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Akos Szekely, Suparna Rajaram & Aprajita Mohanty

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Memory for dangers past: threat contexts produce more consistent learning than do non-threatening contexts

Akos Szekely, Suparna Rajaram and Aprajita Mohanty

Department of Psychology, Stony Brook University, Stony Brook, NY, USA

ABSTRACT

In earlier work we showed that individuals learn the spatial regularities within contexts and use this knowledge to guide detection of threatening targets embedded in these contexts. While it is highly adaptive for humans to use contextual learning to detect threats, it is equally adaptive for individuals to flexibly readjust behaviour when contexts once associated with threatening stimuli begin to be associated with benign stimuli, and vice versa. Here, we presented face targets varying in salience (threatening or non-threatening) in new or old spatial configurations (contexts) and changed the target salience (threatening to non-threatening and vice versa) halfway through the experiment to examine if contextual learning changes with the change in target salience. Detection of threatening targets was faster in old than new configurations and this learning persisted even after the target changed to non-threatening. However, the same pattern was not seen when the targets changed from non-threatening to threatening. Overall, our findings show that threat detection is driven not only by stimulus properties as theorised traditionally but also by the learning of contexts in which threatening stimuli appear, highlighting the importance of top-down factors in threat detection. Further, learning of contexts associated with threatening targets is robust and speeds detection of non-threatening targets subsequently presented in the same context.

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Threatening stimuli such as angry faces, snakes, and spiders are hypothesised to capture attention automatically due to their salience. Studies show that distinct features of threatening stimuli, such as V-shaped eyebrows, or a snake-like body are thought to be perceived in a bottom-up or automatic manner, leading to their faster detection (Ohman & Mineka, 2001). These studies typically do not examine the role of surrounding context within which the target is presented.

Context can be described broadly as the multisensory, diffuse, and continuously present circumstances surrounding an event (Maren, Phan, & Liberzon, 2013). While contextual representations combine the elements that they encompass, this representation can be distinguished from its component elements (Fanselow, 1990). A consideration of context is useful because in the real world threatening stimuli are not perceived in isolation. Rather, threatening or non-threatening stimuli often occur embedded in a rich context of elements that predict their identity and location (Bar, 2004; Barrett, Mesquita, & Gendron, 2011; Summerfield & de Lange, 2014; Sussman, Jin, & Mohanty, 2016). Drawing upon the broad construal of context as multisensory, diffuse, and continuously present circumstances surrounding an event (Maren et al., 2013), the present study specifically focused on spatial context and how learning in spatial context influences threat detection. This spatial context may be composed of stimulus elements as well as their configuration or spatial relations. Recent work has shown that knowledge regarding surrounding contexts can be used effectively to detect existing non-threatening (Chun & Jiang, 1998) or threatening (Szekely, Rajaram, & Mohanty, 2016) targets presented in these contexts.
It is highly adaptive for humans to learn such regularities in contexts that predict threat and use that learning to guide behaviour. Yet it is equally adaptive for individuals to flexibly readjust behaviour when contextual contingencies change in the environment. For example, a soldier deployed in a war torn city may have learnt that a closely clustered configuration of buildings predicted the possibility of a sniper threat. After the war, on repeatedly encountering this configuration with a relatively safe stimulus such as a vendor, it is important for the soldier to learn this change in contingency. Continuing to search for threats in this relatively safe spatial context may lead to anxiety and avoidance. On the other hand, if there is an onset of war hostilities and a previously safe configuration of buildings becomes associated with snipers, it is equally important for the soldier to learn that this spatial context predicts threat and that a failure to do so may result in them overlooking dangerous threats. Hence, flexible adaptation to the change in learning contingencies is critical for healthy functioning and deficits in this adaptation are associated with psychopathology (Britton, Grillon, Lissek, Norcross, & Szuhany, 2013; Chun & Phelps, 1999; Dickstein et al., 2010). The present study examined whether learning of contexts associated with threatening and non-threatening stimuli facilitates their detection speed and how this detection speed changes when a once-threatening context becomes safe or a once-safe context becomes threatening.

