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PATTERNS OF ACTIVITY AND BEHAVIOUR
OF CLETHRIONOMYS GLAREOLUS

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SUMMARY

The short-term activity rhythm of the bank vole, Clethrionomys glareolus, was studied in the laboratory.

Two methods of study were used: an automatic activity monitoring unit, which gave a continuous running length of 15m., covered by wire mesh, and a direct observation study which involved watching an individual in an observation cage.

In the automatic activity monitoring unit, eight voles were used, (six males and two females), one for each month from January to August 1967. They were all subjected to natural daylength, varying with season.

A well-marked four-hourly rhythm was noted. This rhythm was removed by the presence of an intermittent disturbance, i.e. a current of air. The rhythm returned when the disturbance was discontinued.

The rhythm was also removed when the uncovered unit was covered with brown paper strips to provide artificial ground-cover corresponding to that found in the wild.

No definite overall correlation between activity peaks and dusk or dawn were shown.

The direct observation study was made using the vole, (male), subjected to 12 hour daylength. The vole was observed in red light during the dark period. Activity patterns during day and night were similar. The individual was seldom "inactive" i.e. asleep or resting, for any length of time. It showed short periods of activity for a few minutes followed by a rest

period. Above-ground activities took up approximately 35% of both day and night activity.

It is suggested that the diel activity patterns of Clethrionomys glareolus may be more labile and variable than has previously been considered and that the short-term rhythm of 2 - 4 hourly periodicity which has been described in this species may be a reaction to abnormally uniform laboratory conditions, and that it is unlikely that such a rhythm could be maintained in the wild.

INTRODUCTION

This project was originally intended to be a comparative study of the agonistic behaviour patterns of Clethrionomys glareolus and Apodemus sylvaticus. These species live in close proximity to each other, though the former prefers denser cover. It was thought possible that there might be agonistic interactivity between them which might affect the distribution and population densities of the two species. These might be in the nature of direct attacks or alternatively signalled aggression. The importance of intra-specific social signals in small mammals has been well demonstrated by work on laboratory rats. Barnett (1965) has shown that in rats social stress can produce death in a subordinate animal with no major external injuries, where retreat is impossible. A. sylvaticus and C. glareolus are likely to meet frequently in the wild unless there are specially developed behaviour patterns which act to reduce such interspecific contacts. It was hoped to find out what occurred during these encounters and whether interspecific social signals were present.

Ashby (1967) has shown that A. sylvaticus does not show large population fluctuations from year to year with peaks and crash phases while C. glareolus does, behaving in this respect like Microtus sp. and Lemmus sp. It was hoped to discover whether agonistic behaviour acts as an intra-specific density-dependent control of population density in

A. sylvaticus but not in C. glareolus, using levels of aggression in males as the index of aggression. Sadleir (1965) has shown that an increase in aggressiveness in deermice (Peromyscus maniculatus) at the beginning of the breeding season normally greatly limits the rate of increase in population density of the species until the early autumn.

It was found that little work on the agonistic behaviour of either C. glareolus or A. sylvaticus had been published. Therefore, it was necessary to study the range of variation of the behaviour of individuals of the two species in an attempt to establish the normal limits of variability. During the initial stages of setting up this project it became clear that the conclusions drawn from the studies of other authors of trapping and automatic recording studies on the short-term activity cycles in these species did not seem to be borne out by personal observation, and it was decided to investigate them further. In the end this became the topic of investigation and the original aims were not pursued beyond a reconnaissance study.

