Perceived duration is reduced by repetition but not by highlevel expectation

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A repeated stimulus is judged as briefer than a novel one. It has been suggested that this duration illusion is an example of a more general phenomenon-namely that a more expected stimulus is judged as briefer than a less expected one. To test this hypothesis, we manipulated high-level expectation through the probability of a stimulus sequence, through the regularity of the preceding stimuli in a sequence, or through whether a stimulus violates an overlearned sequence. We found that perceived duration is not reduced by these types of expectation. Repetition of stimuli, on the other hand, consistently reduces perceived duration across our experiments. In addition, the effect of stimulus repetition is constrained to the location of the repeated stimulus. Our findings suggest that estimates of subsecond duration are largely the result of low-level sensory processing.

Introduction

Inferring duration is important in a wide variety of natural situations, such as playing sports, learning music, deciding whether one can stop a car in time before a traffic light turns red, inferring whether a conversation partner intends to continue speaking from a pause in their speech, or a predator choosing the right moment to jump onto prey. Psychophysical studies have shown that the perceived duration of a stimulus is not simply a noisy estimate of its true duration but rather can be influenced by irrelevant features (Eagleman & Pariyadath, 2009; Herbst, Javadi, van der Meer, & Busch, 2013; Kanai, Paffen, Hogendoorn, & Verstraten, 2006; van Wassenhove, Buonomano, Shimojo, & Shams, 2008; Xuan, Zhang, He, & Chen, 2007), emotional valence or arousal level (Angrilli, Cherubini, Pavese, & Mantredini, 1997; Droit-Volet, Brunot, & Niedenthal, 2004), and preceding stimuli (Johnston, Arnold, & Nishida, 2006; Pariyadath & Eagleman, 2007, 2008; Tse, Intriligator, Rivest, & Cavanagh, 2004).

In the latter category, the effects of repeated stimuli are particularly striking. In a sequence of repeated stimuli, later stimuli are judged as briefer than the initial stimulus (Kanai & Watanabe, 2006; Pariyadath & Eagleman, 2007; Rose & Summers, 1995). A closely related effect is the temporal oddball effect (Birngruber, Schröter, & Ulrich, 2014; Chen & Yeh, 2009; Pariyadath & Eagleman, 2007, 2012; Schindel, Rowlands, & Arnold, 2011; Tse et al., 2004): When an observer watches a stream of repeated stimuli, a different stimulus (oddball) of the same duration inserted in the stream is judged as lasting longer. The strength of the temporal oddball effect increases both with the number of repetitions preceding the oddball (Pariyadath & Eagleman, 2012) and with the magnitude of the feature difference between the oddball and the repeated stimuli (Kim & McAuley, 2013; Pariyadath & Eagleman, 2012; Schindel et al., 2011).

Repetition of a stimulus in a sequence makes a subsequent occurrence of that stimulus more expected

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than a novel stimulus. This has raised the question of whether duration distortion due to repetition is one instance of a more general phenomenon—namely that perceived duration is reduced whenever a stimulus is more expected (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007; Schindel et al., 2011). However, expectation and repetition are confounded in the typical experimental paradigm of the temporal oddball effect. To determine whether expectation in general reduces perceived duration, one must examine ways of manipulating high-level expectation of a stimulus that is not based on the repetition of that stimulus.

Expectation can be generated not only based on the repetition of a specific stimulus but also based on the repetition of the *relation* between stimuli. Such expectation can be thought of as being of a higher level than the one induced by the repetition of a specific stimulus. In this article, we manipulate expectation based on the repetition of the relation between stimuli and examine whether such expectation reduces perceived duration.

In Experiment 1, we manipulate expectation based on the probability of occurrence of the relation between stimuli. We introduce two *types* of sequences that are distinguished by the relation between the last stimulus in the sequence and its preceding stimuli. One sequence occurs more often than the other in the experiment; thus, it is more expected. To control for the repetition of specific stimuli, the number of repetition of stimuli within a sequence is equal in both sequences, and the repetition of any specific stimulus across the time scale of the experiment is counterbalanced (no specific stimulus occurs more frequently than other stimuli in the whole experiment). If expectation in general reduces perceived duration, then the last stimulus in a sequence of the more frequent type should be judged as lasting shorter than the last stimulus in a sequence of the less frequent type.

Expectation might also be induced by a regular pattern in a stimulus sequence. A regular pattern can be formed by the repetition of a stimulus, as in the typical paradigm of the temporal oddball effect. It can also be formed by the repetition of alternation between two stimuli. For example, an alternating sequence of A-B-A-B (letters A and B denote any two different stimuli) leads one to expect A more than B to be the next stimulus. When people are asked to press one of two buttons as soon as they see the stimulus associated with that button, they respond faster to the last stimulus in A-B-A-B-A than in A-B-A-B-B (Soetens, Boer, & Hueting, 1985). In another study, after observing A-B-A-B, a perceptual bias toward A was found when the next stimulus is ambiguous between A and B (Maloney, Dal Martello, Sahm, & Spillmann, 2005). In Experiment 2, we compare the perceived duration of the last

stimulus in a sequence A-B-A-B-A and that in a sequence A-B-A-B-B. The effect of repetition is presumably stronger in the latter condition because the last stimulus is an immediate repetition of the preceding stimulus. By contrast, the high-level expectation of the last stimulus might be stronger in the former condition because people might expect the alternating pattern to continue.

As a third form of high-level expectation, we examine expectation induced by overlearned sequences—ones that are very common in daily life (e.g., ascending positive integers 1-2-3-4). In this sequence, the relation between two subsequent stimuli (an increment of one) repeats. When viewing such sequences, people might expect the next integer in the sequence to appear. It has been reported that observers judge the first digit in a sequence of ascending numbers (1-2-3-4-5) as lasting longer than the following digits (Pariyadath & Eagleman, 2007). In Experiment 3, we test whether the number 5 in a stimulus sequence 1-2-3-4-5 is judged as briefer than 6 in a sequence 1-2-3-4-6, which violates the expectation based on the overlearned sequence.

Together, these experiments allow us to determine whether perceived duration is reduced only by repetition of stimulus or also by high-level expectation.

Last, we examine whether perceived duration is reduced when the repeated stimulus appears at a different location. This experiment is not aimed at distinguishing repetition and expectation, but rather it provides insight into how the effect of repetition on perceived duration depends on other factors such as location.

Participants and general method

Participants

All experiments were approved by the institutional review board of Baylor College of Medicine. Fifty-nine participants were included in the study. All participants except for one (the first author) were naïve to the purpose of the study. All naïve participants provided informed consent and received compensation. Sixteen participants (nine males and seven females, aged 29 ± 7 years) took part in Experiment 1.1. Twelve of them further took part in Experiment 1.2. Seventeen participants (eight males and nine females, aged 26 ± 4 years) took part in Experiment 2. Twelve participants (10 males and two females, aged 26 ± 4 years) took part in Experiment 3. Thirteen participants (nine males and four females, aged 32 ± 10 years) took part in Experiment 4. Twelve participants (six males and six females, aged 30 ± 5 years) took part in Experiment 5.

The first author participated in all the experiments. Three naïve participants were in both Experiments 1 and 3. One naïve participant was in Experiments 1, 3, and 5. One naïve participant was in Experiments 1 and 4. One naïve participant was in Experiments 2 and 5. All other participants took part in only one of the five experiments.

Apparatus

In all experiments, participants were seated at a distance of approximately 60 cm from a cathode ray tube monitor (Viewsonic G225f, Viewsonic, Brea, CA), which had a screen resolution of 1152×864 pixels and a refresh rate of 100 Hz. Besides the monitor, no other light source was present in the experimental room. Stimuli were presented using Psychtoolbox for Matlab (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). The background luminance of the screen was mid-level gray ($M \pm$ $SEM = 9.2 \pm 0.1 \text{ cd/m}^2$; measured at a viewing distance of 60 cm; Photo Research Lite Mate III 504, Photo Research, Inc., Chatsworth, CA). All stimuli were in white $(20.6 \pm 0.2 \text{ cd/m}^2)$. Each participant wore a pair of earplugs with approximately 33-dB noise reduction to prevent distraction.