While no past work has examined changes in contextual learning as a consequence of changes in associated targets, the closest paradigm that has examined such flexibility in learning is the reversal learning paradigm. In this paradigm, individuals initially learn to associate one stimulus with a relatively safe outcome and another stimulus with threats such as an electric shock or a threatening face (Schiller & Delgado, 2010). Later, these contingencies are reversed such that the once-safe stimulus is presented with threats and the once-threatening stimulus is presented with a safe outcome. This reversal leads to a gradual learning of a safety response to the newly non-threatening stimulus, and a rapidly learned response to the newly threatening stimulus. We extended this research on changing associations between distinct, individual stimuli to examine changing associations between contexts and embedded stimuli. In the present study, we examined whether learning of contexts (spatial configurations of surrounding stimuli) associated with threatening targets changes when these contexts become associated with non-threatening targets, and vice versa.

We presented threatening (angry features) or non-threatening (neutral features) schematic face targets in old (repeated) or new arrays (i.e. contexts) that consisted of non-threatening faces, and we measured contextual learning operationalised as faster target detection for old vs. new arrays (Szekely et al., 2016). To examine the impact of the switch in contextual learning when a once threatening array becomes associated with non-threatening face targets and a once non-threatening array becomes associated with threatening face targets, we pseudorandomly assigned participants to receive one of two sequences. One group of participants received a sequence in which they detected threatening targets in arrays followed by a switch after which they detected non-threatening targets in the same arrays. Another group of participants received the opposite sequence in which they detected non-threatening targets in arrays followed by a switch after which they detected threatening targets in the same arrays.

If detection of threatening targets is driven entirely by stimulus salience, there would be faster detection of these targets compared to non-threatening targets, regardless of configuration (old vs. new) or sequence (threatening targets first vs. non-threatening targets first). Instead, we expected that “top-down” factors such as configuration and sequence would also have an impact on detection of threatening targets. This expectation was based on past findings where contextual learning influenced responses to threatening targets (Szekely et al., 2016). This impact of top-down factors should adaptively improve response times by improving search. Hence, contextual learning (faster responding for old vs. new arrays) was expected to occur initially for arrays associated with both threatening (Szekely et al., 2016) and non-threatening targets (Chun & Jiang, 1998).

Novel to the present study, learning was likely to be impacted by sequence also: in cases where the initial contextual learning was for threatening targets, the learning was expected to be robust and any learning benefits (i.e. faster RTs) were expected to continue when the non-threatening targets were presented in the same contexts. This is because contexts associated with threatening stimuli are remembered robustly (Maren et al., 2013) and these associations can generalise strongly (Lissek et al., 2008). Typically, learning studies have only examined the strength of these
associations, but have not explored their impact on target detection, as the present paradigm did. Conversely, in cases where the initial contextual learning was for non-threatening targets in our study, persistent benefits from contextual learning for threatening targets were unlikely to occur when presented later in the same contexts. This is because target salience associated with negative stimuli can out-compete learning associated with neutral stimuli to guide attention (Sutherland & Mather, 2012). In brief, the benefits of contextual learning for threatening targets were predicted to persist even when non-threatening targets were presented in the same contexts. On the other hand, the same persistent benefits of prior sequence were unlikely to be observed when threatening targets were presented in same contexts that previously contained non-threatening targets. An examination of these hypotheses should clarify the role of contextual learning in the detection of both threatening and non-threatening stimuli as well as how this detection may change when a once-threatening context becomes safe or a once-safe context becomes threatening.

**Material and methods**

**Participants**

Fifty-one undergraduate volunteers (mean age 22 ± 4.54 years) from Stony Brook University participated for course credit. One group (N = 26, mean age 21 ± 4.26 years) received a sequence with threatening targets first and non-threatening targets next and another group (N = 25, mean age 23 ± 4.73 years) received a sequence with non-threatening targets first and threatening targets next. Groups did not significantly differ in age, gender, or levels of anxiety (all ts < 1). Overall count of trials removed were not different by epoch, (F < 1), for emotion or for configuration (all ts < 1). For a power analysis, please see the Supplementary section.

**Apparatus and stimuli**

All stimuli were coloured line drawings of either an angry (threatening) or a non-threatening face (Figure 1; [also Szekely et al. (2016)]). Target faces were drawn with dotted lines while non-target faces were drawn with solid lines. Target faces were presented in arrays of non-target faces. The colour and location of the target and non-target stimuli in an array constituted the configuration of the array. For additional details about stimuli and their physical presentation, please see the Supplementary section or Szekely et al. (2016).

