



An interoceptive illusion of effort induced by false heart-rate feedback

Pierpaolo Iodice^{a,1}, Giuseppina Porciello^{b,c,1}, Ilaria Bufalari^{c,d}, Laura Barca^e, and Giovanni Pezzulo^{e,2}

^aCentre d'Etudes des Transformations des Activités Physiques et Sportives, University of Normandy, 76821 Mont Saint Aignan, France; ^bDipartimento di Psicologia, Sapienza, Università degli studi di Roma, 00185, Rome, Italy; ^cLaboratorio di Neuroscienze Sociali, Fondazione Santa Lucia, 00142, Rome, Italy; ^dDipartimento di Psicologia dei Processi di Sviluppo e Socializzazione, Sapienza, Università degli studi di Roma, 00185, Rome, Italy; and ^eInstitute of Cognitive Sciences and Technologies, National Research Council, 00185, Rome, Italy

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Interoception, or the sense of the internal state of the body, is key to the adaptive regulation of our physiological needs. Recent theories contextualize interception within a predictive coding framework, according to which the brain both estimates and controls homeostatic and physiological variables, such as hunger, thirst, and effort levels, by orchestrating sensory, proprioceptive, and interoceptive signals from inside the body. This framework suggests that providing false interoceptive feedback may induce misperceptions of physiological variables, or “interoceptive illusions.” Here we ask whether it is possible to produce an illusory perception of effort by giving participants false acoustic feedback about their heart-rate frequency during an effortful cycling task. We found that participants reported higher levels of perceived effort when their heart-rate feedback was faster compared with when they cycled at the same level of intensity with a veridical feedback. However, participants did not report lower effort when their heart-rate feedback was slower, which is reassuring, given that failing to notice one’s own effort is dangerous in ecologically valid conditions. Our results demonstrate that false cardiac feedback can produce interoceptive illusions. Furthermore, our results pave the way for novel experimental manipulations that use illusions to study interoceptive processing.

interoception | interoceptive illusion | heartbeat | illusion of effort

Interoception, Predictive Coding, and Illusions

Interoception, or the sense of the internal state of the body, is key to the adaptive regulation of our physiological needs and the formation of our sense of self (1). Recent theories conceptualize interoception within a predictive coding perspective, which emphasizes the predictive aspects of the processing of bodily signals and of physiological regulation (2–7), analogous to predictive perceptual processing (8, 9) and action control (10–12). These theories propose that the brain implements a process of interoceptive inference for physiological sensing and adaptive regulation. It does so by continuously generating top-down predictions about adaptive interoceptive signals (i.e., the signals that a healthy body should generate) and using prediction errors (i.e., mismatches between the expected and sensed interoceptive signals) to steer compensatory autonomic actions that restore homeostasis. Furthermore, it generates predictions about future misregulation and takes anticipatory (allostatic) actions to proactively prevent them (13).

To engage in interoceptive inference and autonomic control, the brain may use internal models (or central representations) of the physiological and homeostatic variables that it regulates, such as hunger, thirst, effort, and fatigue levels (14–17). Using an internal model for interoceptive inference and physiological regulation is analogous to using a bodily postural model (or body schema) that keeps track of spatial properties of the body, such as limb position, for movement control (18). While under normal conditions, the internal models support an accurate estimate of their relevant variables, some ambiguous conditions can lead to misperceptions.

Body illusions, such as the illusion of owning another person’s full body (19), face (20, 21), or limbs (22), are examples of

experimentally induced misperceptions of one’s body representation. Note that in this context, the term “illusion” denotes a transient misperception of some variables, such as the location of one’s body or hand, as an effect of the resolution of a multi-sensory conflict. Thus, body illusions are markedly different from, and significantly more attenuated than, delusional beliefs, hallucinations, and the illusory perception of nonexistent entities, which are associated with clinical and psychopathological conditions (7, 17, 23–25).

In one of the most widely studied body illusions, the “rubber hand” illusion, participants misperceive the actual location of their hand (26). The classical method of inducing this illusion involves placing a rubber hand in the usual position of the participant’s real arm, which is hidden, and then gently stroking the real hand and the rubber hand simultaneously and in the same place. Participants usually report that their hand position lies in between their real hand and the rubber hand, supposedly because they integrate noisy and conflicting sources of information (e.g., visual and tactile), one of which could be considered false feedback (27).

