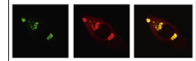


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Research Report

Repetition priming results in sensitivity attenuation

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ABSTRACT

Repetition priming refers to the change in the ability to perform a task on a stimulus as a consequence of a former encounter with that very same item. Usually, repetition results in faster and more accurate performance. In the present study, we used a contrast discrimination protocol to assess perceptual sensitivity and response bias of Gabor gratings that are either repeated (same orientation) or alternated (different orientation). We observed that contrast discrimination performance is worse, not better, for repeated than for alternated stimuli. In a second experiment, we varied the probability of stimulus repetition, thus testing whether the repetition effect is due to bottom-up or top-down factors. We found that it is top-down expectation that determines the effect. We discuss the implication of these findings for repetition priming and related phenomena as sensory attenuation.

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1. Introduction

Repetition priming refers to the change in the ability to perform a task on a stimulus as a consequence of a former encounter with that very same item (for a review see Schacter and Slotnick, 2004). It is usually assessed using tasks in which participants have to identify repeated and non-repeated stimuli, most of the time words or objects, or to make some sort of decision based on features of the item. Repetition priming has been shown to take place on different levels, from perceptual-conceptual (Friese et al., 2012; Sayres and Grill-Spector, 2006) to motor levels (Dobbins et al., 2004; Hsu and Waszak, 2012; Moutsopoulou and Waszak, 2012). On all these levels, repetition results in faster and more accurate performance.

As concerns the underlying brain mechanisms, neuroimaging studies have demonstrated repetition priming to go along with decreased brain activity following item repetition (for reviews see Grill-Spector et al., 2006; Henson and Rugg, 2003). This decrease in activity across stimulus repetition has been referred to as repetition suppression. It has been demonstrated with single-cell recordings in monkeys (Miller and Desimone, 1994), as well as in humans using fMRI (Grill-Spector and Malach, 2001) and EEG/MEG (Henson et al., 2004). Several models have been proposed in the literature to account for neural repetition suppression (see for example Grill-Spector et al., 2006). Initially, the underlying mechanisms were thought to be related to bottom-up factors. The sharpening model assumes that repetition suppression is due to a repeated stimulus being represented more sparsely, because the firing rate of neurons

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responding to irrelevant features decreases across repetitions (Desimone, 1996; Kok et al., 2012a; Wiggs and Martin, 1998). According to the facilitation model, repetition suppression is due to stimuli being processed more quickly when presented more than once (i.e., neurons firing for a shorter period of time) (Henson and Rugg, 2003; James and Gauthier, 2006). The fatigue model, finally, suggests that repetition suppression results from neurons being less responsive when a stimulus is repeated due to firing rate adaptation and synaptic depression (Grill-Spector and Malach, 2001; Kaliukhovich and Vogels, 2011). More recently, however, repetition suppression has been found to be reduced when stimulus repetition is unexpected, suggesting that it reflects a reduction in top-down perceptual “prediction error” due to a repeated stimulus being more expected than an unrepeated stimulus (Summerfield et al., 2008).

Recently, repetition suppression has been discussed as a possible mechanism for a phenomenon called sensory attenuation (cf., Waszak et al., 2012). Sensory attenuation takes two different forms. First there is the finding that self-generated stimuli are perceived as less intense than externally generated stimuli (e.g., Blakemore et al., 1998; Sato, 2008). We are going to refer to this as intensity attenuation. In addition there is the finding that contrast discrimination is impaired for self-generated stimuli (Cardoso-Leite et al., 2010; Roussel et al., 2013). We will refer to this as sensitivity attenuation. Several studies also investigated this effect with neurophysiological correlates of anticipated action effects. It has been shown that when the stimulus is anticipated the neural response is reduced compared to externally triggered or not anticipated stimuli (e.g., Aliu et al., 2008; Baess et al., 2009; Blakemore et al., 1998; Gentsch and Schütz-Bosbach, 2011; Hughes et al., 2013; Hughes and Waszak, 2011; Roussel et al., 2014; Schafer and Marcus, 1973). Waszak et al. (2012) suggest that sensory attenuation of self-produced stimuli (i.e., anticipated action effects) is based on similar if not identical neural mechanisms as repetition suppression. They suggest that action effect anticipation results in the preactivation of the pathway coding for the expected stimulus. If action effect anticipation results in activity similar to the activity triggered by the true perception of the anticipated stimulus, then the activity triggered by a correctly anticipated action effect is actually the repetition of the anticipation-based activity. As a consequence, a correctly anticipated action effect should be subject to the same neural dynamics as a stimulus that is truly repeated, at least to a certain degree. As discussed by Waszak et al. (2012) this also suggests a possible link to the Perkey-effect (Waller et al., 2012) where sensitivity is reduced when a stimulus is imagined, and therefore arguably the internal stimulus representation is activated, at the same time as it is physically presented. Sensory attenuation could, thus, be due to bottom-up neural sharpening, facilitation, and/or fatigue, or to top-down reduction of perceptual prediction error.

