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Perceptual Learning in a Nonretinotopic Frame of Reference

Thomas U. Otto[1,2], Haluk Öğmen[3,4], and Michael H. Herzog[1]
[1]Laboratory of Psychophysics, Brain Mind Institute, École Polytechnique Fédérale de Lausanne (EPFL);
[2]Laboratoire Psychologie de la Perception, Université Paris Descartes; [3]Center for Neuro-Engineering & Cognitive Science,
University of Houston; and [4]Department of Electrical & Computer Engineering, University of Houston

Abstract

Perceptual learning is the ability to improve perception through practice. Perceptual learning is usually specific for the task and features learned. For example, improvements in performance for a certain stimulus do not transfer if the stimulus is rotated by 90° or is presented at a different location. These findings are usually taken as evidence that orientation-specific, retinotopic encoding processes are changed during training. In this study, we used a novel masking paradigm in which the offset in an invisible, oblique vernier stimulus was perceived in an aligned vertical or horizontal flanking stimulus presented at a different location. Our results show that learning is specific for the perceived orientation of the vernier offset but not for its actual orientation and location. Specific encoding processes cannot be invoked to explain this improvement. We propose that perceptual learning involves changes in nonretinotopic, attentional readout processes.

Keywords

perceptual learning, orientation specificity, vernier acuity, attention, consciousness

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Perceptual learning is the ability to improve perception. In human vision, small differences in basic stimulus features that are indistinguishable to an inexperienced observer may be well discriminated after practice. However, these improvements are often very specific to the trained stimuli (e.g., Ahissar & Hochstein, 1997; Crist, Kapadia, Westheimer, & Gilbert, 1997; Fiorentini & Berardi, 1980; Ramachandran & Braddick, 1973; Schoups, Vogels, & Orban, 1995; for an overview, see Fahle & Poggio, 2002). For example, when training improves performance with a vertical vernier stimulus, there is no transfer of learning to a horizontal vernier stimulus (Poggio, Fahle, & Edelman, 1992). Moreover, there is no transfer to a vertical vernier stimulus at a different location in the visual field (Fahle, Edelman, & Poggio, 1995). Observers have to retrain to improve performance with each stimulus. Such findings are usually taken as evidence that the neural changes underlying perceptual learning are restricted to neural mechanisms coding specifically for a certain orientation at a certain retinotopic position (e.g., Ahissar & Hochstein, 2004; Fahle, 2004; Fiorentini & Berardi, 1980; Karni & Sagi, 1991; Schoups et al., 1995; Seitz, Kim, & Watanabe, 2009; but see Mollon & Danilova, 1996).

This interpretation follows the deeply entrenched view that stimulus features are perceived according to the retinotopic location at which they are presented. However, researchers have demonstrated that this assumption is not always accurate (e.g., Breitmeyer, Herzog, & Öğmen, 2008; Cavanagh, Holcombe, & Chou, 2008; Nishida, Watanabe, Kuriki, & Tokimoto, 2007; Öğmen, Otto, & Herzog, 2006; Werner, 1935). In the sequential metacontrast paradigm (Otto, Öğmen, & Herzog, 2006, 2009), for example, a central line appears briefly and is then followed on either side by a sequence of flanking lines consecutively presented along a circular-motion trajectory (Fig. 1a). The central line is invisible because of metacontrast masking; observers perceive two diverging streams of lines, one moving leftward, the other rightward. When the central line contains a small vernier offset, observers perceive a corresponding offset in the lines flanking it, particularly in the terminal flanker of the attended motion stream; this perception occurs even though all flankers are not offset (Fig. 1b). Hence, the offset of the invisible central vernier stimulus is perceived in a different stimulus with a different position and orientation.