An open question is whether a similar process may extend to the interoceptive domain as well. If the brain processes interoceptive and exteroceptive body representation in fundamentally similar ways, then providing participants with false feedback about their interoceptive streams may produce an interoceptive misperception or illusion (where illusion is used in the same sense as for body illusion, not in the clinical sense).

Significance

To ensure our survival, the brain continuously estimates important homeostatic and physiological variables, such as our hunger, thirst, and effort levels. This estimate relies on multiple signals, most prominently on interoceptive signals coming from inside the body (e.g., cardiac and respiratory signals). Here we tested the hypothesis that providing false feedback about these signals produces an interoceptive illusion, that is a misperception of one’s own physiological state. We show that giving participants false (faster) acoustic feedback about their heartbeats during an effortful cycling task induced the illusion of making more effort. Rather, participants did not report lower effort when slower acoustic feedback was provided, suggesting that the brain considers the potential costs of underestimating effort and fatigue levels.

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¹P.I. and G. Porciello contributed equally to this work.

²To whom correspondence may be addressed. Email: giovanni.pezzulo@istc.cnr.it.

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Aims of the Study and Hypotheses

In this study, we tested the idea that providing participants with false cardiac feedback while they performed a physical exercise would make them experience an illusion of perceived effort—that is, a misperception of their actual level of effort.

We asked participants to cycle on a stationary bicycle (cycle-ergometer) at different levels of intensity, which were unknown to them. Crucially, we provided the participants with auditory feedback, via headphones, that was either congruent with the heartbeat frequency recorded when they cycled at the same level of intensity or incongruent with it (i.e., faster or slower). After each cycling session, the participants reported their perceived level of effort using the rate of perceived exertion (RPE) (28), which is widely used in medicine and sports because it accurately indexes physiological variables, such as heart rate (HR) and exercise intensity level (29). We were interested in quantifying the participants' misperception (or illusion) of effort as a function of their cardiac feedback, or the discrepancy between the actual physical effort that they were exerting and the perceived effort that they reported.

We predicted that participants who heard faster heartbeats (i.e., heartbeats recorded when they cycled at a higher intensity level) would experience an illusion of perceived effort and report higher scores in the RPE scale compared with a control condition in which they made the same physical effort (i.e., cycled at the same intensity level) but heard congruent (i.e., heartbeats recorded when they cycled in the same intensity level) auditory feedback or no feedback. We also reasoned that participants who heard slower heartbeats (i.e., heartbeats recorded when they cycled at a lower intensity level) would experience the opposite illusion (i.e., lower effort) in a significantly more attenuated way. This is because underestimating the effort during exertional activities such as physical exercise entails numerous risks, for example, selection of intensity levels that are excessively high. Under these conditions, a risk-avoidant strategy could be more appropriate. This idea is consistent with previous research showing that (mentally) fatigued persons overestimate their physical exertion levels, plausibly as a protection mechanism against the risks of excessive effort (30).

Finally, we hypothesized that persons with lower interoceptive awareness rely more on the false feedback and thus experience a stronger illusion of effort. This prediction is consistent with previous studies reporting that the strength of body illusions, such as the rubber hand (31) and enfacement (32) illusions, is higher in participants with low interoceptive awareness.

Results

We checked the normality of data distribution relative to each dependent variable (i.e., participants' HR and RPE ratings) and condition using the Kolmogorov–Smirnov (K-S) test. When the normality assumption was not respected, a nonparametric approach (i.e., Friedman ANOVA followed by Bonferroni-corrected Wilcoxon matched-pairs test, and Spearman's rank correlations) was used. Given that classical null hypothesis testing is not the ideal statistical tool for drawing conclusions about nonsignificant results (33, 34), in the event of negative results, we also calculated Bayes factors (BFs), which allows quantification of evidence in favor of the alternative or null hypothesis. All statistical analyses but BFs were run using Statistica 7 software. BFs were calculated using the open-source software JASP (35).

Preliminary Analysis

First, we checked that cycling at increasing levels of intensity increased physiological effort (as indexed by HR frequency) and perceived effort (as indexed by subjective ratings on the RPE scale) during the Baseline Exercise (BE) session, where no acoustic interoceptive feedback was provided.