**Design and procedure**

The experiment consisted of a 2 × 2×2 × 5 mixed design with sequence (threatening-first vs. non-threatening-first) as a between-subjects variable, and phase (initial vs. switch), configuration (old vs. new) and epoch (1–5) as within-subject variables. The main purpose of including epoch was to examine learning as it emerges over time across all conditions as well as in interaction with other conditions of interest. Past contextual cueing tasks have expressed learning in terms of epoch (Geyer, Zehetleitner, & Muller, 2010). This grouping of trials into four epochs, with each epoch consisting of five blocks, has been successfully used in earlier contextual learning studies (Chun & Jiang, 1998; Kunar, Flusberg, Horowitz, & Wolfe, 2007) and provides a stable measure of learning performance over time. Participants were pseudorandomly assigned to begin with either a threatening-first or non-threatening-first sequence. Hence, the between-subjects independent variable sequence included two orders. In the threatening-first sequence, threatening target (dotted) schematic faces were presented in arrays of non-threatening (solid) faces in the initial phase (first 10 blocks) of the experiment following which there was a switch in phase (last 10 blocks) and non-threatening target faces were presented in the same arrays of non-threatening faces. In the non-threatening-first sequence, non-threatening target schematic faces were presented in arrays of non-threatening faces in the initial phase (first 10 blocks) of the experiment following which there was a switch in phase (last 10 blocks) and threatening target faces were presented in the same arrays of non-threatening faces. Therefore, for the independent variable phase, arrays initially associated with threatening targets were associated with non-threatening targets after the switch, and arrays initially associated with non-threatening targets began to be associated with threatening targets.

For the independent variable configuration, the spatial configurations of the face arrays in the search display were manipulated. In the old condition, the array of faces repeatedly appeared in consistent locations across blocks of trials such that the visuospatial context predicted the location of face targets. In
the new condition, the locations of the array of faces varied from trial to trial. For additional details about the old and new configurations, please see the Supplementary section or Szekely et al. (2016). To increase the power of the analyses and calculate learning over time, trials were grouped into five epochs per condition, each epoch consisting of two experimental blocks (Chun & Jiang, 1998) for each half (initial, switch) of the task sequence. This allowed us to divide the first and last 10 blocks into even sections. See the Supplementary section for details regarding timeline and task instructions.

After performing the contextual cueing task participants were given a computerised, explicit recognition test following the procedure similar to prior contextual cueing studies (Chun & Jiang, 1998; Chun & Phelps, 1999; Szekely et al., 2016). Participants were asked to indicate whether they noticed repetition of arrays (See the Supplementary section for details).

Results
All reaction time (RT) data were based on correct responses and were trimmed by removing trial RTs greater than three standard deviations above the condition mean for all participants. This resulted in the removal of an average of 4% of target-present trials, in line with other studies (e.g. Chun and Jiang (1998); Geyer et al. (2010)). Consistent with earlier studies on contextual cueing (Geyer et al., 2010), RT data were analysed for the target-present trials only. Accuracy for target detection averaged above 80% correct.

Consistent with our previous findings, the RT results (Figure 2) showed that there was contextual
learning (difference between new and old RTs) not only for non-threatening but also threatening targets when presented in the initial phase of non-threatening-first or threatening-first sequence, respectively. Novel to this study, while the robust contextual learning for threatening targets in the initial phase of the threatening-first sequence continued into the switch phase, the same was not observed for the switch phase of the non-threatening-first sequence. We tested our hypotheses regarding contextual learning via a 2 (sequence: threatening-first vs. non-threatening-first) × 2 (phase: initial vs. switch) × 2 (configuration: old vs. new) × 5 (epoch) repeated measures mixed-model ANOVA (rm-ANOVA). RT results showed a main effect of configuration, $F(1, 49) = 19.79$, $MSE = 0.03$, $p < 0.001$, $\eta_p^2 = 0.29$, phase, $F(1, 49) = 28.92$, $MSE = 0.10$, $p < 0.001$, $\eta_p^2 = 0.37$, epoch, $F(4, 196) = 36.30$, $MSE = 0.02$, $p < 0.001$, $\eta_p^2 = 0.43$, and interactions between phase and sequence, $F(1, 49) = 46.67$, $MSE = 0.10$, $p < 0.001$, $\eta_p^2 = 0.49$, between epoch and sequence, $F(4, 196) = 3.03$, $MSE = 0.02$, $p = 0.02$, $\eta_p^2 = 0.06$, as well as among sequence, phase, and epoch, $F(4, 196) = 4.56$, $MSE = 0.02$, $p = 0.002$, $\eta_p^2 = 0.09$. Most critically for the hypothesis, a significant four-way interaction was observed between sequence, phase, configuration, and epoch, $F(4, 196) = 3.56$, $MSE = 0.01$, $p = 0.008$, $\eta_p^2 = 0.07$ (Figure 2). The nature of this interaction was such that learning for contexts differed depending on whether threatening or non-threatening targets were presented in them in the initial or switch phase of the experiment.