This nonretinotopic processing allowed us to investigate the specificity of perceptual learning in a completely new

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Corresponding Author:
Thomas U. Otto, Laboratoire Psychologie de la Perception, Université Paris Descartes, 45 rue des Saints-Pères, 75006 Paris, France
E-mail: thomas.otto@parisdescartes.fr

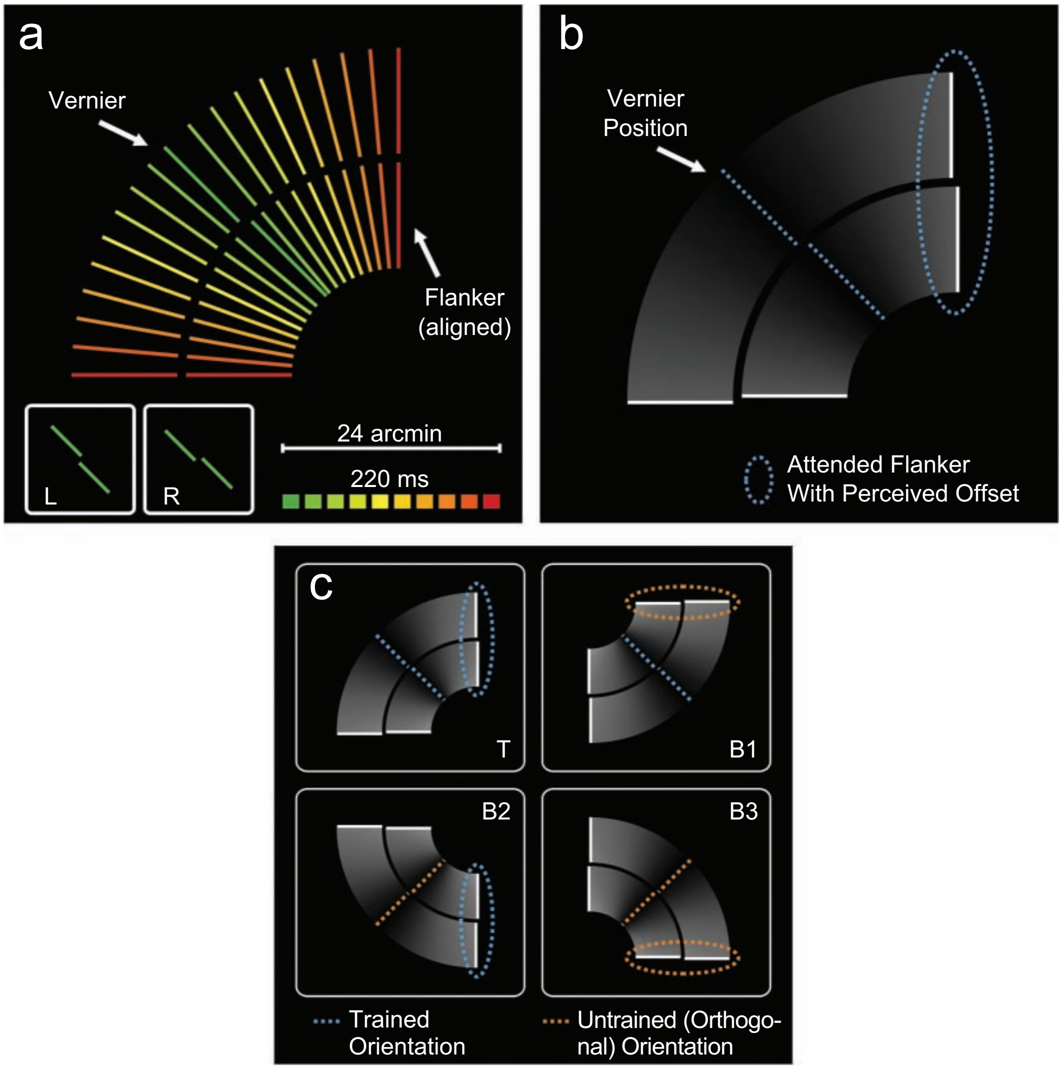

Fig. 1. Procedure used in the experiment. The space-time stimulus diagram of the sequential metacontrast paradigm (a) shows a central vernier stimulus followed by nine consecutive pairs of flankers arranged radially along a circular trajectory. Pairs of flankers were presented one after the other (the time course is color-coded in this figure; actual stimuli were bluish white on a dark background). In each trial, the vernier stimulus was randomly offset either to the left (L) or to the right (R), as depicted in the insets. All flankers were aligned. Observers perceived two circular-motion streams, one of which they were instructed to attend to (b). The vernier stimulus itself was invisible. The last flankers in the stream were most clearly visible because they were not backward-masked by subsequent flankers. At the attended flanker, an offset corresponding to the vernier offset was perceived, although the flanker was physically aligned, as shown in (a). There were four experimental conditions (c). In the training condition (T), the vernier stimulus was oriented diagonally, and the attended flanker was oriented vertically. The three baseline conditions (B1, B2, and B3) were defined by whether the vernier stimulus and the attended flanker were in the same orientation as in Condition T. The figure illustrates the procedure for observers who attended to the rightward-moving motion stream; half of the observers attended to the opposite motion stream in each condition.