Data analysis

We fitted the psychometric functions based on raw responses of an individual subject in a given experimental session as follows. (No conditions were shared between sessions.) We denote by t_{in} the duration of the test stimulus (the fifth stimulus in Experiments 1.1, 2, and 3, and 5 and the first stimulus in Experiment 4) on the *n*th trial in the *i*th experimental condition. We assume that the probability of the participant's response r_n on that trial is

$$p(r_n = \text{``longer''} | t_{in}, \mu_i, \sigma_i, \lambda)$$

= $(1 - \lambda) \Phi(t_{in}; \mu_i, \sigma_i) + 0.5\lambda;$
$$p(r_n = \text{``shorter''} | t_{in}, \mu_i, \sigma_i, \lambda)$$

= $1 - p(r_n = \text{``longer''} | t_{in}, \mu_i, \sigma_i, \lambda),$

where λ is the probability that the participant guesses (lapse rate; can depend on session; Wichmann & Hill, 2001), μ_i is the test duration that a participant perceives as equally long as the other stimuli (point of subjective equality; PSE), σ_i reflects the participants' sensitivity (just noticeable difference; JND), and $\Phi(t_{in};\mu_i,\sigma_i)$ is the cumulative Gaussian distribution function with mean μ_i and standard deviation σ_i . We use boldface μ and σ to denote the vectors of PSE and JNDs across all conditions tested in the session. To calculate the

$$L(\boldsymbol{\mu}, \boldsymbol{\sigma}, \boldsymbol{\lambda}) = p(\text{data}|\boldsymbol{\mu}, \boldsymbol{\sigma}, \boldsymbol{\lambda})$$

= $\prod_{i=1}^{C} p(\text{data}_i | \mu_i, \sigma_i, \boldsymbol{\lambda})$
= $\prod_{i=1}^{C} \prod_{n=1}^{N_i} p(r_n | t_{in}, \mu_i, \sigma_i, \boldsymbol{\lambda})$

where C is the number of conditions in the session and N_i is the number of trials in condition *i*. For each session separately, the parameters μ , σ , and λ were estimated simultaneously to maximize log $L(\mu,\sigma,\lambda)$, using fmincon in Matlab. For example, if an experiment had two conditions in a session, we simultaneously fitted five parameters for that session: $\mu_1, \mu_2, \sigma_1, \sigma_2$, and λ . We quantify the relative duration distortion (RDD) of the test stimulus by the equation $RDD = (t_{ref} - PSE)/PSE$, where t_{ref} is the duration of the first four stimuli (the last four in Experiment 4). For example, an RDD of 0.05 means that the last stimulus was judged to be 5% longer than the other stimuli. All parameter estimates of each experiment are reported in Supplementary Tables S1 through S5.

Experiments and results

Experiment 1: Effect of sequence type probability

Design

To determine whether perceived duration is impacted by high-level expectation based on the probability of the relation between stimuli, we used two types of sequences, A-A-A-B and A-A-A-C, which were identical in the distribution of the first four stimuli but differed in the relation between the fifth stimulus and the first four. We manipulated the expectation for the last stimulus by presenting, within a session, one type of sequence more frequently than the other type. In Experiment 1.1, we measured the effect of this manipulation of probability on perceived duration. To ensure that our manipulation is sufficient to bias expectation, we measured the participants' choice reaction time to the last stimulus of each sequence in Experiment 1.2. If the sequence type of higher probability is more expected, then the reaction time to the last stimulus in that sequence type should be shorter and mistakes should be less frequent.

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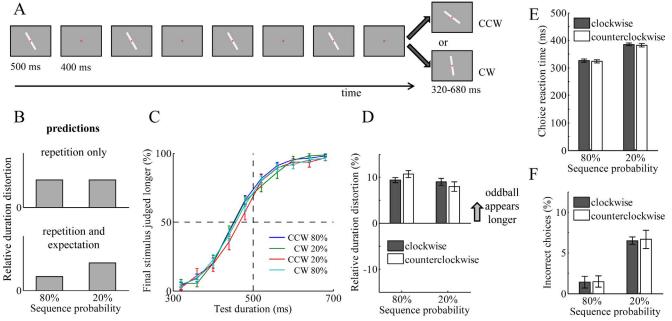


Figure 1. Perceived duration is not influenced by expectation based on the probability of stimulus sequence type. (A) Examples of the two sequence types. The initial orientation A is randomly sampled from a uniform distribution over all orientations. The last stimulus (oddball) is rotated either 22.5° clockwise (CW) or 22.5° counterclockwise (CCW) from A. (B) Predictions. If only repetition of stimulus reduces perceived duration, then the oddball in the high- and low-probability sequence types should be judged as longer by the same extent (top). If expectation based on sequence type probability also reduces perceived duration, then the oddball in the low-probability sequence type should be judged as longer than the one in the high-probability sequence type (bottom). (C) The psychometric curves of each condition averaged over 16 participants. Error bars, here and everywhere, represent the standard error of the mean. (D) The duration distortion of the last stimulus relative to other stimuli in each condition. There was no significant difference between different sequence type probabilities and between oddball change directions. The oddball was judged as longer in each condition. (E) In a separate experiment, the participants viewed the same types of sequences and judged the orientation change of the last bar. The reaction time was significantly shorter for the sequence type of higher probability. (F) Participants made significantly fewer errors when the sequence type was of higher probability.

Method

Examples of the stimulus sequences used in Experiment 1.1 are shown in Figure 1A. On each trial, a participant sequentially viewed five white bars flashing in the center of the screen and judged whether the last bar was on the screen for a longer or briefer duration than the first four bars. Each trial was structured as follows. A red fixation cross spanning a visual angle of 0.5° appeared in the center of the screen. After a duration randomly drawn from a uniform distribution over the range of 400 to 600 ms, the first bar appeared. The first four bars all lasted 500 ms and had the same orientation. We denote this orientation by A; on each trial, it was drawn randomly from a uniform distribution over all orientations. The orientation of the last bar (the oddball) was rotated by 22.5°, either clockwise (denoted by B) or counterclockwise (denoted by C) relative to A. The duration of the last bar was drawn randomly with equal number of incidents from 10 values equally spaced between 320 and 680 ms in 40-ms steps. The bar subtended 9.1° by 0.9° of visual angle. The interstimulus interval was 400 ms. The fixation

cross remained visible throughout the stimulus sequence and disappeared 400 to 600 ms after the disappearance of the last bar. After the fixation cross disappeared, participants were allowed to respond. They pressed the left or the right arrow key to indicate that the duration of the last bar was shorter or longer, respectively, than that of the first four bars. No feedback was provided. After the response, the next trial began after a duration drawn randomly from a uniform distribution over the range of 800 to 1000 ms.

Each participant was tested in two sessions on different days. Each session included 500 trials. In one randomly chosen session, 20% of the sequences were of type A-A-A-B and 80% were of type A-A-A-A-C; in the other session, 20% were of type A-A-A-A-C and 80% were of type A-A-A-B. Within a session, sequence type was randomly interleaved. At the beginning of each session, participants were explicitly informed about the probabilities of the sequence types. Eight additional practice trials (all of the sequence type that was more frequent in the session) were added before the 500 testing trials. From the point of view of the observer, the practice trials were indistinguishable from the testing trials, but we did not analyze them. The testing trials were divided into six blocks, between which participants were asked to take a break for at least 1 min.

Of the 16 participants in Experiment 1.1, 12 also completed Experiment 1.2 after completing Experiment 1.1, in which the choice reaction time to the last stimulus of the two sequences was measured. The experiment and trial structures were identical to those in Experiment 1.1 except for the following differences. The participants were instructed to press one of the two arrow keys as soon as they saw the last bar: the left key if the last bar was rotated counterclockwise from the first four bars, and the right key if the last bar was rotated clockwise. The fixation cross was black. The last bar remained on the screen until the participant pressed one of the two keys. After the key was pressed, the fixation cross turned green if the correct key was pressed or turned red if the wrong key was pressed. The fixation cross then disappeared after 300 ms. The interval from the onset of the fixation to that of the first bar was randomly drawn from a uniform distribution over the range of 200 to 400 ms, and the interval from response to the next trial was drawn from 600 to 800 ms.

Prediction for Experiment 1.1

If only repetition of stimulus reduces perceived duration, then in both sequence types, the last stimulus should be judged as longer than the first four, and by the same amount between the two sequence types. The latter is because the probability of each specific orientation in the fifth position was controlled for both within and across trials. Within a trial, it was controlled for because none of the four preceding orientations were ever identical to the fifth one. Across trials, it was controlled for through the randomization of orientation A.

If perceived duration is also reduced by high-level expectation based on probability, then the fifth stimulus in the high-probability (80%) sequence type should be judged as briefer than the fifth stimulus in the low-probability (20%) sequence type (Figure 1B).

