Long Integration Time for Accelerating and Decelerating Visual, Tactile and Visuo-tactile Stimuli

Monica Gori 1,* , Alessandra Sciutti 1 , Marco Jacono 1 , Giulio Sandini 1 ,
Concetta Morrone 1,2 and David C. Burr 3

1 Robotics Brain and Cognitive Sciences, Istituto Italiano di Tecnologia, via Morego 30,
16163 Genoa, Italy
2 Dipartimento di Scienze Fisiologiche, Facolta` di Medicina, Universita` di Pisa, Italy
3 Dipartimento di Psicologia, Università Degli Studi di Firenze, Via S. Nicolò 89, Florence,
Italy
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Abstract
The human visual system is good at discriminating speed but not acceleration. However, as speed is seldom constant, it is important to be able to extract speed in conditions of acceleration and deceleration. We measured visual, tactile and bimodal speed-matching over a wide range of accelerations and decelerations in a 2IFC procedure. Both visual and tactile stimuli were generated on physical wheels etched with a sinusoidal profile. During different experimental sessions the wheels could be seen, or touched, or both. Comparisons between different unimodal and bimodal matched speeds revealed similar integration times for the two modalities, in both cases around one second, suggesting that it occurs at a relatively high level of processing. Bimodal precision of speed discrimination was better than unimodal discrimination, as predicted by the maximum likelihood model of optimal integration.

Keywords
Vision, touch, multisensory integration, temporal integration, acceleration, deceleration

1. Introduction
During everyday life touch and vision are commonly co-activated when objects are manipulated, providing both visual and tactile dynamic information. As our world is highly dynamic, with many objects moving simultaneously along different trajectories, motion processing is fundamental for all senses.

* To whom correspondence should be addressed. E-mail: monica.gori@iit.it
Specialized flow sensitive mechanisms have been well described for vision (Gibson, 1950), and recently similar mechanisms have been individuated for touch (Bicchi et al., 2005). Several studies (Burr and Santoro, 2001; Melcher and Morrone, 2003; Melcher et al., 2004; Neri et al., 2006) point to at least two, possibly three stages of analysis of optic flow and other complex motion (such as biological motion): an early stage of local visual motion analysis, with a time constant of 200–300 ms; an intermediate stage, with an integration time of around 1000 ms; and a later global-motion integration stage (particularly clear for biological motion) with a much longer time constant, around 3000 ms. There is little information about integration of flow tactile information, but for optimal fusion between the senses one may expect the integration windows of the two systems to be similar. Vision and tactile motion mechanisms seem to share many properties and cross-sensory interactions between these two modalities have been widely reported (e.g. Blake et al., 2004; James and Blake, 2004; see Soto-Faraco et al., 2004 for a review; Tomassini et al., 2011). For example, both are subject to motion flow after-effects (Watanabe et al., 2007), to the ‘aperture problem’ and the Ouchi illusion (Bicchi et al., 2008; Pei et al., 2008) and the motion aftereffects can be transferred between vision and touch (Konkle et al., 2009). In addition, fMRI studies show that both visual and tactile flow may activate the cortical motion area hMT+ (Hagen et al., 2002; Huk et al., 2002; Ricciardi et al., 2004; Summers et al., 2009). These results, together with the correspondence in velocity thresholds (e.g. Gori et al., 2011), indicate a strong similarity in the processing of visual and haptic flow motion.

As we live in an environment subject to gravitational acceleration, real life motion is seldom uniform. Some results suggest that different mechanisms of analysis may be involved in the perception of constant and variable-speed motion (Calderone and Kaiser, 1989). It is therefore interesting to investigate whether the similarity in velocity discrimination thresholds between vision and touch observed for constant speed stimuli (e.g. Gori et al., 2011) can be generalized to other types of motion, in particular to linearly accelerating motion.