Note that, however, the effects of repetition priming and action effect anticipation on performance seem to be contradictory. Repetition priming has been demonstrated to enhance performance (Morton, 1969; Tenpenny, 1995), whereas action effect anticipation results in sensitivity attenuation, i.e., a decrease in perceptual performance (Cardoso-Leite et al., 2010; Roussel et al., 2013). Nevertheless, studies on sensory attenuation

are usually psychophysical studies in which participants are required to detect a stimulus in noise or to indicate the stimulus' intensity. Repetition priming experiments, on the other hand, never used a psychophysical detection protocol. Instead, participants are usually required to issue a motor response, for example to respond as fast as they can to a target stimulus.

Taken together we conclude that, if mechanisms of action effect anticipation and repetition priming are similar, then we should observe the same perceptual effects in case of a repeated stimulus as in case of a stimulus that is anticipated by an action. That is, a repeated stimulus should be perceptually attenuated. The present study tests this notion. In Experiment 1, we adapted a contrast discrimination protocol that has been used before successfully to assess perceptual sensitivity and response bias of anticipated and unanticipated visual action effects (Roussel et al., 2013, 2014). Roussel et al. made participants learn an association between left and right key presses and the presentation of the letters A and H, respectively. They then made participants perform left and right key presses that randomly triggered presentation of either an H or an A at one of two possible contrasts. Participants were required to make a discrimination judgment between the two contrasts. They showed contrast discrimination to be worse when the prediction (H or A, as learned during the association phase of the experiment) matches the true stimulus, demonstrating sensitivity attenuation. The present study uses the same protocol. However, instead of testing contrast discrimination of stimuli that have been correctly anticipated by an action or not, we assessed contrast discrimination when a (Gabor grating) stimulus is presented twice with the same orientation (repetition trial) versus when the orientation is changed from the first to the second presentation (alternation trial). We predicted that contrast discrimination performance will be worse for repeated stimuli. A second experiment was designed to test whether this effect was due to repetition as such or due to expectation. We varied the probability of stimulus repetition, such that in one block repetition trials were more frequent (repetition block) while alternation trials were more frequent in the other block (alternation block). Such a manipulation is commonly assumed to result in participants learning to expect the more frequent stimulus (e.g. Grotheer and Kovács, 2014; Kok et al., 2012b, 2013; Summerfield and de Lange, 2014; Summerfield et al., 2008). If the attenuation is due to repetition as such then it should occur on repetition trials in both blocks, while if it is due to expectation it should occur on repetition trials in the repetition block and on alternation trials in the alternation block where these are more frequent and therefore alternation is expected.

2. Results

2.1. Experiment 1

In Experiment 1 we tested the hypothesis that stimulus repetition, which is found to induce repetition suppression at the neuronal level, is associated with decreased performance in contrast discrimination. Here discrimination performance (d') was lower in the repetition condition (d' repetition: 1.60) than in the alternation (d' alternation: 1.76) condition. A one-tailed t-test

including the factor of repetition showed this effect of repetition on d' to be significant ($t(20)=7.03$, $p=0.038$). At the same time, the criterion was not different in the two conditions ($t(20)=0.17$, $p=0.86$) (repetition: 0.36, alternation: 0.35). In other words, we found that when prime and target are identical, participants are less able to discriminate stimulus intensity.

However, Experiment 1 does not allow us to discriminate whether this effect is based on bottom-up or top-down factors. To do so, we have to dissociate bottom-up stimulus repetition and top-down stimulus prediction (see Summerfield et al., 2008). In Experiment 2, we therefore varied the probability of stimulus repetition between blocks. In one block repetition was more likely than alternation, in the other block alternation was more likely than repetition.

2.2. Experiment 2

We analyzed the contrast discrimination data for each type of expectation (REP block vs. ALT block) and repetition (repetition vs. alternation). We used the 20 first trials of each block to familiarize participants with the block's probabilities. These trials did not enter the analysis.