Results

Experiment 1.1: The participant-averaged psychometric curves and the relative duration distortions for each condition in Experiment 1.1 are shown in Figures 1C and D. In the session in which the sequence type A-A-A-B had higher probability, the oddball was judged to be $9.4\% \pm 0.6\%$ longer than preceding stimuli in the high-probability sequence type and $8.0\% \pm 1.0\%$ longer in the low-probability sequence type. In the

session in which the sequence type A-A-A-C had higher probability, the oddball was judged to be 10.7% \pm 0.8% longer in the high-probability sequence type and 9.0% \pm 0.8% longer in the low-probability sequence type. Each of these was significantly larger than zero (two-tailed t test, p < 0.004), confirming the basic temporal oddball effect. A two-way repeatedmeasures analysis of variance (ANOVA) with factors sequence type probability (20% or 80%) and individualtrial sequence type (clockwise change or counterclockwise change) revealed a trending but nonsignificant main effect of sequence type probability on the relative duration distortion, F(1, 15) = 3.93, p = 0.07, no significant main effect of individual-trial sequence type, F(1, 15) = 0.13, p = 0.73, and no significant interaction between sequence type probability and individual-trial sequence type, F(1, 15) = 0.75, p = 0.40.

We next examined the effects of sequence type probability on JND and reaction time. A repeatedmeasures ANOVA revealed no significant main effect of sequence type probability on JND, F(1, 15) = 0.59, p = 0.46, no significant main effect of individual-trial sequence type, F(1, 15) = 1.21, p = 0.29, and no significant interaction, F(1, 15) = 1.50, p = 0.24. In the session in which the sequence type A-A-A-B had higher probability, the average reaction time was $388 \pm$ 77 ms in the high-probability sequence type and 416 \pm 97 ms in the low-probability sequence type. In the session in which the sequence type A-A-A-C had higher probability, the average reaction time was 403 \pm 57 ms in the high-probability sequence type and 400 \pm 56 ms in the low-probability sequence type. There was no significant main effect of sequence type probability on reaction time, F(1, 15) = 1.88, p = 0.19, no significant main effect of individual-trial sequence type, F(1, 15) =1.33, p = 0.27, and no significant interaction, F(1, 15) =0.00, p = 0.99. The lapse rate was $1.2\% \pm 0.4\%$ in the session in which A-A-A-B had higher probability and $1.8\% \pm 0.6\%$ in the session in which A-A-A-C had higher probability. These were not significantly different (p = 0.49).

Experiment 1.2: The average reaction time for each condition in Experiment 1.2 is shown in Figure 1E. In the session in which the sequence type A-A-A-A-B had higher probability, the reaction time was 326 ± 6 ms in the high-probability sequence type and 382 ± 6 ms in the low-probability sequence type. In the session in which the sequence type A-A-A-C had higher probability, the reaction time was 323 ± 6 ms in the high-probability sequence type and 385 ± 5 ms in the high-probability sequence type. A two-way repeated-measures ANOVA with factors sequence type probability and individual-trial sequence type probability on reaction time, F(1, 11) = 80.30, p < 0.001, no significant main effect of individual-trial sequence type, F(1, 11) =

0.15, p = 0.70, and no significant interaction between sequence type probability and individual-trial sequence type, F(1, 11) = 0.00, p = 0.98. The reaction to the last stimulus was faster in the 80% probability sequence type than in the 20% probability sequence type. The average rate of incorrect responses for each condition in Experiment 1.2 is shown in Figure 1F. In the session in which the sequence type A-A-A-B had higher probability, the incorrect rate was $1.4\% \pm 0.7\%$ in the high-probability sequence type and $6.7\% \pm 1.1\%$ in the low-probability sequence type. In the session in which the sequence type A-A-A-C had higher probability, the incorrect rate was $1.5\% \pm 0.7\%$ in the highprobability sequence type and $6.5\% \pm 0.5\%$ in the lowprobability sequence type. A two-way repeated-measures ANOVA with factors sequence type probability and individual-trial sequence type revealed a significant main effect of sequence type probability on the incorrect rate, F(1, 11) = 13.92, p = 0.003, no significant main effect of individual-trial sequence type, F(1, 11) =0.04, p = 0.84, and no significant interaction, F(1, 11) =0.01, p = 0.92. Fewer incorrect responses were made in the 80% probability sequence type than in the 20% probability sequence type.

Experiment 1.1 suggests that expectation based on sequence probability does not reduce perceived duration. There was even a (nonsignificant) trend that the last stimulus in the more expected (high-probability) sequence was judged as longer than in the less expected sequence. Experiment 1.2 indicated that the probability difference between the sequence types was salient enough to bias expectation, at least when the sequence type was task relevant. We cannot rule out the possibility that the brain does not create any expectations when the feature we manipulated (counterclockwise or clockwise) is irrelevant to the task, as it was in Experiment 1.1. Thus, our results may have been different if the experiment had dual tasks or if the manipulated feature were more ecologically relevant. However, at a minimum, we can state that not every form of probability manipulation that an observer is aware of affects perceived duration.

Experiment 2: Effect of sequence regularity and sequence type probability

Design

Experiment 1 showed that expectation based on sequence type probability does not reduce perceived duration. In Experiment 2, we additionally examined the effects of a different potential source of expectation—namely, sequence regularity. The temporal oddball paradigm is not suitable for distinguishing the effects of sequence regularity and stimulus repetition because the regularity of the sequences used in that paradigm is based on the repetition of a specific stimulus. To overcome this, we investigated the effects of another form of regularity—namely, one based on alternation rather than repetition of a specific stimulus. An alternating sequence such as A-B-A-B may induce an expectation that the next stimulus will be A (Maloney et al., 2005; Soetens et al., 1985).

Method

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Examples of the stimulus sequences are shown in Figure 2A. We denote the orientation of the first stimulus by A, and the orthogonal orientation by B. A was either 45° clockwise or 45° counterclockwise from vertical, with equal probability. We manipulated two factors: sequence regularity and sequence type probability. We used two sequence types: regular (A-B-A-B-A) and irregular (A-B-A-B-B). The probabilities of the two sequence types were manipulated in the same way as in Experiment 1: 80%:20% in one session and 20%:80% in the other. Unlike in Experiment 1.1, participants were not informed of these probabilities. However, they were instructed that at the end of the experiment they would be asked whether the fifth stimulus in each trial was more often the same as or more often different from the fourth one. Other differences from Experiment 1.1 were minor: The size of the bar was 4.7° by 0.6° of visual angle, and no practice trials were given.

Prediction

In irregular sequences of the form A-B-A-B-B, the last stimulus B breaks the alternating pattern started by A-B-A-B but immediately repeats the previous A; in regular sequences of the form A-B-A-B-A, the opposite holds. Therefore, regularity and stimulus repetition might have opposite effects on the perceived duration of the last stimulus in these sequences. If regularity induces expectation and the effect of high-level expectation on perceived duration is stronger than that of stimulus repetition, then the last stimulus in A-B-A-B-A should be judged as briefer than the one in A-B-A-B-B. On the other hand, if the effect of stimulus repetition is stronger than that of expectation, then the last stimulus in A-B-A-B-A should appear longer than the one in A-B-A-B-B. We expect to measure the net effect of stimulus repetition and regularity-induced expectation on perceived duration (Figure 2B).

In this experiment, the probability of a specific orientation (and therefore the total amount of stimulus repetition) was controlled for both within a trial and across the experiment. Within a trial, it was controlled for because in both sequence types, A and B each occurred twice before the last stimulus. Across the experiment, the probability of a specific orientation was

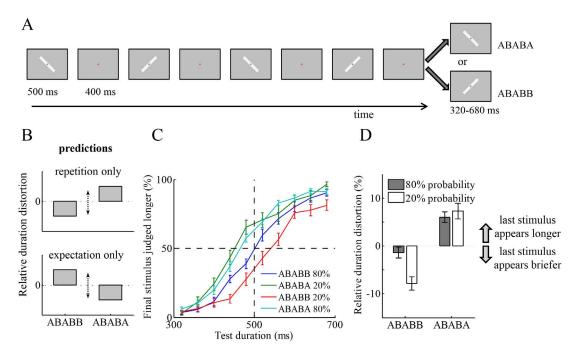


Figure 2. The effect of expectation based on sequence regularity, if any, is weaker than that of stimulus repetition. (A) Examples of the two sequence types: A-B-A-B-A and A-B-A-B-B. The orientation of A occurred as either 45° clockwise or 45° counterclockwise from vertical with equal incidence. (B) Predictions in two extreme scenarios. If only repetition reduces perceived duration, then the last stimulus in sequence A-B-A-B-B should be judged as briefer than that in sequence A-B-A-B-A (top). If only expectation based on sequence regularity reduces perceived duration, then the last stimulus in sequence A-B-A-B-B should be judged as longer than that in A-B-A-B-A (bottom). The double-headed arrow indicates that we are agnostic of any potential response bias that is independent of stimulus sequence. In other words, we can only predict the relation between the duration distortions of the two sequence types will reflect their relative strengths. (C) The average psychometric curves of each condition over 17 participants. (D) The duration distortion of the last stimulus relative to other stimuli in each condition. The last stimulus in A-B-A-B-B was judged to be briefer than in A-B-A-B-A, reflecting a stronger effect of repetition.

controlled for because A can be one of the two orientations that occur exactly equally often.