Several studies have looked at accelerating and decelerating visual motion (Krekelberg et al., 2006; Lisberger and Movshon, 1999; McKee and Nakayama, 1988; Schlack et al., 2007) showing that the human visual system is more sensitive to constant speed discrimination than to acceleration (Bowne et al., 1989; Calderone and Kaiser, 1989; Gottsdanker, 1956; Gottsdanker et al., 1961; Schmerler, 1976; Werkhoven et al., 1992). Thresholds, expressed as Weber fractions, are as low as 0.06 (McKee, 1981; Orban et al., 1984) for temporally separated velocity changes, but increase up to 0.3 (Mateeff et al., 2000; Snowden and Braddick, 1991) or more (Schmerler, 1976).
for contiguous velocity changes and are still more impaired with decreasing temporal periods of modulation (Mateeff et al., 2000; Snowden and Braddick, 1991; Werkhoven et al., 1992). It is well known that information about velocity is integrated over space (Watamaniuk and Duchon, 1992) and over time (McKee and Nakayama, 1988; Nakayama, 1985). In particular, Mateeff et al. (1995) suggest that when temporally-adjacent stimuli with different velocities are presented, velocity information is integrated simply by averaging within a moving temporal window. These processes may be mediated by the cortical motion area MT. Although MT neurons have no explicit representation of acceleration (Lisberger and Movshon, 1999), neuronal responses in this area are affected by stimulus speed changes (Price et al., 2005). More precisely, stimulus relative speed and acceleration can be accurately estimated from the pattern of activity of the MT neuron population (see Price et al., 2005 for more details). Interestingly, as noted above, the MT area is activated also by tactile flow stimulation (Hagen et al., 2002; Huk et al., 2002; Ricciardi et al., 2004). This finding suggests, together with the evidence that speed signals from vision and touch seem to be summated at a low sensory level of analysis (Gori et al., 2011), that visual and tactile temporal flow integration could share similar mechanisms during acceleration and deceleration.

To test this idea, we investigated perception of visual, tactile and visuo-tactile accelerated and decelerated stimuli by measuring speed matching and discrimination thresholds over a wide range of accelerating and decelerating ramp speeds. The results show that visual, tactile and bimodal cues are integrated in a similar way, which is well modeled by averaging the temporally contiguous speeds over time. Moreover, bimodal thresholds are consistent with the prediction of an optimal Bayesian model of multi-modal integration. Similar results were found for acceleration and deceleration, and also for motion stimuli presented in opposite directions to the different sensory systems, as had been shown previously for audio-visual and visual-tactile constant speed (Alais and Burr, 2004; Gori et al., 2011; Wuerger et al., 2003). These results suggest that visual, tactile and bimodal visuo-tactile perception of flow during acceleration and deceleration is subserved by similar mechanisms.

2. Materials and Methods

Six subjects (3 authors and 3 naïve to the goals of the study) gave their informed consent to participate in the experiment. We measured visual, tactile and bimodal speed-matching and detection thresholds over accelerations and decelerations ranging from 6.8 to 4549 cm/s². The stimuli were two physical wheels etched with a sinewave profile. The sinusoidal grating had a spatial fre-
Figure 1. (A) Setup and procedures. Physical wheels etched with a sinewave profile of 10 c/deg. (B) Support where each wheel was inserted. (C) Setup comprising two independent computer-controlled motors. (D) Position of the subject during the experiment. (E) Visual stimulus. (F) Tactile stimulus. (G) Bimodal stimulus: visual and tactile stimulation in the same (gray arrows) or opposite (black arrows) direction of motion. (H) Tactile stimulation for the speed detection threshold measure: the finger simultaneously touches the two wheels (see ‘Materials and methods’ section for details).

Quency of 10 c/cm, corresponding to 10 c/deg as the subject sat 57 cm from the stimulus (Fig. 1A). The wheels were simultaneously driven at specified speeds by two independent computer-controlled motors (Fig. 1B and C). Subjects sat in front of the observed wheel (visual stimulus) and touched the second wheel (tactile stimulus) behind it (Fig. 1D). Room illumination was kept constant. For the ‘visual’ task the visual stimulus was observed through a small window (1 × 3 cm², see Fig. 1E), while for the ‘tactile’ task a shield hid the wheels from view while the subject touched one wheel with the right index fingertip (1 × 2 cm, see Fig. 1F). During the ‘bimodal’ task (Fig. 1G, gray arrows) subjects were instructed to touch and observe simultaneously the two wheels moving in the same direction. The touched wheel was spatially aligned with the visual one to give the impression that both stimuli originate from the same object. In the ‘bimodal, opposite direction’ task (Fig. 1G, black arrows), the two wheels moved in opposite directions.