Regarding the discrimination performance (d') in the REP block, the mean d' for repeated and alternated trials were respectively, 1.61 and 1.63 (SD: 0.86, SD: 0.79). Regarding d' in the ALT block, the mean d' for repeated and alternated trials were, respectively, 1.90 and 1.54 (SD: 0.82, SD: 0.72). A repeated measure analysis of variance on d' including the factors Expectation (here manipulated between blocks: REP block vs. ALT block) and Repetition (here manipulated by the target–prime relationship: repetition vs. alternation) showed a significant main effect of Repetition ($F(1,27)=4.98$, $p=0.03$) and a significant interaction between the two factors ($F(1,27)=4.87$, $p=0.04$). Post hoc t-test revealed that in the ALT block contrast discrimination was significantly lower when the target–prime couple matched the expectation ($t(27)=3.55$, $p=0.001$). This was not the case in the REP block ($t(27)=0.088$, $p=0.93$).

Regarding the criterion a repeated measure analysis of variance revealed a significant interaction between the factors Repetition and Expectation ($F(1,27)=5.72$, $p=0.02$) as well as a significant main effect of Repetition ($F(1,27)=4.52$, $p=0.04$).

Post hoc t-test revealed that the criterion was significantly higher on repetition compared to alternation trials in the ALT block ($t(27)=3.39$, $p=0.002$). In the repetition block there was no such difference ($t(27)=0.18$, $p=0.86$) The means and standard deviation were respectively for REP-block, repeated-trial M: -0.04 , SD: 0.47, alternated-trial M: -0.05 , SD: 0.47, and for ALT-block, repeated-trial M: 0.23, SD: 0.40, alternated-trial M: -0.03 , SD: 0.26.

3. Discussion

We used a contrast discrimination protocol where participants were presented either with rightward or leftward tilted Gabor target stimuli at one of two possible contrasts. Participants were required to make a discrimination judgment between the two contrasts. The Gabor gratings were either a repetition of a prime presented before the target stimulus or an alternation (rightward or leftward tilted). In Experiment 1, repetition probability was

50%. We found that participants are less able to discriminate stimulus intensity when prime and target are identical. This finding resembles a phenomenon from sensory attenuation research, where self-generated, expected stimuli are less discriminable in intensity and more difficult to be detected (e.g., Roussel et al., 2013). Experiment 1 suggests that the repetition of a stimulus results in (sensitivity) attenuation, just as it results in neural suppression (see Grill-Spector et al., 2006). It seems likely that the perceptual attenuation is the phenomenological consequence of the neural suppression. The experiment, thus, also underscores the notion that sensory attenuation of expected action effects is based on mechanisms related to the neural phenomenon of repetition suppression (Waszak et al., 2012).

However, Experiment 1 cannot tell whether the observed effect is due to bottom-up repetition or top-down expectation. Therefore, in Experiment 2, we varied the probability of stimulus repetition/alternation and, thus, the participants' expectation to perceive a stimulus repetition or alternation (see Summerfield et al., 2008). We observed that stimulus repetition/alternation interacts with repetition/alternation probability. When alternation probability is high, participants are less able to discriminate stimulus intensity when prime and target are alternated compared to when they are identical (i.e. an effect in the opposite direction compared to Experiment 1 where repetition and alternation probabilities were equal); this effect was not observed when repetition probability was high. Experiment 2, thus, shows that the perceptual attenuation observed in Experiment 1 is not due to the repetition of the stimulus as such. Instead, it is based on the expectation that the participant has about the upcoming target stimulus (cf., Summerfield et al., 2008). In terms of predictive coding, the observed perceptual attenuation might reflect a reduction in perceptual prediction error, i.e., the signal triggered by a mismatch between expected and true sensory evidence. In Experiment 1, the previously seen stimulus is considered to be more probable than a novel stimulus (see Summerfield et al., 2008). In Experiment 2, this expectation depends on the probability of stimulus repetition/alternation. Bottom-up accounts of the attenuation effect cannot explain how it varies with contextual factors that affect participants' perceptual expectations. Please note also that the results of Experiment 2 render an explanation in terms of forward masking unlikely, as this, too, could not explain the reversal of the effect in Experiment 2.

In Experiment 2 we also found a significant effect on the criterion. Criterion and d' are independent measures and the main purpose of our experiment was to measure the effect on sensitivity (d') not on the criterion. However, criterion could possibly relate to intensity attenuation and is therefore also of some interest. This is because intensity attenuation means that the stimuli are perceived as having lower contrast and one could expect participants to then be biased towards responding that they saw the low contrast, C0. This would result in fewer hits and fewer false alarms, i.e. higher (more conservative) criterion. So if the expected stimuli were subject to intensity, as well as sensitivity, attenuation one might expect higher criterion for expected stimuli. However, the only effect on criterion that we found followed the opposite pattern, i.e. it was for unexpected, not expected stimuli that we found a higher criterion (in combination with increased d'). Note that the criterion depends on the participants' response strategies. One possible

explanation for this finding is therefore that participants expected there to be an equal number of high and low contrast stimuli on repetition and alternation trials and overcompensated when they noticed they were not giving an equal number of C1 and C0 responses. However, it is also possible that our repetition priming paradigm gave rise to only sensitivity attenuation and not intensity attenuation. This remains an open question for future research to address.