We further examined this four-way interaction with two separate rm-ANOVAs for each of the phases, initial and switch, in order to examine the contextual cueing effect in each sequence before and after changing target type. For the initial phase (upper and lower panels before the dashed line in Figure 2), a 2 (sequence: threatening-first vs. non-threatening-first) × 2 (configuration: old vs. new) × 5 (epoch) ANOVA showed a main effect of sequence, $F(1, 49) = 9.96$, $MSE = 0.42$, $p = 0.003$, $\eta_p^2 = 0.17$, configuration, $F(1, 49) = 13.39$, $MSE = 0.02$, $p = 0.001$, $\eta_p^2 = 0.22$, epoch, $F(4, 196) = 23.78$, $MSE = 0.02$, $p < 0.001$, $\eta_p^2 = 0.33$, and an interaction between sequence and epoch, $F(4, 196) = 6.21$, $MSE = 0.02$, $p < 0.001$, $\eta_p^2 = 0.11$. The main effect of sequence indicates a faster overall RT for targets in threatening-first sequences vs. targets in non-threatening-first sequences, $M = 180$ ms, 95% CI [66, 298]. The main effect of configuration with faster RTs for old vs. new configurations, difference $M = 49$ ms, 95% CI [22, 76], demonstrates that learning took place for both non-threatening targets and threatening across non-threatening-first and threatening-first sequences, replicating previous findings (Chun & Jiang, 1998) and our own work (Szekely et al., 2016). The interaction between sequence and epoch indicates that rate of learning in the initial phases of both sequences was different across epochs such that threatening targets were detected faster than non-threatening targets until the last epoch of the phase, where non-threatening target detection speed improved. Overall, in the initial phase, while contextual learning was observed for both threatening and non-threatening targets, target detection was faster for threatening vs. non-threatening targets.

For the switch phase (upper and lower panels after the dashed line in Figure 2), a 2 (sequence: threatening-first vs. non-threatening-first) × 2 (configuration: old vs. new) × 5 (epoch) ANOVA showed main effects of sequence, $F(1, 49) = 4.17$, $MSE = 0.27$, $p = 0.047$, $\eta_p^2 = 0.08$, configuration, $F(1, 49) = 16.08$, $MSE = 0.02$, $p < 0.001$, $\eta_p^2 = 0.25$, and epoch, $F(4, 196) = 15.53$, $MSE = 0.02$, $p < 0.001$, $\eta_p^2 = 0.24$, and an interaction between sequence, configuration, and epoch, $F(4, 196) = 2.93$, $MSE = 0.01$, $p = 0.02$, $\eta_p^2 = 0.06$. The main effect of sequence suggests a faster detection of threatening targets in the switch phase of non-threatening-first sequence vs. non-threatening targets in the switch phase of the threatening-first sequence, $M = 94$ ms, 95% CI [1, 187] ms. The main effect of configuration indicates a contextual learning effect, i.e. faster RTs for old vs. new configurations, $M = 49$ ms, 95% CI [25, 74] ms. The interaction between sequence, configuration, and epoch indicates contextual learning (faster RTs for old than new configurations) across epochs for non-threatening targets presented in the same contexts that were previously associated with threatening targets. This contextual learning was not present for threatening targets presented in the same contexts that were previously associated with non-threatening targets. Simply put, in the switch phase of the threatening-first sequence, contextual learning for threatening targets continued to guide target detection even after the targets switched to non-threatening whereas the same was not observed in the switch phase of the non-threatening-first sequence.