fashion. Because the actual orientation and the perceived orientation of the vernier offset are dissociated, we could show that perceptual learning in the sequential metacontrast paradigm is specific for the perceived orientation but not for the actual orientation of the vernier offset.

General Method

Observers

Data were obtained from 15 naive observers and one of the authors (4 females and 12 males; age range = 19–31 years). We determined each observer's visual acuity using the Freiburg Visual Acuity test (Bach, 1996). To participate, observers had to reach a value of at least 1.0 for one eye (corresponding to a Snellen fraction of 20/20). Observers signed informed-consent forms. All procedures were conducted in accordance with the Declaration of Helsinki and were approved by the local ethics committee.

Apparatus

Stimuli appeared on X-Y monitors (HP-1332A; Hewlett-Packard, Palo Alto, CA; Tektronix 606B & 608; Tektronix, Beaverton, OR) connected to a computer (for more details, see Otto et al., 2006). The refresh rate of the monitors was 200 Hz. The stimulus luminance was 80 cd/m^2. The room was dimly illuminated (~0.5 lux), and background luminance on the screen was less than 1 cd/m^2. The viewing distance was 2 m.

Stimuli

We presented a vernier stimulus followed by a sequence of nine pairs of flankers (Fig. 1a). Each vernier stimulus and flanker consisted of two segments that were 10 arcmin long and placed end to end separated by a gap of 1 arcmin. Flankers were arranged radially along a circular-motion trajectory (radius of the notional circle = 24 arcmin). The vernier stimulus was oriented diagonally. Flankers were added along the trajectory on either side of the vernier stimulus; there was a 5° difference in orientation between flankers. One of the final flankers was oriented horizontally, and the other was oriented vertically.

The vernier stimulus was offset; that is, its two segments were slightly displaced with respect to each other (Fig. 1a). The offset direction (left or right) was randomly chosen at each trial. Offset sizes were chosen according to an adaptive procedure (see the Procedure section). The two segments of each flanker were aligned (i.e., they were not offset).

The vernier stimulus was presented for 20 ms. Each pair of flankers was presented for 10 ms, except for the last pair, which was presented for 30 ms. The screen was blank for 10 ms between the appearance of consecutive pairs of flankers. The duration of the whole sequence was 220 ms. When viewing this stimulus paradigm, observers naturally attend to one motion stream, and particularly to the last flanker, which they perceive as having the same offset as the vernier stimulus (Otto et al., 2006, 2009).

Procedure

We asked observers to attend explicitly to one of the two motion streams and to indicate its offset direction. Half the observers were instructed to attend to the rightward stream (Fig. 1b); the other half were instructed to attend to the leftward stream. Observers indicated whether the offset was to the left or to the right by pressing one of two buttons (binary forced-choice task). Responses not in accordance with the actual vernier offset were followed by an auditory error signal.

Stimuli were presented in blocks of 100 trials (duration of blocks: ~3–4 min). Each trial was initiated with four markers at the corners of the screen and a fixation dot in the center, all of which were presented for 500 ms. A blank screen followed for 200 ms. Then, the stimulus sequence was presented, after which the screen went blank. A new trial was initiated 500 ms after observers made a response. If observers failed to respond within 3 s, the trial was repeated at the end of the block. Observers were allowed to take short breaks between blocks.

