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SPATIAL CODING OF VOLUNTARY SACCADDES IN MAN

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Three experiments are described in which human subjects must direct the gaze to a previously memorized point in visual space after the initial position of the eye has been displaced voluntarily. In Experiment 1 and 2 the visual target is defined as a point on the retina, while in Experiment 3 it is defined as a position of the eye in the orbit. In Experiment 1 and 3 the voluntary movement away from the initial position is a saccade, and in experiment 2 it is a smooth pursuit. The results are in agreement with the hypothesis that the position of visual targets is coded in a frame of reference based in external space. It is suggested that positional information from retinal error inflow and corollary discharge outflow can be both compounded and called upon interchangeably.

INTRODUCTION

In principle, moving the gaze to a point in space where interesting visual information appears might be achieved with a simple strategy which only presupposes plausible physiological mechanisms. In fact, the location of the distal stimulus is uniquely mapped, via the optical system of the eye, onto a specific retinal location. If one admits that the retinal and collicular circuitry can accurately code the vector from the fovea to the proximal stimulus, (Cynader and Berman (1972) ; Schiller and Stryker (1972)), the correct saccade to the target can be planned by transcoding this perceptual vector in terms of motor commands to the extraocular muscles (Robinson (1972)). This idea, sometimes referred to as the "retinocentric coding hypothesis", is appealingly simple inasmuch as it does not presuppose the necessity for the oculomotor system to have access to whatever information is available on the initial position of the gaze in space, or even on the position of the eye in the orbit. Indeed, formal models of target-directed saccades based on this hypothesis have been proposed early on in the literature (Young and Stark (1963) ; Robinson (1973)).

A number of objections can, however, be levelled against the retinocentric hypothesis, the most devastating of them being that if the head moves before the completion of the saccade, the motor vector computed on the sole basis of visual information cannot possibly compensate for the resulting translation of the visual field. Moreover, the displacement resulting from a given pattern of motor commands depends critically on the initial position of the eyeball in the orbit (Robinson (1975a)). Thus, it is unlikely that the saccadic motor plan neglects completely all types of extraretinal information. Theoretical considerations (Robinson (1975b)), clinical data (Zee, Optican, Cook, Robinson and Engel (1976)), and double-step experiments (Hallet and Lightstone (1976a, 1976b)) all point to the conclusion that in fact saccadic planning depends critically on the availability of accurate, real-time information on the position of the eye in the orbit. Considering that on many occasions eyes, head and body move

simultaneously, it certainly makes more sense to suppose that the position of visual targets is coded in an external frame of reference which is unaffected by such movements (the so-called "spatial coding hypothesis" (Robinson (1975b))). Direct evidence in favor of this hypothesis has recently been presented by Mays and Sparks (1980, 1983) who report that if the direction of the gaze is artificially displaced from the original position during the latent period of a target-directed saccade, the correct final position is nevertheless attained. This finding is only explicable with the notion that retinal and extraretinal sources of geometric information are compounded to provide a space-based system of coordinates for locating visual targets. Two sources of extraretinal information can be invoked, proprioceptive inputs from the extraocular muscles and efferent copy from the commands themselves. However, recent results from a deafferented preparation (Guthrie, Porter and Sparks (1983)) suggest that the retinal signal is only compounded with the internally generated representation of the eye position.

The aim of this report is threefold. First we want to replicate the findings of Mays and Sparks in what we consider a more natural experimental condition. It is in fact open to question whether eliciting saccades by electrical stimulation of the colliculus represents for the motor system a condition that it is adapted to cope with. The paradigm proposed in this report is much closer to real-life operating conditions and can be easily implemented in man. Our second aim is to verify the hypothesis that current eye position can be continuously updated also during smooth pursuit displacements. If so, the results of Guthrie, Porter and Sparks (1983) would suggest that efferent information is not only generated by saccadic commands, but by graded motor outputs as well. Finally we will investigate in further detail the role of retinal information in the accurate location of spatial targets. More specifically, having admitted that visual information alone is not in general sufficient for directing the gaze to a particular spatial location, we will address the question of whether such information is actually necessary under all conditions.

METHODS

Subjects

Six subjects (4 males, 2 females) participated in the experiments being paid for their services. They all had normal or corrected-to-normal vision.