Physiological Effort. Three conditions were not normally distributed according to the K-S test [$D(18) > 0.215$; $P < 0.028$ for all]; therefore, Friedman ANOVA was performed to compare participants'

HR recorded at seven different intensity intervals: the targeted ones (60, 75, 90, 105, and 115 W) and those immediately above or below them (from 45 to 125 W). In line with our hypothesis, Friedman ANOVA was significant [$\chi^2(6) = 108$; $P < 0.00000$]. Bonferroni-corrected Wilcoxon matched-pair tests were all significant ($Z = 3.724$; $P < 0.0002$ for all), suggesting that, as expected, HR frequency increases when cycling at increasing levels of intensity (SI Appendix, Fig. S1a).

Perceived Effort. RPE values were normally distributed; therefore, a parametrical approach (i.e., repeated-measures ANOVA followed by Bonferroni-corrected post hoc tests) was used. The repeated-measures ANOVA on the five levels of the targeted intensity as the sole within-subject factor was significant [$F(4, 68) = 180.465$; $P < 0.00000$]. Post hoc tests comparing the perceived effort recorded in each specific interval with the next interval were significant ($P < 0.0001$ for all) and showed that when the level of cycling intensity increased, participants reported higher scores of perceived effort (SI Appendix, Fig. S1b).

Main Analysis

We aimed to test whether perceived effort changes as a function of receiving incongruent auditory feedback about one's own physiological state (i.e., HR frequency). Thus, we compared effort ratings collected after cycling at five different targeted intensities (60, 75, 90, 105, and 115 W) in a "congruent feedback" condition, in which participants listened to a heartbeat sound registered during the BE session at the same intensity level, with two "incongruent feedback" conditions, in which participants listened to faster or slower heartbeat sounds registered during the BE session at higher or lower intensity levels, respectively. To remove baseline interindividual differences, for each participant, we subtracted effort ratings at baseline from those collected after congruent and incongruent Experimental Exercise (EE) conditions. The K-S test showed that these baseline-corrected ratings of perceived effort were not normally distributed [$D(18) > 0.204$; $P < 0.046$ for all].

Friedman ANOVA comparing the baseline-corrected ratings of effort in our experimental conditions (i.e., when participants cycled at the five intensity levels receiving the three types of acoustic feedback: congruent, slower, and faster) was significant [$\chi^2(14) = 76.321$; $P < 0.000$], suggesting that participants perceived different levels of effort in the different experimental conditions. To see whether participants reported more (less) effort when listening to a faster (slower) HR frequency compared with the congruent condition, we performed a Bonferroni-corrected Wilcoxon matched-pairs test (threshold for statistical significance, $P < 0.025$).

The planned Wilcoxon matched-pairs test showed that providing faster vs. congruent heartbeats significantly increased the perceived effort in all ($Z > 2.982$; $P < 0.003$ for all), with the exception of the first level of exercise intensity, which was slightly above the threshold ($Z = 2.197$; $P = 0.028$). The test also showed that providing slower vs. congruent feedback did not significantly change the perceived effort attributed to any of the exercise intensity levels ($Z < 2.045$; $P > 0.041$; BF < 0.283 for all except one value of 3.242). Results of the Wilcoxon matched-pairs tests and Bayesian paired-sample t tests are presented in Fig. 1 and SI Appendix, Table S1.

We performed an additional analysis to exclude that the illusory increase of effort was driven by an entrainment effect—that is, by a real change in HR frequency during exercise, possibly caused by the false feedback. Given that our variables were not normally distributed [$D(18) > 0.219$; $P < 0.023$ for all], we performed Friedman ANOVA on participants' baseline-corrected HR. The Friedman ANOVA comparing the baseline-corrected HR recorded during our experimental conditions (i.e., when participants cycled at the five levels of intensity while receiving the three types of acoustic feedback: congruent; slower; faster) was not significant [$\chi^2(14) = 18.633$; $P = 0.179$]. Bayesian repeated-measures ANOVA confirmed these results by showing

