the screen, and participants clicked the position where they believed the target had been located. Trials were presented in a pseudorandom order: constrained so that there could never be two novel trials in a row and the first three trials of every block were standards. There were 320 trials divided into eight blocks of 40 trials (8 of which were novel trials and 32 of which were standard trials).

Results

The main measure of interest was response error – the distance from the mouse click to the centroid of the target square (in degrees of visual angle). Trials with response error greater than 2.5 standard deviations away from the condition mean for the block were removed as outliers. A two-way repeated measures analysis of variance (ANOVA) with the factors condition (standard vs. novel) and block (blocks 1 to 8) yielded a main effect of condition ($F(1,15) = 8.88$, $p = .009$, $\eta_p^2 = 0.372$; see Figure 2), with response error being significantly greater for novels vs. standards. This effect persisted throughout the experiment, with no significant interaction between condition and block ($F(1,15) = 1.65$, $p = 0.130$).

Response time (RT), defined as the time between when the mouse cursor reappeared in the center of the screen and when participants clicked, did not differ between novels and standards ($t(15) = 1.74$, $p = .103$).

This study thus extended the verbal WM result (Wessel, et al., 2016) by showing that visuomotor WM is also decremented by auditory novels.

Experiment 2

We now tested whether the unexpected-events-induced decrement occurs for stimuli other than birdsongs.

Method

Participants

Given a partial eta squared of 0.372 in Experiment 1, sixteen subjects would give us 99% power to detect an effect. We thus kept N equal to sixteen to be consistent across studies. Sixteen students (10 female; 13 right-handed; mean age 21.0 ± 4.2 years) were recruited and consented as per Experiment 1.

Apparatus, stimuli, and procedure

All aspects were the same as Experiment 1, except 1) set size for the experiment task was now determined as Cowan's $k + 1$ (we reasoned this would make WM even more prone to disruption), and 2) novels were subdivided into two types: half (10% of all trials) were 200 ms birdsong segments used in Experiment 1, and the other half (10% of all trials) were instead long tones (600 Hz sine waves) lasting 500 ms.

Results

ANOVA was conducted with the factors condition (standard vs. novel) and block (blocks 1 to 8), with response error and outliers determined as in Experiment 1. Again, there was a significant main effect of condition ($F(1,15) = 24.98$, $p < .001$, $\eta_p^2 = 0.625$), with greater response errors for novels vs. standards (see Figure 2). There was no main effect of block ($F(1,15) = 0.77$, $p =$

.617), or block by condition interaction ($F(1,15) = 1.15, p = .337$). Furthermore, the effect was there for both types of novels (birdsong vs. standard: $t(1,15) = 3.56, p = .003$; long tone vs. standard: $t(1,15) = 4.48, p < .001$). There was no significant effect of condition on RT ($t(15) = 1.17, p = .260$).

This experiment thus replicated Experiment 1, and went further by showing that a different kind of novel (a longer tone) is also capable of decrementing visuomotor WM.

Experiment 3

Method

Participants

To be consistent across all three studies, we again ran sixteen subjects (14 female; 15 right-handed, mean age 21.8 ± 4.9 years), who were recruited and consented as per Experiment 1.

Apparatus, stimuli and procedure

All aspects were the same as Experiment 2, except that for the main task, only birdsongs were now used. These were now counterbalanced with each acting as a standard or novel depending on block (specifically, the main experiment consisted of nine blocks (360 trials) with nine unique birdsong segments used throughout the experiment; for each block, one of the birdsong segments served as the standard with the other 8 serving as novels, and this rotated across blocks), We also increased the number of trials (now 72 instead of 64 novels) and standardized the stimulus locations to a fixed eccentricity (i.e. each box occurred at some point on an invisible circle ringing the screen).

Data analysis

The increased number of trials and standardized stimulus locations now allowed us to attempt to measure differences in capacity and precision. For each trial, we calculated the response

error as the angular distance between the correct and the reported location. We then modeled these error distributions as a mixture of a circular normal distribution (centered around the correct location) and a uniform distribution (random guesses), with two parameters – a mixture parameter (G ; indicating how many trials were “guess”¹ trials), and a SD parameter (indicating how wide the normal distribution was; i.e. precision) (Zhang & Luck, 2008). Data were fit using MemToolbox (Suchow, et al., 2013) and parameter estimates were derived using Markov Chain Monte Carlo to find the maximum a posteriori values. The model was fit separately for each subject and task condition (novel vs. standard). We also analyzed the data using a modified model that estimated how frequently participants reported one of the other square locations as the target location (‘swap errors’ Bays, et al., 2009). The results converged across the two models and parameter estimates for this alternate model are listed in the Supplementary Material.

Results

ANOVA was run with the factors condition (standard vs. novel) and block (blocks 1 to 9) revealing a significant effect of condition ($F(1,15) = 17.19, p = .001, \eta_p^2 = 0.534$). This showed, again, that response error was increased on novel vs. standard trials (see Figure 2). There was no significant main effect of block ($F(1,15) = 0.84, p = .566$) or interaction ($F(1,15) = 1.84, p = .076$). Interestingly, the interaction was at trend level, and this trend was in the direction of unexpected-events-induced decrement of WM *increasing* over time. Indeed, the effect was still significant, even in the last block ($t(15) = 2.79, p = .014$). Again, there was no significant effect of condition on RT ($t(15) = 1.57, p = .137$).

Fitting the mixture model to the response error data revealed that participants guessed significantly more often for novels (16.1%) vs. standards (12.6%), $t(15) = 2.44, p = .028$ (Figure

¹ We refer to these as guess trials but recognize that they may also include low resolution memories (van den Berg, Shin, Chou, George, & Ma, 2012) or incorrect item reports (Bays, Catalao, & Husain, 2009).