Results

The participant-averaged psychometric curves and the relative duration distortions for each condition are shown in Figures 2C and D. In the session in which the sequence type A-B-A-B-B had higher probability, the last stimulus was judged to be $1.4\% \pm 1.1\%$ briefer than the preceding stimuli in A-B-A-B-B and 7.3% \pm 1.6% longer in A-B-A-B-A. In the session in which the sequence type A-B-A-B-A had higher probability, the last stimulus was judged to be $7.8\% \pm 1.4\%$ briefer in A-B-A-B-B and $6.0\% \pm 1.1\%$ longer in A-B-A-B-A. A two-way repeated-measures ANOVA with factors sequence regularity (A-B-A-B-B or A-B-A-B-A) and sequence type probability (20% or 80%) showed a significant main effect of sequence regularity on the relative duration distortion, F(1, 16) = 40.82, p < 0.001, a significant main effect of sequence type probability, F(1, 16) = 5.42, p = 0.03, and a significant interaction, F(1, 16) = 5.43, p = 0.03. Post hoc paired t tests between conditions revealed that there were significant differences between all pairs of conditions (p < 0.003), except for between A-B-A-B-A being a high-probability sequence and it being a low-probability sequence (p = 0.56). The last stimulus in the regular sequence A-B-A-B-A was judged to be longer than in the irregular sequence A-B-A-B-B. Surprisingly, the last stimulus was judged to be longer in the high-probability sequence than in the low-probability sequence only for sequence type A-B-A-B-B. After each session, the experimenter verbally asked the participants whether the fifth stimulus was more often the same as or more often different from the fourth one. In three sessions, the experimenter forgot to ask immediately after the experiment and queried through email. Twenty-seven out of the 29 responses immediately obtained after the experiment from naïve participants were correct, and one out of the three responses obtained through email was correct.

A repeated-measures ANOVA revealed no significant main effect of sequence regularity on JND, F(1, 16) = 0.28, p = 0.61, no significant main effect of sequence type probability, F(1, 16) = 0.77, p = 0.39, and no significant interaction, F(1, 16) = 0.54, p = 0.47. In the session in which A-B-A-B-B had higher probability, the average reaction time was 442 ± 46 ms in A-B-A-B-B and 486 ± 53 ms in A-B-A-B-A. In the session in which A-B-A-B-A had higher probability, the average reaction time was 522 ± 59 ms in A-B-A-B-B and 513 ± 55 ms in A-B-A-B-A. There was a significant main effect of sequence probability on reaction time, F(1, 16) = 9.27, p = 0.0082, no significant main effect of sequence regularity, F(1, 16) = 0.98, p = 0.34, and no significant interaction, F(1, 16) = 1.34, p = 0.26. Reaction times were shorter for the high-probability sequence. The average lapse rate was $4.5\% \pm 1.5\%$ in the session in which A-B-A-B-B had higher probability and $10.3\% \pm 2.5\%$ in the other session.

The finding that the last stimulus in A-B-A-B-B was judged to be shorter than in A-B-A-B-A demonstrates that the effect of expectation based on sequence regularity in reducing perceived duration, if any, is weaker than that of stimulus repetition. This experiment could shed light on the origins of the reduction in the perceived duration of the repeated stimulus in the temporal oddball effect. In the current experiment, the effect of stimulus repetition is probably weaker than in the temporal oddball paradigm (e.g., in sequence of A-A-A-A-B). This is because the temporal oddball effect is stronger if there are more repeating stimuli before the oddball (Pariyadath & Eagleman, 2012), suggesting that the effect of repetition may accumulate with consecutive repetitions. In the current experiment, there is no consecutive repetition, and repetition differs between the two sequences only in whether the last stimulus immediately repeats its preceding one. Therefore, the size of the effect of stimulus repetition in Experiment 2 is likely comparable to the size of the temporal oddball effect when there is only a single repetition. In Pariyadath and Eagleman (2012), the duration of the oddball was overestimated by about 6% when there was a single repetition, which is close to the average difference between the duration distortions of the two sequence types in the current experiment. This suggests that the effect of repetition dominates the net difference between the two sequences. On the other hand, because the alternating pattern is maintained until the fourth stimulus in the sequence of type A-B-A-B-B, the effect of regularity is likely similar to that in the sequence of type A-A-A-B. For these reasons, we believe that in the temporal oddball paradigm, the contribution of expectation based on sequence regularity to the temporal oddball effect, if any, is very small compared with the effect of stimulus repetition. On the other hand, the finding that the last stimulus in a higher probability sequence was judged to be longer in one type of sequence suggests that if expectation based on probability influences perceived duration at all, the effect might be expansive rather than compressive. This would further argue against the hypothesis that the temporal oddball effect is due to the oddball being less expected, as opposed to simple repetition of the standard stimulus (Pariyadath & Eagleman, 2008).

Experiment 3: Effect of overlearned sequences Design

Experiment 1 showed no effect of expectation based on sequence type probability. Experiment 2 showed that any effect of expectation based on sequence regularity in reducing perceived duration is much weaker than that caused by immediate repetition of the stimulus. The current experiment further examined whether expectation based on a sequence overlearned in daily life, such as 1-2-3-4-5, reduces perceived duration.

Method

The experiment manipulated two factors: sequence type and sequence order. The stimuli were sequences of digits, differing in whether the last digit violated an overlearned sequence and whether it was a repeat of the preceding digit. Participants compared the duration of the last stimulus against other stimuli in the sequence. The first four digits were in ascending order (1-2-3-4) in one random session of the experiment and in descending order (9-8-7-6) in the other session. The purpose of including both ascending and descending sequences was to control for the potential confound that larger digits may bias the judgment of duration toward *longer* (Xuan et al., 2007). The last digit of each sequence was repeating the previous one (1-2-3-4-4 or 9-8-7-6-6), expected from the overlearned sequence (1-2-3-4-5 or 9-8-7-6-5), or unexpected from the overlearned sequence and not repeating (1-2-3-4-6 or 9-8-7-6-4); we denote these sequence types as Repeating, Expected, and Unexpected, respectively. An example of the three types of sequences with the first four digits in ascending order is shown in Figure 3A. Trials of the three sequence types were randomly interleaved with equal occurrence. The trial structure and the task were the same as in Experiments 1.1 and 2. The digit stimuli were on average 6.3° of visual angle in height. There were six practice trials, two of each sequence type, presented in interleaved order before the testing trials. They were indistinguishable from the testing trials. Each of the two sessions had 450 testing trials.

Prediction

If repetition reduces perceived duration, then a 4 after 1-2-3-4 should be judged as briefer than a 6, and a

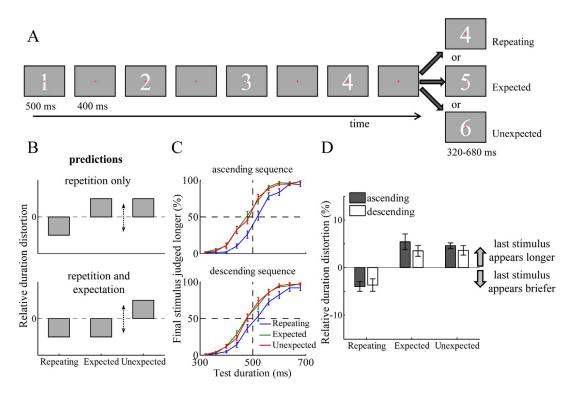


Figure 3. Perceived duration is not influenced by expectation based on overlearned sequences. (A) Examples of the three sequence types (Repeating, Expected, and Unexpected) of ascending order. (B) Prediction of the results. If only stimulus repetition reduces perceived duration, then only the last stimulus in Repeating should be judged as briefer than that in Unexpected (top). If expectation based on overlearned sequences also reduces perceived duration, then the last stimulus in Expected should also be judged as briefer than that in Unexpected (bottom). (C) Average psychometric curves of each condition over 12 participants. (D) Only the last stimulus in Repeating was judged as briefer than that in Unexpected.