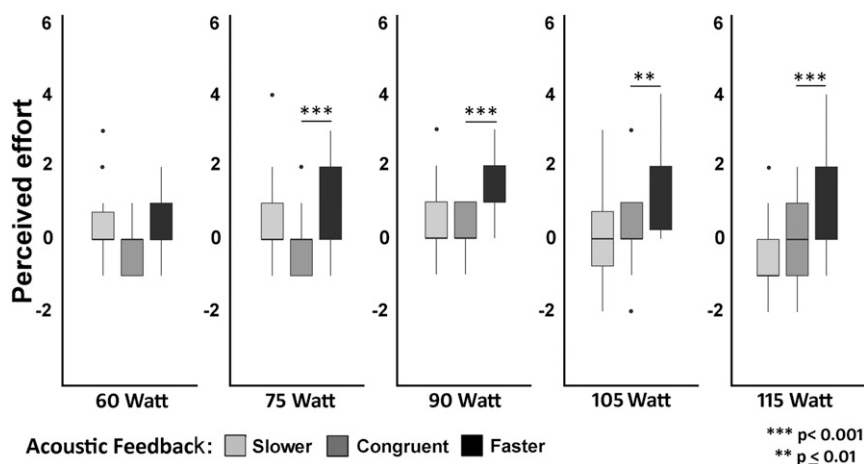


Fig. 1. Results of the EE session. Changes in perceived effort (measured using the RPE scale) compared with the baseline session, as a function of five cycling intensity levels and with three types of acoustic feedback: slower, congruent, and faster. See the main text for explanation.

evidence in favor of the null hypothesis (types of acoustic feedback \times levels of intensity interaction; $BF = 0.014$). Taken together, these results indicate that providing a faster (or slower) incongruent auditory heartbeat-related feedback did not increase (or decrease) participants' HR, thus permitting the exclusion of confounding entrainment effects. Note also that during the debriefing, none of the participants reported having noticed that the acoustic feedback was manipulated.

To exclude the possibility that the illusory increase of perceived effort was due to the acoustic feedback, we compared participants' RPE ratings collected after the congruent condition of the EE task, in which congruent acoustic feedback was provided, with those collected during the BE, in which no acoustic feedback was provided. The K-S test showed that some of the ratings of perceived effort were not normally distributed [$D(18) > 0.201$; $P < 0.054$ for all]; therefore, Friedman ANOVA was performed. Although Friedman ANOVA was significant [$\chi^2(9) = 149.848$; $P < 0.000$], in line with our hypothesis, the Wilcoxon matched-pairs test showed that participants perceived the same level of effort in each of the targeted frequencies when no acoustic feedback (baseline condition) was provided and when congruent HR feedback was provided ($Z < 1.334$; $P > 0.182$; $0.683 < BF > 0.243$ for all). In summary, we found no evidence that providing congruent acoustic feedback changed participants' RPE.

Finally, we tested whether interindividual differences in interoceptive awareness correlate negatively with the illusory increase of perceived fatigue when listening to faster heartbeat sounds, as was previously reported in the context of the rubber hand (31) and enfacement illusions (32). We assessed interoceptive awareness using the Multidimensional Assessment of Interoceptive Awareness (MAIA) (36, 37), focusing on the Noticing and Body Listening MAIA subscales, which relate more directly to bodily processes. For each participant, we computed a global index of illusory perceived effort, by averaging the increase of perceived effort (calculated as the difference between incongruent and congruent scores) in the four faster incongruent feedback conditions that we found to be significant. Finally, we correlated the Noticing and Body Listening scores with the illusory perceived effort index. Unexpectedly, the correlations were not statistically significant ($\rho < 0.197$; $P > 0.05$; $BF < 0.210$ for all). We found no significant correlations with personality traits assessed by the Body Awareness Questionnaire (38), the Body Perception Questionnaire (39), the State-Trait Anxiety Inventory (40), and the Big Five—short version (41) (*SI Appendix, Table S3*).

Discussion

We tested the possibility of inducing an illusion of perceived effort—that is, a misperception of one's physiological state (here effort level)—by providing participants with false feedback about their bodily signals (here false acoustic feedback about their HR). Our results show that providing faster cardiac feedback during physical exercise consistently induces an illusory perception of increased effort.