Accuracy performance was also analysed by conducting a four-way rm-ANOVA (Figure 3). The accuracy patterns were generally consistent with the RT patterns, with two patterns reaching statistical
significance for a main effect of phase, $F(1, 49) = 6.80$, $MSE = 0.03$, $p = .012$, $\eta^2_p = 0.12$, and an interaction between phase and sequence, $F(1, 49) = 12.77$, $MSE = 0.03$, $p = .001$, $\eta^2_p = 0.21$. This interaction suggests that changing from initial to switch phase reduced accuracy overall, and this reduction effect was stronger in the threatening-first sequence.

Finally, recognition task results demonstrated that information about any consistency within arrays was not consciously available to participants. Additional information is available in the Supplementary section.

**Discussion**

It has been hypothesised that perception of threatening stimuli is driven by “bottom-up” factors such as their evolutionary salience or physical characteristics (Mogg, Holmes, Garner, & Bradley, 2008). However, research has shown that contexts surrounding the stimuli can be implicitly learned and used to guide detection of both non-threatening (Chun & Jiang, 1998; Chun & Phelps, 1999; Geyer et al., 2010; Kunar, Flusberg, & Wolfe, 2008) and threatening stimuli (Szekely et al., 2016). In the present study we showed that not only contextual learning but also the sequence of contextual learning (once-threatening context becomes non-threatening or a once-non-threatening context becomes threatening) differentially impacted target detection. This finding is important because in real life, our environment is constantly changing in terms of what it predicts for our safety and it is important to understand the mechanisms by which humans flexibly adjust threat detection within changing contextual contingencies.
We presented threatening or non-threatening face targets in new or old spatial configurations and midway into the experiment switched and presented non-threatening or threatening targets, respectively, in the same contexts. While the new configurations may have been more distracting due to their novelty, this distraction was constant across the blocks as well as for threatening and non-threatening targets, indicating that the old vs. new configuration effects were best accounted for by learning. Hence, the contexts (i.e. configurations) remained the same but the targets associated with the context changed in emotional salience. In the initial phase, the contextual learning effect was observed for both threatening and non-threatening targets such that targets presented in old configurations were detected faster than targets presented in new configurations. This effect replicated our previous findings (Szekely et al., 2016) and showed that detection of threatening targets was driven not only by stimulus properties as theorised traditionally but also by the learning of contexts in which threatening stimuli appeared. Our novel results showed that the standard contextual learning effect changed depending on whether the target associated with a specific context shifted from threatening to non-threatening or vice versa. In the switch phase, the contextual learning effect was observed for non-threatening targets presented in the same arrays that previously held threatening targets but the contextual learning effect was not observed for threatening targets presented in arrays that had previously held non-threatening targets.

The differential effect observed in the switch phase suggested that, (1) learning of contexts initially associated with threatening targets was robust enough to generalise and it guided target detection even after

**Figure 3.** Target-present Accuracy results in the experiment. Mean accuracies for detection of targets that were in the threatening-first versus non-threatening-first sequences presented in old versus new configurations, as a function of phase and epoch. All error bars represent 95% confidence interval.
targets became non-threatening and (2) learning of context initially associated with non-threatening targets was out-competed by “bottom-up” factors such as stimulus salience of threatening targets presented later in the same contexts. Further, switching the context from being associated with a threatening target to being associated with a non-threatening target slowed overall responding, while the converse sped up overall responding, suggesting the influence of bottom-up factors in processing the threat targets. In addition, the influence of top-down learning on target detection was also clearly evident and indexed by an observable difference between old and new trials. Participant accuracy also decreased from initial to switch phase in the threatening-first sequence; however accuracy consistently remained high in both phases of the non-threatening-first sequence as threatening targets in general produced greater accuracy. The combination of RT and accuracy data suggested that participants used both learned associations (“top-down factors”) and target salience (“bottom-up factors”) to aid target detection when initially presented with a threatening target, but after switching to a non-threatening target participants primarily relied on learned associations to aid detection. In this scenario, participants could not rely on salience to improve detection speed, and this reduced accuracy after shifting to non-threatening targets. Reduced accuracy did not offset contextual learning indexed by RTs in the switch phase of the threatening-first sequence, as this effect of reduced accuracy was amplified when targets were presented in new arrays that had not been learned.