4B, left). There was no significant difference in the quality with which the locations were stored, with *SD* estimates for novels 10.0° , and 9.7° for standards, $t(15) = 0.53$, $p = .606$ (Figure 4B, right). However, we note that such a model can have more power to detect differences in guessing than precision (Fougnie, Suchow, & Alvarez, 2012; Suchow, Fougnie, Brady, & Alvarez, 2014), and there were only 72 novels. Yet Monte Carlo simulations showed that with this number of subjects and this number of trials per condition, we would have 91% power to detect a *SD* change as small as one degree.

General discussion

An earlier study showed that novel sounds decrement verbal WM, and it suggested a neural mechanism (Wessel, et al., 2016). Here we expanded on that work by testing a *visuomotor WM* paradigm with several promising features. In Experiment 1, we showed that visuomotor WM is also decremented by auditory novels (birdsongs). In Experiment 2, we again showed that auditory novels (birdsongs) decrement WM, as do standard tones that are merely extended in time. In Experiment 3, we showed that it is the effect of unexpected events and not novel vs. standard physical stimulus differences that count. We also showed that novels decrement WM by increasing guessing. The effect sizes for the novel-decrementing-WM results were in all cases bigger than 0.26, which is typically defined as large (Eta-squared of 0.372 (Exp. 1), 0.625 (Exp. 3) and 0.534 (Exp. 3)). Moreover, the decrement did not abate with time – indeed in Experiment 3 the decrement even increased across time. Taken together these results show statistically robust, and enduring, impacts of unexpected events on visuomotor WM. They also show an increase of guessing, which is consistent with a neuroscience-inspired theory of the mechanism of distraction.

This large, enduring effect is to be contrasted with the verbal WM paradigm (Wessel, et al., 2016), which while showing significant effects in several subject groups, was not of so dramatic a magnitude and did not last as long. We conjecture that visuomotor WM is more

fragile – i.e. rehearsing a motor sequence of spatial locations is more easily interruptible than verbal WM, which is presumably rehearsed via the phonological loop. We also showed that even stimuli well-balanced on physical characteristics interrupt WM when they are unexpected. All these features make the current paradigm an excellent vehicle for further explorations of distractibility – providing a reliable effect that can be studied across many trials and is not confounded by stimulus differences.

It is notable that novels decremented WM by increasing guessing, without any apparent effect on precision. This is interesting in relation to our neural theory that visuomotor WM is maintained via thalamocortical drive. A stop-induced interruption in that drive might be expected to produce a disruption of memory for a visuomotor sequence, which may manifest as a loss of one or more item representations, rather than an overall “blurring” of precision.

An interesting question is whether there is something special about visuomotor and also verbal WM with regard to interruptibility relative to other kinds of WM, such as that for colors or faces. It is likely that both visuomotor WM and verbal WM are motor-based. In that sense, an unexpected event-driven stop system may interrupt them in the same way it ‘suppresses’ the skeletomotor system (Wessel & Aron, 2013). More generally this theory provides new perspectives on the connection between the basal ganglia and WM (c.f. Chatham & Badre, 2015).

Notably, the impact of distraction on WM has been difficult to demonstrate empirically, and many such studies are ones in which the distractor (e.g. visual) ‘shapes’ the (visual) WM representation (Ester, Zilber, & Serences, 2015; Hakun & Ravizza, 2016; Rademaker, Bloem, De Weerd, & Sack, 2015; Yoon, et al., 2006) (however, see Awh, Vogel, & Oh, 2006; Cools, Miyakawa, Sheridan, & D’Esposito, 2010; Ester, et al., 2015; Gazzaley, Cooney, Rissman, & D’Esposito, 2005; McNab & Klingberg, 2008; Zanto & Gazzaley, 2009). Yet in the real world, distraction is often in a different modality than the target information (e.g. a cell phone chirping while trying to remember the exit from the highway) and moreover, the distractor is typically

unexpected. In these ways, the current approach is a more realistic paradigm for understanding distraction, and, as we have shown it is statistically robust and endures across trials. Further studies could test whether unexpected events interrupt visuomotor WM and induces guessing via 'erasing' current traces through the stopping system, and if this extends to non-motor forms of WM, and if this explains clinical conditions of under and over-distractibility.

	Error distance (in deg. of visual angle)		Response time (in seconds)	
	Novel	Standard	Novel	Standard
Experiment 1	1.71° (0.40°)	1.54° (0.24°)	1.18 (0.36)	1.15 (0.37)
Experiment 2	2.41° (0.75°)	1.96° (0.58°)	1.08 (0.19)	1.10 (0.19)
Experiment 3	2.64° (1.16°)	2.08° (0.83°)	1.11 (0.19)	1.07 (0.18)

Table 1: Mean values for the novel and standard conditions, for response error distance and response time. Standard deviations are presented in parentheses.

Figure 1: Schematic for the main task (span test not shown). SOA refers to stimulus offset asynchrony. Note that for Exp. 2, the tone duration was sometimes 500 ms, instead of 200 ms (10% of trials).

Figure 2: Overall response error (as measured by error distance between mouse click position and centroid of target box, in degrees of visual angle). Error bars represent within-subject standard deviation.

Figure 3: A) Response error histograms for the novel condition (left) and the standard condition (right) collapsed over all subjects. The solid line indicates the standard mixture model. B) Model parameter estimates for each condition for the guess rate (left) and *SD* (also known as precision, right). Error bars represent within-subject standard deviation.

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Response Error

A)

B)