Visual display and task

Experiments were run in a totally dark room. Subjects sat within the eye movement recording apparatus with their head immobilized by a biteboard and a forehead brace. The visual display was provided by a HP 1321A, large screen (35.6 by 30.5 cm) oscilloscope driven by the DAC output of the computer. Luminance of the trace (aluminized P31 phosphor) was also controlled via the z-axis input. The distance between the subject's eye and the screen was 57 cm. A 2 mm red LED placed at the center of the screen provided a fixation point in the straight-ahead direction. Point-like visual targets could appear in one among eight symmetrical locations at 10 degrees from the fixation point. In all three experiments to be reported a trial begins with a brief auditory stimulus and comprises four phases: fixate the LED at the center of the field, localize a first spatial location (T1) randomly chosen among the eight possible ones, move to a different random location (T2) and, from there, make a final saccade in total darkness to where T1 had been presented. Subjects were informed neither of the experimental design, nor of the purpose of the experiment. Upon subsequent questioning, none of them was able to indicate whether or not a fixed set of stimuli had been used. A complete session comprised 64 trials corresponding to all possible pairings of first and second location. Each subject participated in three sessions spaced by at least one week. The following experimental paradigms were used in the three successive sessions.

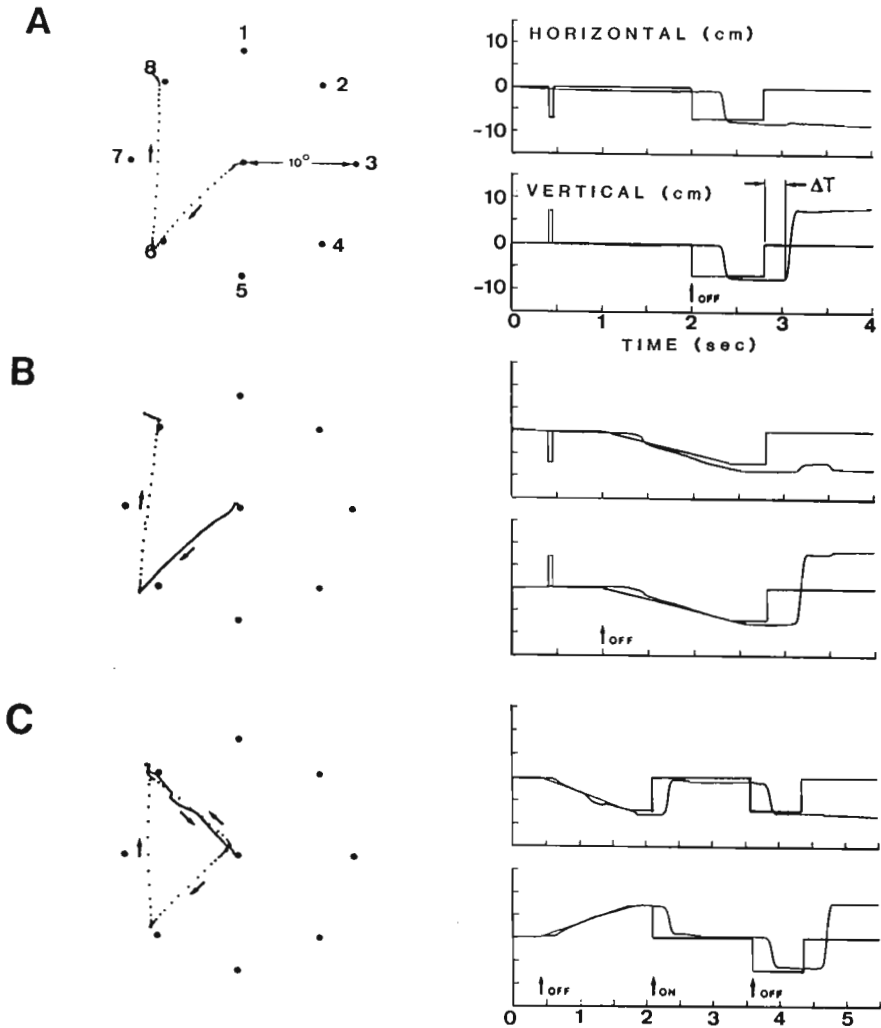


Figure 1.