Another possible mechanism for the sensitivity attenuation we found is that the stimuli with the unexpected orientation more effectively attracted the participants' attention. There is some evidence that unexpected stimuli involuntarily attract attention (Corbetta and Shulman, 2002; Ranganath and Rainer, 2003) in the auditory (Escera et al., 1998) as well as the visual (Itti and Baldi, 2009) modality. Interestingly a unique singleton among distracters can capture attention even without awareness of the difference between the singleton and the distracters (Zhaoping, 2008). Because attention is known to increase contrast sensitivity (Carrasco et al., 2000; Liu et al., 2009) and is thought to affect perception in effectively the same way as an increase of stimulus contrast (Carrasco et al., 2004), an involuntary increase of attention to the unexpected stimuli would predict a contrast sensitivity difference between expected and unexpected stimuli, consistent with our results as well as a difference in perceived intensity, consistent with previous experiments finding intensity attenuation (e.g., Blakemore et al., 1998; Sato, 2008). This hypothesis, that unexpected stimuli attract attention, is consistent with a recent predictive coding model of visual saliency (Spratling, 2012).

We are aware that it is surprising that, in the REP condition of Experiment 2, participants did not show any d' difference between repeated and alternated trials. This might be taken to indicate that top-down prediction is not only dependent on event probability. It may also depend on other contextual factors like the particular content of the predicted/unpredicted events. The current data would indicate that rare alternations in an event environment of mostly stimulus repetitions are less unexpected than rare repetitions in an event environment of mostly stimulus alternations. This might be because predicting an alternation in the ALT blocks necessitates a particularly strong predictive set to off-set the default prediction of a stimulus repetition (as shown in Experiment 1), whereas predicting a repetition in the REP blocks necessitates only a weak predictive set. However, more research is needed to investigate this issue. A related issue is whether our manipulation of repetition and alternation frequency really caused participants to form the right expectations. One way to investigate both of these issues would be to manipulate the strength of the expectation. If sensory attenuation is stronger when unexpected stimuli are less frequent (more unexpected) this would support the claim that it is really fulfilled expectation that causes the sensory attenuation.

4. Methods and materials

4.1. Experiment 1

4.1.1. Stimuli

Experimental stimuli were generated and presented with Matlab 2007b using the psychophysics toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). The stimuli were two tilted Gabor gratings (45° left, 45° right) displayed on a 15 in. CRT monitor at a refresh rate of 80 Hz and fitted into a virtual square

of 2.9° of visual angle. The screen resolution was set at 800*600 pixels. These two stimuli were presented at two different contrast values (C0 and C1; see contrast determination phase) at the center of the screen. The primes were identical to the target stimuli except for the contrast which was set at 10% more than C1 (to be sure that the prime exceeded the detection threshold). We used in all phases of the experiment a uniform noise texture to increase perceptual variance. This noise was a 100*100 matrix filled with an equal number of white and black pixels. The matrix was re-sampled (using the randperm function in Matlab) on each screen refresh. The mean luminance of the noise was then equal to the gray background.

4.1.2. Contrast determination phase

A procedure with two phases was used in order to determine individual contrast values C0 and C1 yielding a discrimination d' of about 2. In the first phase, C0 was determined as the contrast yielding 85% correct responses in an orientation identification task, involving discriminating between Gabor gratings with two different orientations (45° left, 45° right). In the second phase C1 was determined as the contrast (higher than C0) which could be discriminated from C0 85% of the time.

In the first phase we employed an adaptive staircase to manipulate stimulus contrast using an accelerated stochastic approximation algorithm as described by Kesten (1958). Contrast was manipulated by changing the transparency of the Gabor, defined as the weight given to the Gabor in a linear combination of the Gabor and the gray background (thus, the amplitude of the Gabor was proportional to the transparency level and 100% transparency would correspond to the largest amplitude possible given the luminance range of the monitor). Two interleaved staircases were run, starting at 50% and 15% transparency. The initial step size used in the staircases was 20% and we stopped the staircases when the step size was 1% (in transparency). The first two steps the transparency was updated according to the following equation (see Treutwein, 1995):

$$T_{n+1} = T_n - \frac{(0.2/0.85)}{n} (Z_n - 0.85)$$

and after the second step this equation was used:

$$T_{n+1} = T_n - \frac{(0.2/0.85)}{2 + m_{\text{shift}}} (Z_n - 0.85)$$

where T_n is the transparency at the n th step, m_{shift} is the number of reversals (i.e. changes from responding C1 to responding C0 or vice versa) and Z_n is one if the latest response was C1 and 0 if it was C0.