Our finding that contexts associated with threatening targets continued to improve detection even after non-threatening targets were presented in the same context are in line with earlier research. This research used associative learning paradigms to show that threat-associated contexts were learned better than non-threat-associated contexts (Maren et al., 2013). For example, humans or animals experiencing repeated pairings of conditioned stimuli (e.g. tone) and unconditioned stimuli (e.g. shock) subsequently displayed a fear response to both conditioned stimulus and the context in which the stimuli occurred (Malin & McGaugh, 2006; Maren et al., 2013). Other studies showed that even in the absence of a conditioned stimulus, a context previously paired with shock elicited a fear response compared to a context not previously paired with shock in both animals and humans (Alvarez, Biggs, Chen, Pine, & Grillon, 2008; Maren et al., 2013). Our findings extend this research further by showing that humans were able to extract regularities within threat-related contexts and use this knowledge effectively to detect embedded threatening targets as well neutral targets presented later in the threat-related contexts.

Our paradigm also addresses new questions regarding the change in contingencies when a previously threat-target-related context becomes associated with a relatively neutral target and vice versa. Previous research using reversal learning paradigms shows that learning is stronger for the stimuli currently associated with threats compared to stimuli currently associated with safety, before or after reversal of contingencies (Schiller & Delgado, 2010). Using a paradigm where a richer context was used, our results showed that learning of contexts associated with threatening stimuli continued to have robust effects on detection even after these contexts became associated with non-threatening stimuli. Contextual learning can provide information regarding stable spatial layouts, probability, salience, identity, and location of embedded targets as well as covariation between different elements comprising the context. Hence, contextual learning has a stronger top-down influence (Chun, 2000) than can be measured by associative learning between two stimuli measured via reversal learning. Furthermore, our findings have important theoretical implications in that they show that threat detection is not driven simply by bottom-up factors but also by top-down influences. Specifically, while there is evidence showing how explicit threat cues facilitate detection of threatening targets (Sussman, Szekely, Hajcak, & Mohanty, 2016; Sussman, Weinberg, Szekely, Hajcak, & Mohanty, 2016), our study shows how implicit learning can facilitate detection of threatening targets in a top-down manner. Our task is also ecologically valid in that we do not always have access to explicit cues in our environment signalling specific threat; rather, we often have to use implicitly learned regularities in our environment to detect threats. Finally, our paradigm allows for a carefully controlled manipulation of context which is not always possible in real-world scenes (Chun, 2000) in which threatening stimuli are typically studied.

While our paradigm and most reversal learning paradigms are often implicit learning paradigms where participants are not explicitly instructed to learn associations, our contextual learning paradigm offers additional features relevant to understanding
threat learning. Reversal learning paradigms measure learning as a change in physiological reactivity to the target stimulus that is paired with a threatening outcome and demonstrate the result of reversing this pairing. In contrast, using the contextual learning paradigm, we measured learning as the rapid and accurate detection of targets embedded in arrays that were paired with threatening targets and observed the result of reversing this pairing. Consequently, the contextual learning paradigm allows us to examine how well the spatial regularities in the surrounding context are learned and how this learning influences subsequent allocation of attention and target detection. While earlier research shows how perception of threatening and non-threatening stimuli is strongly influenced by explicit cues signaling stimulus presence or absence, or their position in space (Mohanty, Egner, Monti, & Mesulam, 2009; Summerfield & de Lange, 2014; Sussman et al., 2016), we add to this body of knowledge by demonstrating that implicit knowledge of spatial context can guide the perception of threatening targets. This is a more ecologically valid account of perception since most times we do not have access to explicit cues regarding threats in our environment but have to extract this knowledge based on complex contexts. As such, the present research opens avenues for future theoretical and empirical development in understanding the role of contextual learning in threat detection across a range of functioning from adaptive improvements to search to maladaptive slowing of search due to reduced ability to modify excepted target.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Akos Szekely http://orcid.org/0000-0002-3333-4424
Aparajita Mohanty http://orcid.org/0000-0003-0983-3343

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