Description of the experimental paradigms. On the left, two-dimensional display of the eight locations on the screen and of representative trajectories of the gaze in the three experimental conditions. On the right, the time course of the horizontal and vertical components of the eye displacements shown on the left is superimposed on a schematic representation of the target position.

A : After localizing visually the position T1 (8 in this example), the subject makes a saccade to a second location T2 (6 in this example). As soon as this stimulus is turned off, he/she tries to reach with a saccade in total darkness the first location T1.

B : Same as A, but the position T2 is reached with a smooth pursuit.

C : Position T1 is reached with a smooth pursuit. After a second fixation of the center, the trial continues as in A.

Notice that in the three situations, the position of T1 must be memorized for the same amount of time (2350 msec).

Experiment 1 (Figure 1A) - While the subject keeps the gaze on the fixation point, a brief (50 msec) spot appears in one of the peripheral locations (T1). 1550 msec thereafter, the fixation point is turned off and a second location (T2) is simultaneously selected by the spot which stays on for 800 msec. The subject is requested to fovealize the spot with a saccade until it disappears, leaving a totally blank screen. Then, the subject must try and reach with a saccade the first position T1 and remain there until an auditory stimulus signals the end of the trial.

Experiment 2 (Figure 1B) - The first two phases of the experiment are identical to those of Experiment 1. However, when the fixation point is turned off, the subject must follow the spot with a smooth pursuit. This drives the gaze at 7.14 degrees/sec from the center to the selected location T2 and it remains there for 400 msec. As soon as the driving spot disappears leaving a blank screen, the subject must also in this case try to localize the initial position T1 with a saccade and remain there till the end of the trial.

Experiment 3 (Figure 1C) - After an initial 400 msec fixation phase, the subject must smoothly follow the spot from the center to the first position T1 and remain there for 400 msec. When the stimulus is turned off, the fixation point reappears and the subject must come back to it, maintaining the fixation for 1550 msec. Thereafter, the trial continues as in Experiment 1.

Eye movement recording and data analysis

Angular position of the gaze with respect to head and space was measured by the scleral search-coil technique (Collewijn, van der Mark and Jansen (1975); Robinson (1963)). A calibration always preceded each experimental session. Twenty-five locations on the screen, arranged in a 5 by 5 square array and spaced by 5 degrees were sequentially indicated by a spot that the subject was requested to fixate for 5 seconds. The computer then calculated the parameters of a two-dimensional power series mapping of the plane into itself that minimizes the quadratic error between the measured and the actual coordinates of the screen-based matrix. This optimal mapping was finally applied to the raw experimental data. With this procedure the absolute position of the gaze on the display could be determined to within 2 mm. Because the small-angle approximation is extremely accurate in this case results will however be presented in the equivalent angular units.

RESULTS

According to the experimental plan, each subject in a given experimental condition provided eight independent estimates of each location T1, one for every position of the intermediate target T2 (for reasons of symmetry, trials in which T1 is diametrically opposed to T2 were repeated twice). Individual estimates of the accuracy with which localization is possible in every condition are provided by the spatial distribution of the final fixations that, in total darkness, subjects make on the presumed location of T1. Figure 2A,B,C illustrates the results in one subject for the three experimental conditions. For the sake of clarity, we have chosen a subject who was rather accurate both in terms of the average mislocation of the target T1 and of the spatial dispersion of the fixations. Indeed, significant differences exist among subjects for both these two measures of performance. However, the point of the figure that is relevant to the issue discussed here is not the absolute accuracy of the localization, but rather the comparison among the three experimental conditions and, in this respect, the results shown are quite typical. A two-way analysis of variance (8 locations x 3 experimental treatments) was performed both on the distance of the average fixation from T1 and the scatter of the

fixation distribution measured by the surface of the confidence ellipses. No significant difference emerged in either case ($F(2,10) = 2.80$ and $F(2,10) = 2.98$ respectively) among experimental conditions.