In the second phase we used a contrast discrimination task with C0 as reference contrast. We used method of constant stimuli and a 2AFC paradigm, with constant stimuli ranging from C0 to C0+12%, in order to find the contrast value of C1 yielding 85% correct responses. For an ideal observer, this contrast yields a discrimination d' of around 2 (Macmillan and Creelman, 1991). Previous experiments showed this procedure to work reliably (Roussel et al., 2013).

For each subject the prime contrast was set at C1+10% transparency to ensure perfect visibility of it.

4.1.3. Test phase

Participants fixated on a square at the center of the screen, just as in the contrast determination phase. The offset of the prime was followed after a fixed interval of 100 ms by the target onset. Both prime and target had a 200 ms duration. The right or left orientation were presented randomly, such that on 50% of trials the prime and the target had the same orientation (repetition trial), and on 50% of trials the target had the opposite orientation compared to the prime (alternation trial). The target stimuli appeared randomly (but in equal proportions) with the contrast C0 or the contrast C1. Participants were told that there were two contrast values and examples of these two were shown before each test block. After the target stimulus had disappeared participants were required to judge the contrast value of the stimulus in a forced choice format. Participants completed 10 test blocks of 40 trials (Fig. 1).

4.1.4. Participants

Twenty-one participants took part in the experiment. They were naive to the purpose of the experiment.

4.1.5. Analysis of discrimination performance

The contrast discrimination task was considered to be a yes/no protocol, with C1 being the target. That is, a C1 response to a C1 stimulus is a hit, a C1 response to a C0 stimulus is a false alarm, etc. d' and c are calculated using $d' = z(\text{hit rate}) - z(\text{false alarm rate})$ and $c = -0.5 \times [z(\text{hit rate}) + z(\text{false alarm rate})]$. d' and c were calculated separately for repetition and alternation trials.

4.2. Experiment 2

4.2.1. Stimuli and contrast determination phase

Stimuli and contrast determination phase were identical to Experiment 1.

4.2.2. Test phase

The test phase was identical to Experiment 1, with the following exceptions. In Experiment 2, the test phase consisted of 2 blocks of 200 trials. One of the two blocks was a

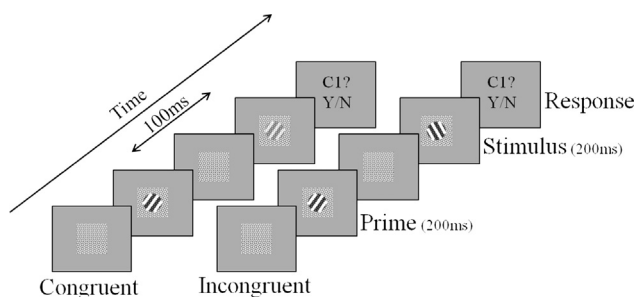


Fig. 1 – Illustration of the procedure/design. The match between the prime and the target was manipulated such that the target sometimes had the same orientation as the prime (repetition trial) and sometimes had the opposite orientation (alternation trial). The target could appear at two different contrast values, C0 or C1. The participant had to indicate the contrast at which the target appeared.

repetition block (i.e., “REP-block”). In this block the probability of the orientation of the prime and the target stimulus being identical was 0.75. The other block was an alternation block (i.e., “ALT-block”). Here the probability of prime and target having opposite orientations was 0.75.

4.2.3. Participants

Based on sample sizes used in previous experiments on sensory attenuation we decided to test 28 participants (seven participants for each response mapping and block order (REP-block/ALT-block)). Two participants were rejected and replaced due to very poor performance. That is, we tested 30 participants and analyzed the data from 28 of them. All participants were naive to the purpose of the experiment and were given a remuneration.

4.2.4. Analysis of discrimination performance

Just as in Experiment 1, the contrast discrimination task was considered to be a yes/no protocol, with C1 being the target. That is, a C1 response to a C1 stimulus is a hit, a C1 response to a C0 stimulus is a false alarm, etc. d' and c are calculated using $d' = z(\text{hit rate}) - z(\text{false alarm rate})$ and $c = -0.5 \times [z(\text{hit rate}) + z(\text{false alarm rate})]$. d' and c were calculated separately for repeated/alternated trials and REP/ALT blocks

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