2.1. Unimodal and Bimodal Speed Matching

Subjects were presented with two stimuli — a test and a probe in randomized order. The test was speed-ramped in acceleration or deceleration of the same mean speed in any session (Fig. 2A and B), while the probe was moved at a
constant velocity that varied from trial to trial (Fig. 2C). The constant velocity stimulus was characterized by a step-like velocity profile, with a very fast ramp of acceleration (4549 cm/s²) followed by a plateau and an analogous deceleration. The transients were extremely rapid, as the maximum time required for the wheel to reach the maximal final velocity considered in our experiment was 0.0057 s. The acceleration and deceleration stimulus presentation was randomly chosen for each session. Subjects were required to discriminate in a two-interval forced-choice (2IFC) task which interval seemed to be faster. The QUEST algorithm (Watson and Pelli, 1983) selected the speed of the probe (from a range of 0 to 17 cm/s) to home in on threshold. The accelerations and decelerations used for the test stimuli were 6.8, 13, 15.92, 20.47, 27.3, 36.4 and 4549 cm/s². The 4549 cm/s² accelerated (or decelerated) stimulus corresponded to a constant velocity stimulus. The motion of the wheel was accurately calibrated with a visual tracking system (NDI Optotrak Certus system). Each stimulus lasted 1 s. The ramps that reached the maximum speed of 13 cm/s in less than that time were speed-clamped at 13 cm/s for the remaining presentation time. The data were fitted with a cumulative Gaussian function, asymptotic at 0 and 1, from which PSEs and thresholds were evaluated. The standard errors of both were estimated by bootstrap (Efron and Tibshirani, 1993). One hundred iterations of bootstrapping were used and the standard error was computed as the standard deviation of the bootstrap distribution. For each condition 160 trials were collected.
2.2. Evaluation of Minimum Perceived Tactile Speed

We also measured the minimum perceived tactile speed (speed detection thresholds) for three different accelerations and decelerations (6.8, 13 and 20.47 cm/s²) on 5 subjects (3 authors and 2 naïve). In this task the subjects were instructed to do a temporal order judgment by simultaneously touching with the two sides of their index finger the two wheels (Fig. 1H) and to choose which started (or stopped) first. As before, one of the two wheels was accelerating ('standard’) while the comparison stimulus had constant velocity (Fig. 6A). The asynchrony between the two stimuli was determined by QUEST. For each condition 160 trials were collected.

2.3. Tactile Detection of Acceleration

In order to assess if the analysis of the stimulus occurred at a sensorial level, we measured tactile acceleration detection thresholds in three subjects (two authors and one naive), before evaluating the unimodal and bimodal speed matching. The subjects indicated in a 2IFC procedure which of two stimuli, one linearly accelerating (3.25, 6.8, 9.1, 13, or 15.92 cm/s²) and one with constant speed (13 cm/s), was the accelerated one. Each stimulus lasted 1 s. As before, the constant speed stimulus was characterized by a step-like velocity profile with very fast transients (acceleration of 4549 cm/s², rising time less than 6 ms) — see Fig. 2C, fourth panel. For each condition 160 trials were collected.

3. Results

3.1. Comparisons Between Visual, Tactile and Bimodal Speed Matching

We first asked subjects to discriminate tactually in 2IFC which stimulus was more accelerated between a sequence of two stimuli, randomly presented, one accelerating and the other moving at a constant speed. All the data lie under threshold (0.75) suggesting that under these conditions tactile acceleration is not detected (Fig. 3). Nevertheless all subjects show high performances in matching with high precision the apparent velocity of an accelerating stimulus with one of constant speed. This result suggests that the analysis of the stimulus velocity occurred at a sensorial level.

We then measured the apparent speed of the accelerated stimuli in order to understand the similarities between the visual and tactile systems. Figure 4 shows the matched speeds of all subjects (different symbols represent different subjects) for tactile (left), visual (center) and bimodal (right) tasks in acceleration (top panel) and deceleration (bottom panel). The similarity between different modalities is also confirmed by the overlapping of the corresponding average matched speeds in Fig. 5 (top panel). Interestingly, both the unimodal
Figure 3. Acceleration detection. Performances of three subjects in the discrimination between constant speed and linearly accelerating stimuli. The dark gray dashed line represents the chance performance at 0.5, while the light gray dashed line indicates the threshold level (at 0.75). Error bars represent standard errors.