6 after 9-8-7-6 should be judged as briefer than a 4 (Figure 3B). If overlearned sequences induce expectation and high-level expectation reduces perceived duration, then a 5 after 1-2-3-4 should be judged as briefer than a 6, and a 5 after 9-8-7-6 should be judged as briefer than a 4 (Figure 3B).

Results

The participant-averaged psychometric curves and the relative duration distortions for each condition are shown in Figures 3C and D. The last stimulus was judged to be $4.0\% \pm 1.0\%$ briefer than the preceding stimuli in the sequence 1-2-3-4-4, $5.4\% \pm 1.7\%$ longer in the sequence 1-2-3-4-5, $4.6\% \pm 0.6\%$ longer in the sequence 1-2-3-4-6, $3.7\% \pm 1.3\%$ briefer in the sequence 9-8-7-6-6, $3.5\% \pm 1.1\%$ longer in the sequence 9-8-7-6-5, and $3.6\% \pm 1.0\%$ longer in the sequence 9-8-7-6-4. A two-way repeated-measures ANOVA with factors sequence type and sequence order showed a significant main effect of sequence type (Repeating, Expected, and Unexpected) on the relative duration distortion, F(2, 22) = 31.84, p < 0.001, no significant main effect of sequence order, F(1, 11) = 0.28, p = 0.60, and no significant interaction, F(2, 22) = 0.89, p = 0.41.

After averaging the relative duration distortions of corresponding conditions between the two sessions, a post hoc paired *t* test found a significant difference between Repeating and Expected, t(11) = -5.7, p < 0.001, and between Repeating and Unexpected, t(11) = -9.06, p < 0.001 (both passing the Holm-Bonferroni correction [Holm, 1979]), but none between Expected and Unexpected, t(11) = 0.30, p = 0.77. The last stimulus was judged to be shorter in Repeating than in the other two conditions.

A repeated-measures ANOVA revealed no significant main effect of sequence type on JND, F(2, 22) =0.27, p = 0.76, no significant effect of sequence order, F(1, 11) = 3.37, p = 0.09, and no significant interaction, F(2, 22) = 1.00, p = 0.38. The average reaction time was 365 ± 58 ms in the sequence 1-2-3-4-5, 360 ± 49 ms in the sequence 1-2-3-4-5, 351 ± 52 ms in the sequence 1-2-3-4-6, 320 ± 31 ms in the sequence 9-8-7-6-6, 351 ± 31 46 ms in the sequence 9-8-7-6-5 and 344 ± 40 ms in the sequence 9-8-7-6-4. There was no significant main effect of sequence type on reaction time, F(2, 22) = 1.20, p =0.32, no significant main effect of sequence order, F(1,(11) = 0.37, p = 0.55, and no significant interaction, F(2, p) = 0.5522) = 1.08, p = 0.35. The average lapse rate was 2.0% \pm 0.8% in the session of ascending sequences and 1.3% \pm 0.5% in the session of descending sequences.

These results suggest that expectation based on overlearned sequences had no effect on perceived duration. The 5 in 1-2-3-4-5 and the 6 in 1-2-3-4-6 differed only in whether the digit was expected based on an overlearned sequence but did not generate a difference in their perceived duration. By contrast, the repetition of the 4 in 1-2-3-4-4 reduced its perceived duration. We cannot rule out that the strength of the expectation based on an overlearned sequence gradually diminishes as the experiment continues. Future studies may test this hypothesis by conducting experiments consisting of only a few trials per participant and combining the responses from many participants for analysis.

One may worry that the use of different digits may bias judgments of duration (larger numbers may be judged as longer; see Xuan et al., 2007), causing the difference between conditions. This possibility is ruled out by the results from the session in which descending sequences were used. For example, if the difference between conditions in ascending sequences (e.g., the last digit in 1-2-3-4-4 was judged as shorter than the last digit in 1-2-3-4-5) were due to the bias caused by the digits, then we would expect the opposite pattern of results in the descending sequence (e.g., the last digit in 9-8-7-6-6 would be judged as longer than the last digit in 9-8-7-6-5) and we would have found an interaction between sequence type and sequence order. The absence of either a main effect or an interaction effect of sequence order on either the relative duration distortion or reaction time suggests that the value of digits did not cause a significant bias in duration judgment.

Experiment 4: Attempt to replicate the previous results

Design

In Experiment 3, we found that perceived duration is not reduced by expectation based on overlearned sequences. This seems to conflict with the finding of an experiment in Pariyadath and Eagleman (2007), in which the duration of the first digit in an overlearned sequence of 1-2-3-4-5 was judged to be longer than its succeeding digits, which was not the case in a scrambled sequence (e.g., 1-3-5-4-2). Therefore, we attempted to directly replicate their result.

Method

We randomly interleaved sequences of three types: the sequence 1-1-1-1, the sequence 1-2-3-4-5, and various scrambled sequence (a 1 followed by a random permutation of 2, 3, 4, 5, with the constraint that the 2 could not follow 1 immediately). We denote these sequence types as Repeating, Ordered, and Scrambled, respectively. (Note that the Repeating sequence, although named the same as one sequence type in Experiment 3, has more repetition within a trial.) Examples of the stimulus sequences are shown in Figure 4A. Instead of varying the duration of the last stimulus as in Experiments 1 through 3, we followed the design of Pariyadath and Eagleman (2007) and drew the duration of the first stimulus randomly from 10 possible values equally spaced between 320 and 680 ms, with the other stimuli each lasting 500 ms. Participants reported whether the first digit appeared longer or briefer than other digits. Because of this difference, a positive relative duration distortion indicates that the first stimulus in a sequence is judged as longer than the following stimuli. The duration of fixation, the duration of the interstimulus interval, and the time from the participant's response to the start of the next trial were the same as in Experiments 1.1, 2, and 3. Each participant completed 420 trials in one session.

Prediction

If stimulus repetition reduces perceived duration, then the last four stimuli in Repeating should be judged as briefer than those in Scrambled. Thus, the participants should judge the first stimulus as longer in Repeating than in Scrambled. If high-level expectation based on an overlearned sequence also reduces perceived duration, then the last four stimuli in Ordered should be judged as briefer than those in Scrambled. Thus, the first stimulus should be judged as longer in Ordered than in Scrambled (Figure 4B).

Results

The participant-averaged psychometric curves and the relative duration distortions for each condition are shown in Figures 4C and D. The first digit was judged to be $29.9\% \pm 4.0\%$ longer than the succeeding stimuli in Repeating, $2.5\% \pm 2.0\%$ briefer in Ordered, and $2.1\% \pm 2.2\%$ briefer in Scrambled. We found a significant effect of sequence type on the relative duration distortion, F(2, 24) = 28.13, p < 0.001, oneway repeated-measures ANOVA. Post hoc paired t test (with Holm-Bonferroni correction [Holm, 1979]) found a significant difference between Repeating and Ordered, t(12) = 5.54, p < 0.001, and between Repeating and Scrambled, t(12) = 5.23, p < 0.001, but not between Ordered and Scrambled, t(12) = -0.29, p = 0.77. We conclude, contrary to a previous study (Pariyadath & Eagleman, 2007) but consistent with Experiment 3, that stimulus repetition but not expectation based on overlearned sequences reduces perceived duration.

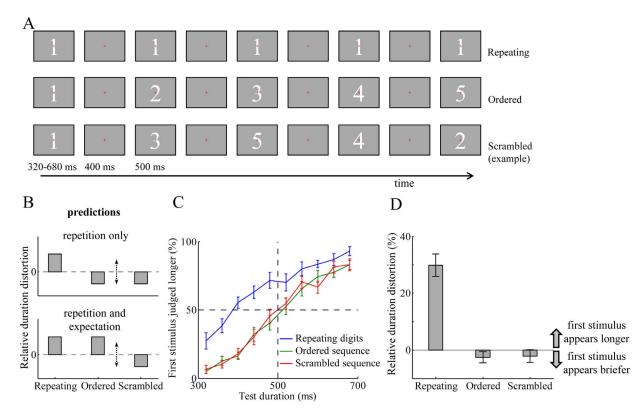


Figure 4. An attempt to replicate a previous result failed to find the effect of expectation. (A) Examples of the three sequence types (Repeating, Ordered, and Scrambled). In each trial of the Scrambled sequence, the second to fifth stimuli were random permutations of digits 2, 3, 4, and 5, without 2 occurring at the second position. (B) Prediction of the results. If only repetition reduces perceived duration, then the first stimulus should be judged as longer than the succeeding stimuli only in Repeating. There should be no difference between Ordered and Scrambled (top). If expectation also reduces perceived duration, then the first stimulus should be (top). If expectation also reduces perceived duration, then the first stimulus should be (bottom). (C) Average psychometric curves of each condition over 13 participants. (D) The first stimulus was judged to be longer than the succeeding stimuli only in Repeating. There was no significant difference between Ordered and Scrambled. The difference between Repeating and Ordered and between Repeating and Scrambled was significant.