Our results can be explained within theories of interoceptive (or embodied) inference (2–7), which assume that the brain both estimates and controls critical homeostatic and physiological variables. From this perspective, effort and other relevant interoceptive variables may be estimated on the basis of sensory (e.g., interoceptive) streams and prior information. Providing participants with false (faster) cardiac feedback may have induced them to misperceive their effort, that is, to overestimate their perceived effort compared with the actual effort that they would report based on their current exercise intensity level and physiological state (e.g., HR). This “illusion of effort” suggests that interoceptive information—perhaps made more salient by the acoustic feedback—is considered in the internal estimate of one's own physiological state.

We found the illusion of effort to be asymmetrical. Participants reported more exertion when they received faster feedback about their HR frequency, but did not report less exertion when provided with slower feedback. At four of the five intensity levels that we tested (60–105 W), Bayesian analyses indicated strong to moderate evidence for the (null) hypothesis that the ratings of perceived effort with congruent feedback and slower feedback are the same. These findings are less conclusive at the fifth intensity level (115 W); although Bayesian analysis indicated moderate evidence for the opposite hypothesis (higher perceived effort with congruent feedback vs. slower feedback), the effect did not reach statistical significance using nonparametric analysis.

The asymmetry between effort perception with faster vs. slower cardiac feedback points toward a risk-averse strategy that takes into consideration the potential costs of a wrong estimate. Indeed, while overestimating effort level is relatively safe for an organism, underestimating it can be more maladaptive, especially during exerting tasks such as physical exercise. Several lines of research suggest that perceived levels of effort and fatigue influence the selection of exercise intensity levels and the efficacious regulation of bodily parameters (13, 42–45). Thus, it is possible that the potential costs of underestimating perceived effort (e.g., poor allostatic regulation) favor risk aversion strategies. The same form of risk aversion has been reported in the case of mentally fatigued persons who overestimate their physical exertion levels (30).

Taken together, these asymmetric results suggest that (top-down) factors, such as a concern for safety, may limit the plasticity of the interoceptive schema, preventing it from making dangerous inferences (e.g., that one is not exerted). Note that this asymmetry permits us to rule out alternative explanations for our findings—namely, that participants may have estimated their effort levels by using only the false auditory feedback or by counting their heartbeats, and also that the false feedback would have enhanced the salience of, and increased the attention to, interoceptive or exteroceptive stimuli (46, 47).

Another possible explanation for our findings is that the acoustic feedback—either congruent or incongruent—may have rendered the estimation of effort more difficult (e.g., we normally hear our heartbeats at quite a low volume) or noisier (e.g., the acoustic feedback was not synchronized with the online heartbeats), thus biasing the participants' ratings. This interpretation is not tenable, however, given that we found no differences between the participants' ratings during the experimental (with congruent feedback) and baseline (without feedback) sessions, and that we found an asymmetric effect of acoustic feedback (with faster but not slower feedback). Another alternative explanation for our findings is a putative entrainment effect; if participants' heartbeats align to the false auditory feedback (i.e., become faster), then their perceived exertion cannot be considered a misperception. The fact that participants' heartbeats do not significantly change with false feedback rules out possible entrainment effects.

A limitation of the present study is its small sample size, which may have hindered the ability to describe differences in the illusory strength of the effect in relation to interindividual differences in self-reported measures of interoceptive awareness. Future studies should examine whether the results reported here can be generalized to other populations (e.g., women, older or less fit individuals) or to other stimuli (e.g., fast or slow non-biological rhythms), especially when participants are not induced or find it difficult to associate stimuli with their HR.

Our findings significantly extend the literature on bodily illusions, such as the rubber hand (26, 27), full body (19, 48), and enfacement (20, 21, 49) illusions, by showing that false feedback about interoceptive streams (here false cardiac feedback) can produce misperceptions of one's own physiological state (here one's own effort level). The false feedback mechanism has proven effective for probing interoceptive processing in different cognitive and emotional domains. A previous study that manipulated participants' physiological feedback during exercise reported that emotional intensity and salience of neutral faces was enhanced by false feedback of increased HR (50). Other studies have reported that providing feedback on HR influences the perceived attractiveness of stimuli (51), and that increasing HR by exercise sensitizes to fearful stimuli (52). Our present study and the aforementioned studies show that providing false physiological feedback is an effective method for probing interoceptive processing and producing interoceptive illusions.