(visual and tactile) and bimodal conditions produced similar results (see the overlapping of unisensory (triangle and circle) and multisensory (squares) perceived speeds in the top panel of Fig. 5), suggesting the action of similar mechanisms. The similarity was confirmed statistically by a two-way repeated measures ANOVA with ‘acceleration magnitude’ and ‘modality’ as factors: there was no significant effect of modality or interaction of modality × acceleration ($p > 0.05$, both for the acceleration and the deceleration conditions).

Evaluation of subject responses can reveal the process behind the perception of speed of accelerating stimuli. Subjects could have based their estimation on the final speed reached by the varying stimulus (gray lines in Figs 4 and 5, top panel); or they could have integrated over time the different speeds sensed during the entire stimulation time, thus perceiving the average stimulus speed (dashed black lines); or they could have integrated the different perceived speeds over a time window shorter than the stimulus duration. In
Figure 4. Comparison within each modality. Matched speeds (PSEs) of six subjects, illustrated with different symbols and colors, for tactile (on the left), visual (in the center) and bimodal (on the right) stimuli, in acceleration (top panel) and deceleration (bottom panel). Error bars on individual data points are obtained by bootstrap (Efron and Tibshirani, 1993). The light gray solid line represents the maximal velocity reached by the wheels, while the black dashed line represents their average speed. The red solid line corresponds to the mean matched speed of all the subjects. Error bars in this case correspond to ±1 SEM of the group measurements.

In this case, in the acceleration condition the matched speeds should be lower than the average stimulus speed, as the restricted time window would have truncated the later — and faster — speed information. The opposite should happen for deceleration, where a time window shorter than 1 s would have neglected the lowest speeds.

The results show that the perceived speed is always lower than the maximal speed reached by the stimulus, with the mean of the data (red solid line) falling close to the average speed of the wheel (black dashed line). These results suggest that subjects integrated the speed signal linearly for the entire duration of the stimulus (1 s; see below for a more detailed comparison between acceleration and deceleration).

Interestingly, the unimodal thresholds for the two modalities are similar (triangles and circles in Fig. 5, bottom panel), and the bimodal thresholds (squares) are well predicted by a Bayesian fusion of the two individual estimates (dash-dotted orange line, computed with Equation 1, Ernst and Banks, 2002; Landy et al., 2011). Indeed, for the bimodal condition the precision in-
Figure 5. Comparison between modalities. Mean matched speeds (top panel) and thresholds (bottom panel) for tactile (triangles), visual (circles) and bimodal (squares) stimuli in acceleration (on the left) and deceleration (on the right). The light gray solid line in the top panel represents the maximal speed of the stimulus while the black dashed one represents its average speed. The dash-dotted orange line in the bottom panel refers to the Bayesian bimodal prediction (computed according to Equation 1, see Materials and methods). Error bars correspond to ±1 SEM of the group measurements.

3.2. Speed Perception of Accelerating and Decelerating Visual, Tactile and Visuo-tactile Stimuli

The average velocity of accelerating stimuli is equal to that of the decelerating stimuli in the 1 s period. However, if sensory integration were shorter than the stimulus duration, the speed perceived for accelerating and decelerating stimuli should be different. The speed history to be integrated is different for acceleration and deceleration, with higher velocities later in time in an accelerated velocity profile, compared with deceleration. A window of integration shorter than 1 s would therefore exclude different parts of the stimulus

\[ \sigma_{VT}^{-2} = \sigma_V^{-2} + \sigma_T^{-2}, \]  

where \( \sigma_V \) and \( \sigma_T \) are the visual and tactile unimodal thresholds and \( \sigma_{VT} \) is the bimodal visuo-tactile threshold.
Figure 6. Detection threshold measure, methods and results. (A) Experimental procedure. Subjects had to answer which of the two wheels started (in acceleration) or stopped (in deceleration) first. One wheel was linearly accelerating or decelerating (‘standard’) while the other (‘comparison’) was moved at a constant velocity, reached almost instantaneously during motion onset. (B) Mean detection time for acceleration (pink circles) and deceleration (green squares). Error bars correspond to ±1 SEM of the group measurements. (C) Tactile detection thresholds for acceleration (pink circles) and deceleration (green squares). Error bars correspond to ±1 SEM of the group measurements. (D) Mean matched speeds among all modalities in acceleration (pink solid line) and deceleration (green solid line). The light gray solid line represents the maximal velocity reached by the wheel, the black dashed one represents its average speed and the blue short-dashed line represents the average stimulus speed computed over an interval corresponding to the time when the velocity was above detection threshold.