In each block, the offset sizes presented were selected according to an adaptive staircase method (parameter estimation by sequential tracking, or PEST; start value = 2.5 arcmin, maximum value = 3 arcmin; Taylor & Creelman, 1967). However, we used the method of constant stimuli with five predefined test offset sizes for 2 observers (because these results did not differ from the results achieved with PEST, data were collapsed). Then, we recorded whether the observers' responses were in accordance with the vernier-offset direction. We estimated the threshold of the psychometric function (cumulative Gaussian function; chance level = 50%; rate of response lapses = 2.5%) by means of a maximum likelihood analysis (the two offset directions were pooled). If this analysis failed because observers did not reach a performance level greater than 75% correct responses even for the largest test offset, we recorded a threshold of 3 arcmin. If the estimated threshold was smaller than the smallest test offset, we recorded the smallest test offset as the threshold.

Experimental protocol

Pretraining familiarization. Before we began the experiment, we provided up to two sessions to familiarize observers with the procedures. We presented single nonflanked vernier stimuli of different orientations in each session to familiarize observers with the offset-discrimination task. Then, we introduced the sequential metacontrast paradigm with a linear (i.e., noncircular) stimulus sequence (Otto et al., 2006). Finally, we presented the experimental stimulus sequence in different orientations (Fig. 1c). To avoid the possibility of practice effects influencing the results, we ensured that observers attending leftward streams during familiarization attended rightward streams during the experiment proper, and vice versa. Moreover, we terminated the introduction as soon as the PEST procedure yielded reliable thresholds (below 3 arcmin). We excluded 8 out of 24 recruited subjects from the actual experiment because they did not meet this criterion after the second session. The actual experiment started at least 1 day after the last familiarization session.

Pretraining baseline measurements. On the first day of the experiment, we measured pretraining performance. This session included four test conditions with sequential metacontrast stimuli (Fig. 1c). In Condition T (which was also the condition for the subsequent training phase), the vernier stimulus was oriented diagonally; half the observers attended to the leftward stream (in which the attended flanker was oriented horizontally), and the other half attended to the rightward stream (in which the attended flanker was oriented vertically). In the first baseline condition (B1), the vernier stimulus had the same orientation as in Condition T, but the attended flanker was orthogonal to the corresponding flanker in Condition T. In the second baseline condition (B2), the vernier stimulus was orthogonal to the vernier stimulus in Condition T, but the attended flanker had the same orientation as the flanker in

Condition T. In the third baseline condition (B3), both the vernier stimulus and the attended flanker were oriented orthogonally to their counterparts in Condition T. In addition, the pretraining sessions included three test conditions with nonflanked vernier stimuli in different orientations: the same orientation as the trained vernier stimulus (135°), the same orientation as the trained attended flankers (90° or 180°), and a control orientation (22.5° or 67.5°).[1]

We measured each observer's performance in each condition in two blocks. The order of conditions was randomized across observers (nonflanked vernier stimuli were always tested first). After every condition had been measured once, the order of conditions was reversed for the second set of measurements to reduce, at least partly, the influence of possible learning or fatigue effects in the averaged data. To determine pretraining performance, we collapsed the two thresholds in each baseline condition for each observer individually.

Training. After completing the pretraining session, observers trained in four sessions on 4 consecutive days. Each session contained 10 blocks of Condition T (Fig. 1a); stimuli were always the same except for offset directions and sizes. To determine changes in performance during training, we fitted regression lines to the data of each observer. The slopes of regression lines were subjected to a two-tailed, one-sample *t* test that compared the slopes of regression lines with the null hypothesis of no change in performance (i.e., a slope of zero).

Posttraining baseline measurements. After the last training session, we repeated the pretraining tests to determine posttraining performance (nonflanked vernier stimuli were tested last). To compare pretraining and posttraining performance, we determined the percentage of improvement in each baseline condition. To test for changes in performance, we computed two-tailed, one-sample *t* tests with the null hypothesis of no change. We also analyzed the percentage of improvement as a function of vernier-stimulus orientation (trained vs. untrained) and attended-flanker orientation (trained vs. untrained) in an analysis of variance (ANOVA) with repeated measures. Specificity was indicated by a main effect of either orientation.

Results

As in most studies on perceptual learning, performance strongly improved with training (Fig. 2a; $p < .001$; a large share of the improvement occurred overnight). The improvement in observers' offset discrimination occurred despite the invisibility of the vernier stimulus. Hence, perceptual learning occurred unconsciously (cf. Watanabe, Nanez, & Sasaki, 2001).