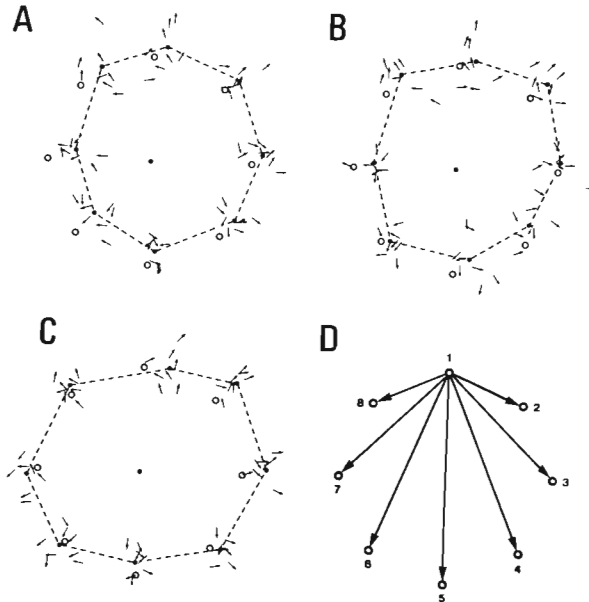


Figure 2.

Distribution of fixations on the invisible target. A,B,C, example in one subject of the distribution of final fixations on T1 in the three experimental conditions. Each arrowhead marks the endpoint of the saccade from T2 to T1 and the direction of the arrows indicate the target from which the movement originates. Dots connected by dashed lines represent the center of gravity of the distribution and unfilled circles indicate the actual position of the target T1.

D : The diagram shows how saccades originating from one point can have 7 different directions and 4 possible amplitudes. Since there are two possible orientations for each direction, and considering the extra direction not represented in the diagram (7-3) the experiments covered altogether 16 different orientations.

A more detailed comparison of the performances in the three experimental conditions can be obtained by breaking down the set of all localizing saccades in each condition according to their direction and amplitude. As shown diagrammatically in Figure 2D, there are 16 possible directions (twice the number of distinct orientations) and four possible amplitudes (7.65, 14.14, 18.48 and 20 cm). The accuracy with which subjects locate the invisible target T1 can then be measured by comparing the theoretical vector T2 T1 with the final saccade leading to the presumed location. Statistical analysis demonstrates that both amplitude and direction errors are independent of the intended saccade amplitude. Instead, they are significantly correlated with the intended saccade direction. In particular, direction errors are larger for oblique movements than for horizontal and vertical ones. At any rate, errors seldomly exceed 10 degrees

and, more importantly, their distribution across orientation does not depend on the experimental condition. This is best appreciated in Figure 3 which displays the relation between theoretical and actual values of both amplitude and direction of the localizing saccade in the three experiments. The scatter of data points in both types of regression plots is mostly due to the fact of pooling the results of all subjects, and does not differ significantly across subjects. The visual impression that amplitudes are less accurately programmed than direction is largely a consequence of the scales involved.

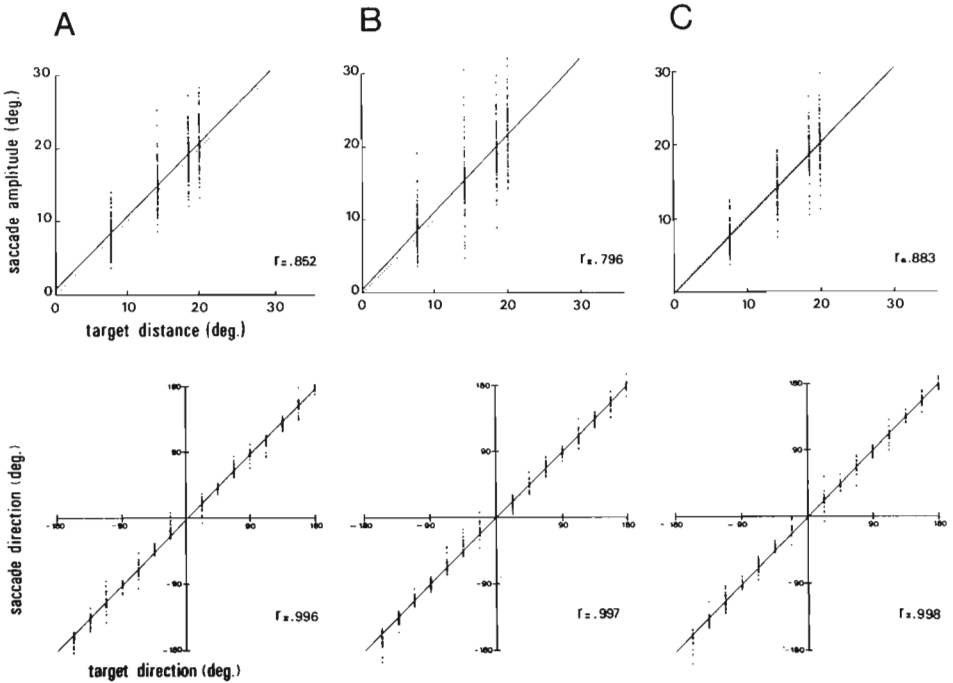


Figure 3.