There was a significant effect of sequence type on JND, F(2, 24) = 5.14, p = 0.01. On average the JND in Repeating was larger than in Ordered, paired *t* test, t(12) = 2.48, p = 0.03, and larger than in Scrambled, paired *t* test, t(12) = 2.24, p = 0.04, although the significance level did not pass the Holm-Bonferroni correction threshold. There was also a significant effect of sequence type on the reaction time, F(2, 24) = 4.69, p = 0.02. On average, reaction time was shorter in Repeating than in Scrambled, t(12) = -2.66, p = 0.02, and shorter in Ordered than in Scrambled, t(12) = -2.87, p = 0.01. Only the latter pair of comparisons passed the Holm-Bonferroni correction (Holm, 1979). The average lapse rate was $8.2\% \pm 2.5\%$.

This experiment failed to find a significant difference in duration distortion between Ordered and Scrambled sequences; this is consistent with a recent study using a closely related paradigm (Herai & Mogi, 2010). After inspecting the design and data of Pariyadath and Eagleman (2007), we think the discrepancy might have two causes. First, their paper tested one group of participants on Repeating and Ordered and a second group on Repeating and Scrambled. Here, we tested the same participants on all three sequence types. Second, their low number of trials (63 per condition, compared with our 150 in Experiment 3 and 140 in Experiment 4) makes their estimation of duration distortion less reliable. We further estimated the statistical power of this experiment. By assuming that the effect size is equal to that estimated in Pariyadath and Eagleman (2007), our sample size ensures a statistical power of 97% to detect a difference between Ordered and Scrambled at the significance level of 0.05. Therefore, it is unlikely that our finding results from a type II statistical error.

It is not entirely clear why there is a difference in JND and reaction time between conditions. One possible reason why the JND is larger in the Repeating condition is that participants might occasionally confuse their memory of the perceived duration of the first stimulus in a sequence of 1-1-1-1 with the memories of the following stimuli, which are reduced by repetition. The different reaction times between Scrambled and other types of sequences may suggest a stronger expectation of the later stimuli in Repeating and Ordered sequences. If this is the case, this and the fact that the relative duration distortion in Ordered is no larger than in Scrambled argue against the hypothesis that expectation reduces perceived duration.

The average value of the digits after the first stimulus in Repeating was smaller than that in the other conditions. We cannot rule out the possibility that the value of digits can bias participants' responses (Xuan et al., 2007). However, the fact that we did not observe such an effect in Experiment 3 suggests that this bias, if any, is very small in our experiment design. Therefore, it is unlikely to be the major cause of the difference observed between Repeating and the other two sequences.

Experiment 5: The interaction between repetition and stimulus location

Design

Stimulus repetition appears to be the only factor that reduces perceived duration in Experiments 1 through 4. The effect of repetition may occur because the repeated stimulus affects the neural population responding to that stimulus. If this is the case, then the size of the receptive field of such neural population should determine the spatial specificity of the effect. If the receptive fields are relatively small, then the perceived duration of a repeated stimulus should be reduced only when it appears at the same location as its preceding stimuli. If the receptive fields are relatively large, then the perceived duration should also be reduced when the repeated stimulus appears at a different location. Typically, neurons at a higher level of the sensory processing hierarchy have larger receptive fields. Therefore, understanding whether the effect of repetition is specific to the location of the repeated stimuli may shed light on the stage in sensory processing hierarchy where duration perception takes place. In this experiment, we measure the interaction of a change in stimulus feature and a change in stimulus location to determine the spatial specificity of the effect of repetition on perceived duration.

Method

Example stimulus sequences are shown in Figure 5A. The size and luminance of the stimuli, the timing structure of each trial, and the task were identical to those in Experiment 2. On any trial, the first four stimuli were of identical orientation and appeared at the same location. Their orientation was either 45° clockwise or 45° counterclockwise, with equal probability. Their location was 4.6° visual angle (estimated at a distance of 60 cm) to either the left side or the right

side of fixation. The experiment had four conditions, defined by the relation between the last stimulus and the first four stimuli: The last stimulus could appear at the same location with the same orientation as the first four stimuli (we denote this condition as SS), at the same location with a different (orthogonal) orientation (SD condition), at a different location (on the other side) with the same orientation (DS condition), or on the other side with an orthogonal orientation (DD condition). Participants judged whether the last stimulus lasted for a longer or shorter duration than the first four. There were 120 trials in each condition. All four conditions were randomly interleaved.

Prediction

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If repetition of a stimulus reduces perceived duration, then we expect the perceived duration of the last stimulus in the SS condition to be shorter than in the SD condition. If perceived duration is reduced by the repetition of a specific stimulus and if this effect is through the influence on a neural population with small receptive fields, then the effect of repetition should be constrained to the location of the stimulus: The last stimulus in the SS condition should be judged to be shorter than in the DS condition, and there should be no difference between the DS and DD conditions. If the effect of repetition is through the influence on a neural population with large receptive fields, then there should be a difference between DS and DD conditions, but small or no difference between SS and DS conditions and small or no difference between SD and DD conditions.

This experiment is not aimed at distinguishing whether the distortion of perceived duration is due to repetition or expectation. If the distortion is due to expectation, then the prediction may be similar, depending on how a change of stimulus location influences expectation.

Results

The participant-averaged psychometric curves and the relative duration distortions for each condition in Experiment 5 are shown in Figure 5B and C. In the SS condition, the last stimulus was judged to be $2.3\% \pm$ 2.4% shorter than the preceding stimuli. In the SD condition, the last stimulus was judged to be $8.9\% \pm$ 0.9% longer. In the DS condition, the last stimulus was judged to be $11.8\% \pm 1.2\%$ longer. In the DD condition, the last stimulus was judged to be $12.2\% \pm$ 1.6% longer. A two-way repeated-measures ANOVA with factors orientation (same or different) and location (same or different) of the last stimulus showed a significant main effect of orientation on the relative duration distortion, F(1, 11) = 11.55, p = 0.006, a

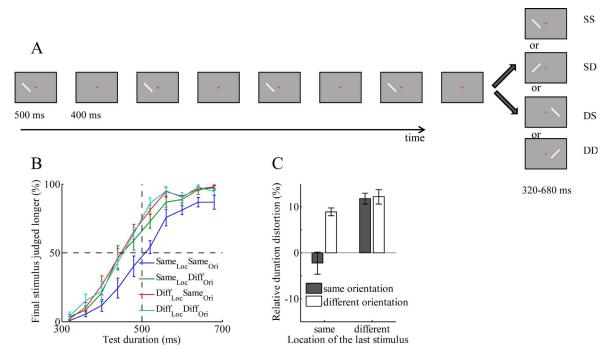


Figure 5. The effect of repetition is constrained to the location of the stimulus. (A) Examples of the four sequence types: SS, SD, DS, and DD. The orientation of the first four stimuli occurred as either 45° clockwise or 45° counterclockwise from vertical and appeared either to the left or to the right of fixation with equal incidence. (B) The average psychometric curves of each condition over 12 participants. (D) The duration distortion of the last stimulus relative to other stimuli in each condition. When the last stimulus was not an exact repetition of preceding stimuli at the same location, the duration was judged as longer than the preceding stimuli.

significant main effect of location, F(1, 11) = 12.14, p =0.005, and a significant interaction, F(1, 11) = 19.64, p =0.001. The last stimulus was judged as longer when it appeared on the opposite side from the preceding stimuli than when it appeared at the same location. It was judged as longer when it changed its orientation from the preceding stimuli than when it did not change. Post hoc paired t test between each pair of conditions (with Holm-Bonferroni correction [Holm, 1979]) revealed that the last stimulus was judged to be significantly shorter in the SS condition than in all other conditions: t(11) = -4.21, p = 0.001 compared with the SD condition; t(11) = -4.09, p = 0.002compared with the DS condition; and t(11) = -3.71, p =0.003 compared with the DD condition. There was no significant difference between any other pairs of conditions.