velocity profiles: the faster (and later) speeds in acceleration and the lower speeds in deceleration. Figure 6D shows that the accelerating stimuli matches seemed as fast as the decelerating stimuli ones and no major differences are evident. The average speed of the stimulus (black dashed line) fits quite well the mean matched speeds for both acceleration (pink solid line) and deceleration (green solid line) with just a slight underestimation of the latter. A two-way repeated measures ANOVA with ‘condition’ (acceleration/deceleration) and ‘acceleration magnitude’ as factors run on the collapsed data from all the three modalities (tactile, visual and bimodal) showed a significant effect of condi-
tion \((p = 0.004)\) and a significant interaction between acceleration magnitude and condition \((p = 0.008)\). However, a Tukey post-hoc analysis highlighted that the only significant difference between deceleration and acceleration occurred for the 13 cm/s\(^2\) stimulus \((p < 0.001)\). A set of one-tailed pair-sample \(t\)-tests run for each modality for this acceleration value showed that the decelerating stimulus was perceived significantly faster than the accelerating stimulus (tactile \(p < 0.001\); visual \(p = 0.03\); bimodal \(p = 0.1\)) and this was true especially in the ‘tactile’ condition.

This small difference in velocity perception (on average 6.53 ± 0.27 (SEM) cm/s for acceleration and 8.29 ± 0.36 cm/s for deceleration) might be due to a different speed detection threshold for the deceleration and acceleration conditions. It is possible that the integration period for speed is limited to the interval in which motion is above some threshold. Using a tactile temporal order judgment for three accelerating or decelerating ramp stimuli we measured the corresponding speed detection thresholds. We asked subjects to simultaneously touch with the two sides of their index finger the two wheels (one driven at constant speed and the other in acceleration or deceleration) and to choose which started (or stopped) first (Figs 1H and 6A). We assume that the speed of the wheel at the time instant at which the subject perceives the motion onset (or offset) corresponds to the speed detection threshold. The time at which the detection occurs and the corresponding speeds of the wheel are plotted in Fig. 6B and C, respectively (see ‘Materials and methods’ section for more details). Again, no difference was found in speed detection thresholds between acceleration (Fig. 6C, pink circles) and deceleration (Fig. 6C, green squares), excluding the possibility that the difference in matched speed could be explained by a difference in speed detection thresholds. However, when the average of the stimulus velocity is calculated only for the intervals when the velocity was above threshold, the fit with the decelerating data improves. The short-dashed blue curve reports the average for the supra-threshold interval, shifted horizontally with respect to the black curve (average over 1 s of duration). This curve has an intermediate value between the accelerating and the decelerating data, indicating that both data sets are consistent with an integration of the velocity signal over the supra-threshold detection period.

3.3. No Direction-Specific Facilitation for Bimodal Stimuli

Several studies show cross-modal interactions in motion perception: visual motion can influence the apparent speed of tactile motion when in the same direction (Bensmaia et al., 2006; Craig, 2006) and also affect the perceived speed and direction of auditory motion (Lopez-Moliner and Soto-Faraco, 2007; Mays and Schirillo, 2005). In real life it may be important to fuse signals of motion in the same direction. However, audio-visual (Alais and Burr, 2004; Wuerger et al., 2003) and visual-tactile motion studies (Gori et al., 2011) show
Figure 7. Bimodal perception of same and opposite directions of motion. Mean matched speeds (A) and thresholds (B) for acceleration (circles) and deceleration (squares) in same (black filled symbols) and opposite (open gray symbols) direction of motion. Error bars correspond to ±1 SEM of the group measurements. The light gray solid line in panel A represents the maximal velocity reached by the wheel.

that motion in opposite directions is integrated as well as motion in the same direction. We evaluated whether the same occurs for accelerating and decelerating stimuli by comparing the bimodal threshold for visual and tactile motion in the same (filled symbols in Fig. 7) or opposite direction (open symbols in Fig. 7). As with the previous studies, no direction specific facilitation was found in matched speeds (Fig. 7A) and thresholds (Fig. 7B), either for accelerating (circles) or decelerating (squares) stimuli.