Correlation analysis. Plots in A, B, and C summarize the results from the three experiments.

Upper plots : relation between the theoretical distance from T2 to T1 (abscissa) and the actual amplitude of the localizing saccade (ordinate).

Lower plots : Relation between the theoretical direction of the vector T2 T1 (abscissa) and the direction of the localizing saccade (ordinate).

Data for all subjects. Lines through the data points are linear regressions. Dotted lines indicate the ideal regression.

Figure 4 demonstrates this point on the basis of the results in two subjects. Each diagram in this figure represents in polar coordinates the joint variation of direction and amplitude errors of the final localizing saccade for each of the 16 possible directions. The radius of the reference circle is 10 degrees and its circumference is the locus of all saccades whose amplitude is equal to the distance between T2 and T1 (no amplitude error). Ticks on the circumference

indicate the 16 theoretical directions. The variability in both amplitude and direction are measured by the two orthogonal standard deviations around the means. For each direction, four saccades with different amplitudes are averaged. Thus, the fact that the variability of amplitude errors is small (about 2 degrees across subjects) demonstrates that these errors are almost constant and independent of the saccade amplitude. The figure illustrates in further detail the type of individual differences observed in our experiments. Subjects S1 and S2 were actually selected to illustrate the case of extreme undershooting and overshooting in the planning of the final saccade. However, over and above these differences, the data provide a strong confirmation that no significant difference exists in individual performances across experimental conditions. Finally, the polar diagrams illustrate the systematic (but idiosyncratic) distortions of the perceived location of the targets that were observed in all subjects.

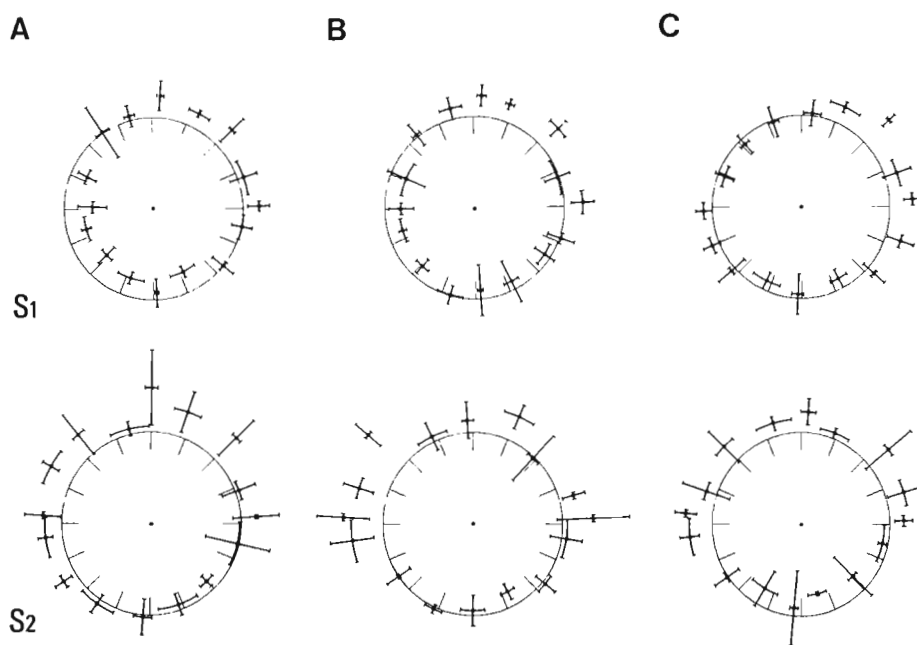


Figure 4.