The most widely known interoceptive illusion is the thermal grill illusion, a sensation of burning heat when the arm is placed on a "grill" composed of several interleaved cold and hot metallic bars (53). As none of the bars is so hot as to produce a sensation of burning heat per se, this is considered an illusion, which may depend on the peculiar way in which our thermoreceptors integrate conflicting (cold vs. hot) peripheral information about temperature (53). The thermal grill can be conceptualized as interoceptive, if one assumes that the unmyelinated C-fibers that convey cutaneous temperature (and pain) sensations are part of the interoceptive system (1). Following similar arguments, other illusions may be considered at least partly interoceptive, such as those that use affective touch (54) or cardiovascular feedback (55, 56) to induce the illusory feeling of owning a body part or the full body (57; see also ref. 58 for different results).

While the relationships between bodily illusions and interoceptive streams remain to be fully tested, the results of the foregoing studies raise the possibility that body representations may be tightly linked to allostatic processes. Furthermore, a more

integrative view should also consider proprioceptive and action-related contributions to body representations and illusions. For example, manipulating the neural command to the musculature via vibration of muscle afference induces an illusion of movement and cardiovascular and respiratory responses (59–61). The extent to which the brain maintains coherent internal models across several dimensions (e.g., postural, interoceptive) remains incompletely understood.

Several other facets of interoceptive processing are still unclear, such as the way in which the brain may combine multimodal sources of evidence to estimate physiological or homeostatic variables (e.g., hunger or effort). In principle, the information source that is temporarily more accurate may dominate and uniquely contribute to the perception of current effort and other relevant physiological variables. However, in the present study, manipulating the putatively most reliable (or at least most salient) information source—auditory feedback—produced asymmetric effects; participants reported higher effort levels with faster feedback but not lower effort levels with slower feedback. This result suggests that the brain may use more sophisticated mechanisms than selection of the most reliable source of evidence.

The optimal approach to multisensory integration involves considering prior information plus all available sources of evidence—interoceptive, proprioceptive, and exteroceptive—and weighting them based on their precision (i.e., inverse uncertainty). It has been reported that the brain can optimally weight and integrate multiple exteroceptive sources of (visual and haptic) information to form a robust percept (62). Along similar lines, it is possible to speculate that the brain maintains a central representation of physiological variables and bodily signals coming from inside the body. Such a putative interoceptive schema would be the equivalent of a body schema (i.e., an internal representation of bodily variables, such as the shape of our body, the position of our limbs) (18) for the interoceptive domain. It may support homeostatic and allostatic regulation by orchestrating and predicting interoceptive signals coming from inside the body (e.g., heartbeats, ventilation) as well as from the outside (e.g., muscular signals due to effort). However, the idea that the brain maintains an interoceptive schema for (optimal) multimodal integration is speculative and remains to be investigated in future studies. Novel experiments should assess which physiological and homeostatic variables (e.g., hunger, thirst, effort and fatigue levels) the brain estimates and controls, the relative contribution of different (interoceptive, proprioceptive, and exteroceptive) streams to these processes, and whether the different streams are integrated in an optimal way. For this, in addition to heartbeat signals, which have slow transmission and limited perceptual access, it may be worth manipulating other interoceptive signals (e.g., respiratory signals) that may be more accessible and precise. This would permit the testing of whether cross-modal conflicts arise and if so, whether they are resolved by considering the relative precision of the information sources, as is assumed by optimal integration schemes.

Another open question involves the behavioral effects of the illusion of effort (or other interoceptive illusions). Various studies in the sports literature suggest that for athletes, the selection of exercise intensity is not a simple function of muscle fatigue but rather is mediated by top-down mechanisms and perceived levels of effort and fatigue (42, 43, 63, 64). These studies suggest that an illusion of effort should induce participants (or athletes) to select lower exercise intensity levels. Similarly, one can hypothesize that participants who report being more exerted would discount future rewards more steeply if they required some effort to be secured (44). Future studies should test these predictions. Another open question concerns the relationship between implicit processes of interoceptive processing and explicit (self-reported) measures of interoceptive awareness that, according to a recent model proposed by Garfinkel and collaborators (65), may target different components of interoceptive awareness, namely interoceptive accuracy and interoceptive sensibility. Previous studies have reported that participants

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