4. Discussion

Our results suggest that similar mechanisms can be present for visual and tactile flow perception of accelerating and decelerating stimuli as well for bimodal combinations of the two. Moreover, the integration window over which the speed of visual and tactile stimuli is judged is extensive — at least one second. This finding is interesting, as the integration time of early sensorial processes appears to be much shorter — about 200 ms. Integration times of this magnitude are similar to those demonstrated for integration of flow motion, probably achieved at intermediate stage of global analysis (Burr and Santoro, 2001) after contrast thresholding. With our manipulation we cannot exclude the possibility that integration time could also be longer than 1 s, as for instance happens in vision, where it has been shown to last even for 3 s (Burr and Santoro, 2001). The use of longer stimulus durations would be needed to define exactly the width of the temporal integration window; however, we have shown that it cannot be smaller than 1 s. MT can be the responsible cor-
tical region for this neural processing (Hagen et al., 2002; Huk et al., 2002; Ricciardi and Pietrini, 2011; Ricciardi et al., 2004), as it is activated by both visual and tactile flow stimulation (Hagen et al., 2002; Morrone et al., 2000; Ricciardi and Pietrini, 2011; Ricciardi et al., 2004; Zeki et al., 1991) and its activation is affected by stimulus speed changes (Price et al., 2005). Under all conditions the stimulus average speed was a good estimate of the speed perceived by the observer. When the average was restricted to the supra-threshold detection period the prediction of the data improved further.

Accelerating and decelerating signals seem to be perceived very similarly for both modalities, supporting the idea of similar processes behind visual and tactile flow perception. The speed comparison of accelerating and decelerating stimuli showed only a slight tendency for the decelerating stimuli to be perceived as faster (marginally for vision and significantly for touch in the 13 cm/s^2 condition). Asymmetries between positive and negative acceleration have been reported by others authors (Babler and Dannemiller, 1993; Calderone and Kaiser, 1989; Gottsdanker et al., 1961; Schmerler, 1976). This difference is unlikely to be a consequence of an asymmetry in acceleration and deceleration speed detection thresholds, as they were very similar, especially in the tactile domain. Schlack et al. (2008) observed that accelerating and decelerating stimuli can affect visual speed discrimination thresholds of a constant-speed stimulus presented immediately after the accelerating stimulus. In particular, the exposure to a linear acceleration leads to a speed underestimation, more pronounced for accelerations than for decelerations. This dependency of speed perception on ‘speed history’ has been taken as evidence for the existence of speed-dependent adaptation mechanisms, probably in MT. ‘Speed history’ might well affect our visual and tactile ramp stimuli perception causing larger or smaller differences between accelerating and decelerating conditions depending on the different speed profiles.

An interesting result of the present study is that all the bimodal thresholds were well predicted by the Bayesian model (Ernst and Banks, 2002; Landy et al., 2011) indicating optimal integration of accelerating visuo-tactile flow information (as observed for constant flow perception, see Gori et al., 2011). However, the bimodal integration is not selective to the motion direction between the two unimodal signals, suggesting that the direction of motion has no influence in cue integration.

The similarity of the performance and integration times of vision and touch suggests that the two systems share common mechanisms, as indicated by other psychophysical (e.g. Bicchi et al., 2003, 2005) and neurophysiological (Hagen et al., 2002; Ricciardi et al., 2004) studies.

In conclusion, vision and touch seem to share common strategies in the analysis of both constant motion (Gori et al., 2011) and stimuli characterized by time-varying velocity. One possible neural substrate for the integration of
such motion signals is MT, a visual motion area that is activated by both visual and tactile motion stimuli (Hagen et al., 2002; Morrone et al., 2000; Ricciardi and Pietrini, 2011; Ricciardi et al., 2004; Zeki et al., 1991) and that seems to respond to speed changes (Price et al., 2005). It is highly possible that the brain has developed optimal strategies to process the complexity of motion signals. In particular, the implementation of the same mechanism in all senses, possibly in a supramodal way, allows handling similarly not only constant speed stimuli but also accelerating signals, most common in everyday life.

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