To determine the specificity of the improvement, we analyzed the percentage of improvement in the four conditions in which the orientation and position of the vernier stimulus and the attended flanker were independently varied. We found a strong improvement for the trained condition, that is, Condition T (Fig. 2b; $p < .001$). We found no improvement in Condition B1 (Fig. 2b). If learning had changed retinotopic encoding processes related to the vernier offset, improvements would have occurred because the vernier stimulus was identical in these two conditions. An improvement of performance

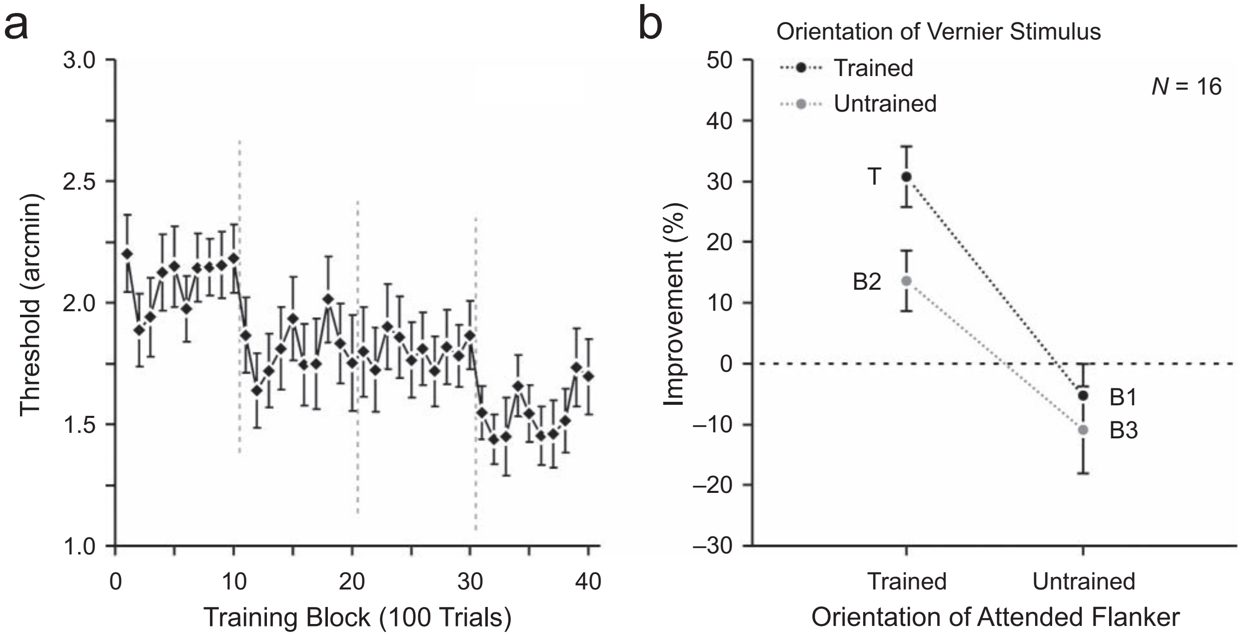

Fig. 2. Performance during training and performance improvements in posttraining. Mean offset-discrimination thresholds are plotted as a function of training block in (a). A vertical dotted line indicates the beginning of each session. In (b), percentage of improvement in posttraining (compared with the pretraining baseline) is plotted for each of the four experimental conditions (positive values indicate learning). See Figure 1c for an explanation of the conditions. Error bars indicate standard errors of the mean.

occurred in Condition B2 (Fig. 2b; $p = .015$; the improvement was smaller than in Condition T, possibly because the motion streams differed). Considering the orthogonal orientation of the vernier stimulus in Condition B2, this improvement is best explained by neural changes related to the attended flanker, at which the vernier offset is perceived, rather than by changes related to the vernier stimulus itself. No improvement occurred in Condition B3; a two-way ANOVA showed no significant interaction, a trend for a main effect of vernier-stimulus orientation, and a significant main effect of attended-flanker orientation, $F(1, 15) = 37.02$, $p < .001$.