There was no significant effect of orientation on JND, F(1, 11) = 1.18, p = 0.30, no significant effect of location, F(1, 11) = 2.98, p = 0.11, and no significant interaction, F(1, 11) = 1.64, p = 0.23. There was no significant effect of orientation on the reaction time, F(1, 11) = 0.00, p = 0.97, no significant effect of location, F(1, 11) = 0.77, p = 0.40, and no significant interaction, F(1, 11) = 4.58, p = 0.06. The lapse rate was $6.2\% \pm 1.8\%$.

That there is no significant difference between the DS and DD conditions suggests that only repetition of

a stimulus at the same location reduces its perceived duration. The significant difference between the SS and DS conditions is consistent with the hypothesis that the effect of repetition may occur because the repeated stimulus influences a neural population with relatively small receptive fields. The result of this experiment does not rule out the hypothesis that expectation reduces perceived duration. But if one were to accept the expectation hypothesis, then these results suggest that the expectation that a stimulus will appear at a different location is smaller than the expectation that a stimulus will appear at the same location and that the expectation of any stimulus at a different location is equal regardless of the stimulus property.

General discussion

Repeated stimuli are judged to be briefer than nonrepeated ones. However, it has been difficult to determine whether perceived duration is reduced by stimulus repetition only or by expectation in general. Manipulating three sources of high-level expectation sequence type probability, sequence regularity, and overlearned sequences—we found that repetition consistently reduces perceived duration, whereas high-level expectation does not. If anything, we found in Experiment 2 a hint that expectation based on sequence type probability *increased* perceived duration.

Even though we have used the term *perceived duration*, there is debate about whether the shift in a psychometric curve of a discrimination task truly reflects a change in perception or a cognitive bias in decision (Schneider & Komlos, 2008). A recent investigation of the temporal oddball effect suggests that the effect is more likely due to a perceptual change than to a cognitive bias (Birngruber et al., 2014). Still, we cannot rule out the possibility that participants' responses are vulnerable to certain biases. In Experiment 2. the duration of the last stimulus in the A-B-A-B-A sequence was judged as slightly longer than the first four stimuli. The same effect was seen with the last stimuli in the Expected and Unexpected sequences of Experiment 3. There are at least two possible reasons for this. First, participants might have a tendency to balance their overall responses of *longer* and *shorter* judgments. Because they made more shorter judgments for the A-B-A-B-B sequence in Experiment 2 and the Repeating sequence in Experiment 3, this tendency may cause them to make more *longer* judgments in the other conditions. Second, for an unknown reason, people might have a subtle tendency to judge the last stimulus in any sequence of five stimuli as longer. Regardless of whether a tendency to balance response or a bias toward answering *longer* exist in our experiment, either mechanism should have the effect of a global shift of the apparent relative duration distortion in all conditions. Because we care only about the differences in relative duration distortion between conditions, neither mechanism is likely to change our conclusion.

In Experiment 1.1, participants were explicitly informed of the probabilities of the sequences, while in Experiment 2 they were instead instructed to pay attention to the frequencies of the sequences. This difference was introduced in order to determine whether explicitly knowing the probability influenced the result. We found a significant effect of sequence probability only in Experiment 2, suggesting that explicitly knowing the probability does not make participants judge a stimulus from a high-probability sequence as longer, but paying attention to this probability might. One may worry that the explicit information about probability in Experiment 1.1 could have introduced a higher expectation to the last stimulus than to the preceding stimuli in all trials. We cannot rule out this possibility. But, as discussed above, this should only introduce a global effect on all conditions, whereas our conclusions were based on a comparison between conditions.

Because the stimulus sequences all had the same length in Experiment 1.1, a concern may be that participants could have based their judgments solely on comparing the perceived duration of the last stimulus against a reference duration stored in memory, neglecting all preceding stimuli. We think this is unlikely because if this were the case, then we would not see a strong overestimation of the duration of the last stimulus, as we did. On the contrary, the relative duration distortion of the last stimulus in Experiment 1.1 was larger than those in Experiments 2 and 3, where the amount of repetition of stimulus was much less.

The mechanisms underlying the effect of repetition are unknown. In the context of the temporal oddball effect, two major hypotheses have been proposed, and these may generalize to the conditions that we examined. The attention hypothesis (Tse et al., 2004) states that the oddball draws more attention, which potentially increases the rate of information processing, or the speed of an oscillator under the internal clock model of time perception (Gibbon, 1977; Treisman, 1963). The neural energy hypothesis attributes perceived duration to the total amount of neural activity expended to encode a stimulus (Eagleman & Pariyadath, 2009); it has been proposed to explain the parallel between the reduced perceived duration of repeated stimulus and neural repetition suppression (Henson & Rugg, 2003; Noguchi & Kakigi, 2006; Sadeghi, Pariyadath, Apte, Eagleman, & Cook, 2011) as well as other parallels between duration illusions and neural response amplitude (Eagleman, 2008; Eagleman & Parivadath, 2009: Parivadath & Eagleman, 2007, 2012). These hypotheses might not be mutually exclusive: The effect of increasing attention to a stimulus might primarily be to increase the neural response to the stimulus (Desimone & Duncan, 1995; Moran & Desimone, 1985; Treue & Martínez Trujillo, 1999).

Because our data show that repetition of a stimulus, but not high-level expectation, reduces perceived duration, they point to a primary role for bottom-up processes in time perception. This would be compatible with the neural energy hypothesis as well as with the attention hypothesis if attention is bottom-up. However, higher-level cognitive factors such as expectation are unlikely to provide a unifying explanation of the observed distortion in duration perception on the subsecond time scale.

Our results are in line with a series of studies that demonstrate compression of perceived duration by lowlevel sensory adaptation in both the visual (Bruno, Ayhan, & Johnston, 2010; Johnston et al., 2006) and tactile (Watanabe, Amemiya, Nishida, & Johnston, 2010) modalities. Together, these studies suggest that time perception may be achieved by a distributed network that includes sensory cortices (Eagleman, 2008; Ivry & Schlerf, 2008; Merchant, Harrington, & Meck, 2013) instead of by a centralized clock. Specifically, Johnston et al. (2006) demonstrated that the adaptation to a visual stimulus of high temporal frequency can distort the perceived duration of a subsequent stimulus of low temporal frequency only when the subsequent stimulus appears at the location of the adapting stimulus. Both this result and our finding in Experiment 5 that the effect of repetition is location-specific support the hypothesis that low-level neural processing of sensory stimuli, where the sizes of receptive fields are relatively small, largely contributes to duration perception in the subsecond range.

We did not find in any of our experiments that the expectation of a stimulus *sequence* reduces perceived duration. This seems to conflict with a study that found that when the probability of *a single stimulus* is manipulated, the more frequent stimulus is judged as briefer (Ulrich, Nitschke, & Rammsayer, 2006). However, the latter finding might also be accounted for by the repetition of the frequent stimulus over the course of their experiment. By contrast, all single stimuli appeared equally often in our Experiments 1.1 and 2. Ulrich et al. (2006) explained their finding by suggesting that the unexpected stimulus increases arousal, which in turn speeds up the pacemaker of the hypothetical internal clock, giving rise to an increase in perceived duration (Ulrich et al., 2006). Our study cannot rule out this possibility because we did not measure any physiological responses that could reflect arousal. Future studies that measure skin conductance or pupil dilation (Bradley, Miccoli, Escrig, & Lang, 2008) may help test the arousal hypothesis.

Matthews (2015) manipulated the probabilities of sequences comprising two consecutive identical stimuli and the probabilities of sequences comprising two consecutive different stimuli. Increasing the probability of one type of sequence should make that type of sequence more expected, as was the logic underlying our Experiments 1 and 2. This study found that the duration of the second stimulus in the sequence of identical stimuli is judged as longer when the probability of that type of sequence is higher than when it is lower (Matthews, 2015). This result is similar to the pattern observed in Experiment 2. Both these results and our results show that high-level expectation based on the probablity of a sequence type does not reduce perceived duration, as repetition of a stimulus does. Both the results are against the hypothesis that expectation in general reduces perceived duration. However, we find a positive effect of expectation on perceived duration only in Experiment 2 and only in one type of sequence. We have no good explanation for this.