Amplitude and direction error as a function of direction. Polar diagrams of the covariation of amplitude and direction errors for each of the 16 possible directions of the vector T2 T1. The circumference is the locus of all saccades with no amplitude error. Points within and outside the circumference correspond to undershoots and overshoots respectively. The scale is provided by the radius of the circle which is set to 10 degrees. Data points represent the average errors over the four saccades made by each subject in the indicated direction. Orthogonal bars encompass 2 standard deviations. Data in two subjects (S1 and S2).

DISCUSSION

Experiment 1 has demonstrated that the gaze can be directed to a briefly presented visual target even if the original viewpoint is changed between stimulus offset and saccade onset. While the localization of the invisible target under these conditions is not as accurate as in the usual one-step situation, this result is in keeping with the hypothesis set forth by several authors that retinal inputs are combined with extraretinal position information to provide the oculomotor system with an invariant spatial coding of visual stimuli. We actually maintain that, on several counts, the results improve on the supporting experimental evidence recently supplied by Mays, Sparks and coworkers (cf. Introduction). To begin with, end-point invariance is demonstrated in a far less contrived experimental situation. Both saccades from the fixation point to T2, and from T2 to T1 are normal movements, voluntarily triggered by the subject. The interval between saccades is relatively long (about 800 msec.). Thus, there can be no doubt that the second saccade is planned quite independently of the first one. This in turn rules out the hypothesis that end-point invariance in eye movements is achieved via a stiffness-setting mechanism as it has been suggested for other body segments (Feldman (1966)) and leaves the vectorial composition hypothesis as the only viable one. Notice that the intersaccadic latencies typically observed when the first saccade is electrically stimulated (Mays and Sparks (1980, 1983); Guthrie, Porter and Sparks (1983)) are intriguingly short (20 to 60 msec) for such a composition to take place. However, similar short latencies have also been documented in the spontaneous correction of goal-directed saccades (Viviani and Swenson (1982)). Finally, since both intermediate (T2) and final (T1) targets are precisely specified, it is possible to address the question of whether errors of localization are due to perceptual coding or motor commands (Viviani and Velay, in preparation).

Having confirmed that extraretinal information must necessarily come into play in the saccadic capture of visual targets, the question then arises of the nature of this information. The results of experiment 2 bear directly on this issue. Two putative sources of position sense are classically considered (Skavenski and Steinman (1970); Skavenski, Haddad and Steinman (1972)): proprioceptors in the extraocular muscles and corollary discharge. While the two possibilities are not mutually exclusive, the permanence of end-point invariance after deafferentation (ophthalmic nerve section) led Guthrie, Porter and Sparks (1983) to the conclusion that the corollary discharge associated with the stimulus-induced saccades is the major source of extraretinal information. The only difference between experiment 1 and 2 is that in the latter the gaze is displaced from the original fixation by a smooth pursuit, while in the former the gaze is displaced by a saccade. Thus, if we accept the suggestion of Guthrie, Porter and Sparks, the similarity of the results in the two experiments can be taken to imply that smooth pursuit commands give rise to corollary discharge just as saccades are supposed to do. If so, one would predict that the positional visual information and information provided by corollary discharge be somehow interchangeable. In particular, it should make no difference whether the final target T1 is localized visually or via a smooth pursuit eye movement. Experiment 3 affords precisely a test of this hypothesis. Since no significant difference could be detected between the performance in this experiment and that in the two previous conditions, it follows that the existence of a retinal input is not necessary to memorize the location of the final target. As suggested, different types of positional information can be both compounded and called upon interchangeably.

To conclude in a somewhat speculative vein, we would like to argue that such an apparent interchangeability of positional clues is hardly compatible with too "hardwired" a view of the sensori-motor coordination of eye movements (a view

for instance that would emphasize the rigidity and reflex-like nature of collicular interfacing). The data are instead more in keeping with the idea of a two-level hierarchical structure, where the lower level comprises an array of mutually independent sensory mechanisms, each measuring a different type of positional clues, and the upper, computational level marshals amodal information from the bottom to conjure up the desired spatial coordinates. As long as the head is fixed, spatial and cephalocentric coordinates coincide and only eye position clues are needed. However, the same general scheme can be generalized to include the possibility of head movements, by adding the vestibular and neck proprioceptive inputs to the array of sensory modules in the lower level.

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