No improvement occurred for a nonflanked vernier stimulus with the same orientation as the vernier stimulus presented during training (Table 1; performance seemed to deteriorate in these conditions). This finding provides further evidence that the orientation of the vernier stimulus carrying the signal related to learning is of no importance for perceptual learning in the sequential metacontrast paradigm. Likewise, no improvement occurred for a vernier stimulus with the same orientation as the attended flanker presented during training (Table 1). Hence, learning seems to be specific to the orientation of the attended flanker only in the context of the motion stream.

Discussion

Perceptual learning improved performance in Condition T, the training condition, and in Condition B2, in which the orientation of the attended flankers, but not the orientation of the vernier stimuli, was the same as in Condition T. No improvement occurred in Condition B1, in which the position and orientation of the vernier stimulus were the same as in Condition T, but the position and orientation of the flanker were different. Hence, we found specific perceptual learning that seems not to rely on changes in early retinotopic encoding processes related, for example, to a fine-tuning of receptive fields specifically adjusted to the vernier stimulus. Instead, we found perceptual learning that was specific to the perceived vernier offset.

The improvement of performance reveals a strong attentional component. We instructed half of the observers to attend to the leftward stream and the other half to attend to the rightward stream during training. In the two cases, the stimuli were exactly the same. Observers in these conditions showed a specific improvement for the horizontal and vertical terminal flankers, respectively. Hence, specificity of perceptual learning depended on attention, in accordance with the findings of previous studies (Ahissar & Hochstein, 1993; Fahle & Morgan, 1996; Li, Piëch, & Gilbert, 2004; Shiu & Pashler, 1992). In contrast to these studies, our method focused observers' attention not on the vernier stimulus, which carried an offset, but on the terminal flanker, which did not carry an offset. Therefore, we claim that perceptual learning improved attentional readout from the terminal flanker rather than from retinotopic encoding processes specific to the vernier stimulus.

Perceptual learning occurs for unattended and invisible stimuli when observers perform a primary task with clearly visible and attended stimuli (task-irrelevant perceptual learning; Seitz et al., 2009; Watanabe et al., 2001). Hence, attention and consciousness seem not to be necessary for perceptual learning. However, without feedback in the primary task, no improvements occur for the unattended and invisible stimuli. In our paradigm, the task-relevant central line was invisible, whereas the task-relevant feature—the vernier offset in the central line—was nonretinotopically visible at the attended flanker. Hence, we found complex dissociations among the retinotopic vernier offset, attention, and the perceived (nonretinotopic) vernier offset.

Specificity is considered the hallmark of perceptual learning. Recent studies have shown, however, that perceptual learning can transfer to stimuli of different orientations and positions (e.g., Aberg, Tartaglia, & Herzog, 2009; Jeter, Dosher, Petrov, & Lu, 2009; Xiao et al., 2008). In these studies, learning improved performance for a trained stimulus and for a second, untrained stimulus at a different location or with a different orientation. In our study, performance improved specifically only for one orientation, the orientation of the flanker with the illusory offset. Thus, our results attribute specificity to nonretinotopic and attentional processes, but do not contribute to the debate regarding the conditions under which specific improvements occur.

We can only speculate on what exactly changes during training. Improvements in Condition B2 were smaller than improvements in Condition T. This indicates that learning is related not only to the terminal-flanker orientation, but also to the entire motion stream. Moreover, as there is no transfer of learning to nonflanked vernier stimuli, it seems that flanker orientation per se is not the primary target for training-induced changes. We suggest that perceptual learning specifically improves the flow of information within the motion stream (i.e., from the vernier stimulus to the attended flanker) and the attentional readout process from this stream, particularly from

Table 1. Percentage of Improvement for Nonflanked Vernier Stimuli

Vernier stimulus orientation	Mean improvement	*p* (one-sample *t* test)
135° (same as the trained vernier stimulus)	−17.6 (10.3)	.106
90° or 180° (same as the trained flanker)	−14.7 (10.6)	.187
22.5° or 67.5° (control orientation)	−19.6 (12.1)	.125

Note: Standard errors of the mean are given in parentheses.

the terminal flanker. However, these considerations remain speculative at the moment.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Note

1. Offsets for nonflanked vernier stimuli were smaller than offsets in the sequential metacontrast conditions by approximately a factor of 10.

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