Our results point to lower sensory cortices as the neural basis of time perception. Traditionally, a common model of time perception is the internal clock model (Gibbon, 1977; Treisman, 1963), according to which the brain integrates an approximately constant signal to encode duration. It is unclear where this signal comes from. If one were to take this perspective, then our results suggest that the neural response in low-level sensory cortex may be a candidate signal for this integration. Although mechanistic models of how time may be encoded by neural networks exist—for example, a state-dependent network model (Karmarkar & Buonomano, 2007), a model based on neural integration (Simen et al., 2011), and a beat frequency timing model (Matell & Meck, 2000; Richelle & Lejeune, 1980)—it is not clear what these models predict for our experiments. Mimicking the manipulation of factors such as repetition and expectation in neural simulations might increase understanding of the neural basis of duration illusions.

Keywords: time perception, expectation, predictability

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References

- Angrilli, A., Cherubini, P., Pavese, A., & Mantredini, S. (1997). The influence of affective factors on time perception. *Perception & Psychophysics*, 59, 972– 982.
- Birngruber, T., Schröter, H., & Ulrich, R. (2014). Duration perception of visual and auditory oddball stimuli: Does judgment task modulate the temporal oddball effect? *Attention, Perception, & Psychophysics, 76,* 814–828, doi:10.3758/ s13414-013-0602-2.
- Bradley, M. M., Miccoli, L., Escrig, M. A., & Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology*, *45*, 602–607.
- Brainard, D. H. (1997). The Psychophysics Toolbox. Spatial Vision, 10, 433–436.
- Bruno, A., Ayhan, I., & Johnston, A. (2010). Retinotopic adaptation-based visual duration compression. *Journal of Vision*, 10(10):30, 1–18, doi:10. 1167/10.10.30. [PubMed] [Article]
- Chen, K. M., & Yeh, S. L. (2009). Asymmetric crossmodal effects in time perception. *Acta Psychologica*

(*Amsterdam*), 130, 225–234, doi:10.1016/j.actpsy. 2008.12.008.

- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222, doi:10.1146/annurev.ne. 18.030195.001205.
- Droit-Volet, S., Brunot, S., & Niedenthal, P. M. (2004). Perception of the duration of emotional events. *Cognition and Emotion, 18,* 849–858, doi:10.1080/ 02699930341000194.
- Eagleman, D. M. (2008). Human time perception and its illusions. *Current Opinion in Neurobiology*, 18, 131–136, doi:10.1016/j.conb.2008.06.002.
- Eagleman, D. M., & Pariyadath, V. (2009). Is subjective duration a signature of coding efficiency? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364, 1841–1851, doi: 10.1098/rstb.2009.0026.
- Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, 84, 279–325, doi:10.1037/0033-295X.84.3. 279.
- Henson, R. N., & Rugg, M. D. (2003). Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia*, 41, 263– 270.
- Herai, T., & Mogi, K. (2010). Effect of numeric order on subjective duration of following stimulus. *Australian Journal of Intelligent Information Processing Systems*, 11, 1–23.
- Herbst, S. K., Javadi, A. H., van der Meer, E., & Busch, N. A. (2013). How long depends on how fast—Perceived flicker dilates subjective duration. *PLoS One*, 8, e76074, doi:10.1371/journal.pone. 0076074.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70.
- Ivry, R. B., & Schlerf, J. E. (2008). Dedicated and intrinsic models of time perception. *Trends in Cognitive Sciences*, 12, 273–280.
- Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, 16, 472–479, doi:10.1016/j.cub.2006. 01.032.
- Kanai, R., Paffen, C. L., Hogendoorn, H., & Verstraten, F. A. (2006). Time dilation in dynamic visual display. *Journal of Vision*, 6(12):8, 1421– 1430, doi:10.1167/6.12.8. [PubMed] [Article]
- Kanai, R., & Watanabe, M. (2006). Visual onset expands subjective time. *Perception & Psychophysics*, 68, 1113–1123.

- Karmarkar, U. R., & Buonomano, D. V. (2007). Timing in the absence of clocks: Encoding time in neural network states. *Neuron*, 53, 427–438.
- Kim, E., & McAuley, J. D. (2013). Effects of pitch distance and likelihood on the perceived duration of deviant auditory events. *Attention, Perception, & Psychophysics, 75,* 1547–1558, doi:10.3758/ s13414-013-0490-5.
- Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychoolbox-3? *Perception*, 36(Suppl.), 14.
- Maloney, L. T., Dal Martello, M. F., Sahm, C., & Spillmann, L. (2005). Past trials influence perception of ambiguous motion quartets through pattern completion. *Proceedings of the National Academy of Sciences, USA, 102,* 3164–3169, doi:10.1073/pnas. 0407157102.
- Matell, M. S., & Meck, W. H. (2000). Neuropsychological mechanisms of interval timing behavior. *Bioessays*, 22, 94–103.
- Matthews, W. J. (2015). Time perception: The surprising effects of surprising stimuli. *Journal of Experimental Psychology: General, 144,* 172–197, doi:10.1037/xge0000041.
- Merchant, H., Harrington, D. L., & Meck, W. H. (2013). Neural basis of the perception and estimation of time. *Annual Review of Neuroscience*, 36, 313–336.
- Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, 229, 782–784.
- Noguchi, Y., & Kakigi, R. (2006). Time representations can be made from nontemporal information in the brain: An MEG study. *Cerebral Cortex*, *16*, 1797– 1808, doi:10.1093/cercor/bhj117.
- Pariyadath, V., & Eagleman, D. (2007). The effect of predictability on subjective duration. *PLoS One*, 2, e1264, doi:10.1371/journal.pone.0001264.
- Pariyadath, V., & Eagleman, D. M. (2008). Brief subjective durations contract with repetition. *Journal of Vision*, 8(16):11, 1–6, doi:10.1167/8.16.11.
 [PubMed] [Article]
- Pariyadath, V., & Eagleman, D. M. (2012). Subjective duration distortions mirror neural repetition suppression. *PLoS One*, 7, e49362, doi:10.1371/ journal.pone.0049362.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442.
- Richelle, M., & Lejeune, H. (1980). *Time in animal behaviour: Comparative studies*. Oxford, United Kingdom: Pergamon Press.

- Rose, D., & Summers, J. (1995). Duration illusions in a train of visual stimuli. *Perception*, 24, 1177–1187.
- Sadeghi, N. G., Pariyadath, V., Apte, S., Eagleman, D. M., & Cook, E. P. (2011). Neural correlates of subsecond time distortion in the middle temporal area of visual cortex. *Journal of Cognitive Neuroscience*, 23, 3829–3840, doi:10.1162/jocn_a_00071.
- Schindel, R., Rowlands, J., & Arnold, D. H. (2011). The oddball effect: Perceived duration and predictive coding. *Journal of Vision*, 11(2):17, 1–9, doi:10. 1167/11.2.17. [PubMed] [Article]
- Schneider, K. A., & Komlos, M. (2008). Attention biases decisions but does not alter appearance. *Journal of Vision*, 8(15):3, 1–10, doi:10.1167/8.15.3.
- Simen, P., Balci, F., Cohen, J. D., & Holmes, P. (2011). A model of interval timing by neural integration. *The Journal of Neuroscience*, 31(25), 9238–9253.
- Soetens, E., Boer, L. C., & Hueting, J. E. (1985). Expectancy or automatic facilitation? Separating sequential effects in two-choice reaction time. *Journal of Experimental Psychology: Human Perception and Performance*, 11, 598–616, doi:10.1037/ 0096-1523.11.5.598.
- Treisman, M. (1963). Temporal discrimination and the indifference interval. Implications for a model of the "internal clock." *Psychological Monographs*, 77, 1–31.

- Treue, S., & Martínez Trujillo, J. C. (1999). Featurebased attention influences motion processing gain in macaque visual cortex. *Nature*, 399, 575–579, doi:10.1038/21176.
- Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception & Psychophysics*, 66, 1171–1189.
- Ulrich, R., Nitschke, J., & Rammsayer, T. (2006). Perceived duration of expected and unexpected stimuli. *Psychological Research*, *70*, 77–87, doi:10. 1007/s00426-004-0195-4.
- van Wassenhove, V., Buonomano, D. V., Shimojo, S., & Shams, L. (2008). Distortions of subjective time perception within and across senses. *PLoS One*, *3*, e1437, doi:10.1371/journal.pone.0001437.
- Watanabe, J., Amemiya, T., Nishida, S. Y., & Johnston, A. (2010). Tactile duration compression by vibrotactile adaptation. *Neuroreport*, 21(13), 856–860.
- Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63, 1293–1313.
- Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision*, 7(10):2, 1–5, doi:10.1167/7.10.2. [PubMed] [Article]