Miller (1955) studied the feeding activity of Apodemus and Clethrionomys in response to different daylengths. He noted the amount of activity during the diel cycles with controlled daylengths of sixteen, twelve and eight hours duration respectively. He found that the activity rhythms of both species were readily modifiable according to the daylength and seemed to vary in pattern as a function of each

species nocturnal preferences and food habits. He found that the percentage of diurnal activity was greatest when daylength was 16 hrs. at 51.4%. Twelve hour daylength gave 33% diurnal activity and eight hours, 28%. The amount of activity outside the nest decreased considerably when food storing became part of the behaviour pattern of each species but was otherwise approximately constant. Apodemus began food storing when the daylength was reduced from 16 to 12 hrs., and Clethrionomys when it was decreased from 12 to 8 hrs. The corresponding reductions in amount of activity (mean number of active periods per diel cycle) were of the same relative proportion for each species. Progressive decreases in daylength produced parallel changes in nocturnal preference between the two species. He suggested that the role of activity rhythms in the community relations of Apodemus and Clethrionomys is a critical one and an important feature of any competition between them. His results were obtained by using a largely automatic recording system.

Brown (1956) showed by trapping that the above ground activity of Apodemus peaked during the night and Clethrionomys during the day. This activity pattern would effectively prevent many meetings between Apodemus and Clethrionomys individuals in the wild, though a considerable amount of dusk and dawn activity was noted for both species.

In order to discover whether meetings did occur in the wild and what effect, if any, they had on the behaviour of

each species, the author found it necessary to try to watch the animals in the wild. An area in Houghall Wood near Durham was selected, it was in a fairly open oak and beechwood on a slope giving a good view from the top, but containing a few patches of brambles to provide cover for the animals. After many days and nights observation, though no encounters between Clethrionomys and Apodemus were seen, some daylight activity by Apodemus was noted, i.e. coming to the mouth of the burrow and looking out then returning. In one case an Apodemus was seen apparently sunbathing in the area immediately in front of the burrow. This behaviour in a supposedly nocturnal animal was surprising. Clethrionomys were also observed moving about late at night.

The author began to suspect that small mammal activity patterns were, perhaps, more complex and variable than either Miller's or Brown's results indicated. Also, the experience of spending days and nights in the same environment as the small mammals studied showed that many random stimuli acted on them, which could affect their activity rhythms.

A particular aspect of activity reported by many observers e.g. Davis (1933), Hadfield (1940), Southern (1954), Miller (1955), was the short-term rhythm of between 2 - 4 hourly periodicity shown by many small rodents. Experience in the field watching Clethrionomys and Apodemus and the changing conditions of their environment led the author to doubt that a rhythm of this kind could be maintained in natural conditions.

The study by automatic recording methods while giving useful data on activity, provides information on only limited aspects of the animal's behaviour. The research on activity carried out by the author using such devices has therefore been supplemented by visual study of an individual's total behaviour to reveal in particular what the animal was doing during the long periods when, according to automatic recording data, it was inactive. In addition, when using automatic recording the habitat of the animal being studied was made as natural as possible to avoid the production of artefacts of behaviour resulting from abnormal environmental conditions.

The study was commenced using Clethrionomys owing to its greater docility and therefore ease of handling in comparison with Apodemus. At the beginning of the study, the work by St. Girons (1960, 1961) was unknown to the author as was that of Stebbins (1968) and Grodzinski (1963), but their work and that of others is considered in the Discussion. Had these results been known, however, the variability in small rodent behaviour would have been more immediately evident to the author.

The period of study was curtailed from three to one year during the course of the work, which made it impossible to carry out the parallel, comparative study with Apodemus which had been intended.

METHODS

Automatic Monitoring of Movement

Most laboratory studies of small mammal activity using automatic recording apparatus have been concentrated on monitoring the occurrence of feeding. For example, Miller (1955) and Stebbins (1971) used separate compartments for food and nesting space and monitored the number of journeys through the intervening door as an index of activity. The space allowed each animal has usually been very small and opportunities for activities not involving feeding, such as exploration, territory marking, searching for food, food storage and social interactions, etc. have been restricted. It was decided, therefore, to construct an automatic monitoring unit (which will be referred to as the "run") which would give the animal a much larger area in which to pursue its activities. In this way it was hoped that the results obtained might be more representative of the behaviour of animals in the wild.

The unit was designed to provide as much space as possible within the laboratory conditions available. It was constructed from mild steel to prevent the animals from gnawing their way out and was designed as a self-contained semi-portable unit to facilitate transport from one test area to another.

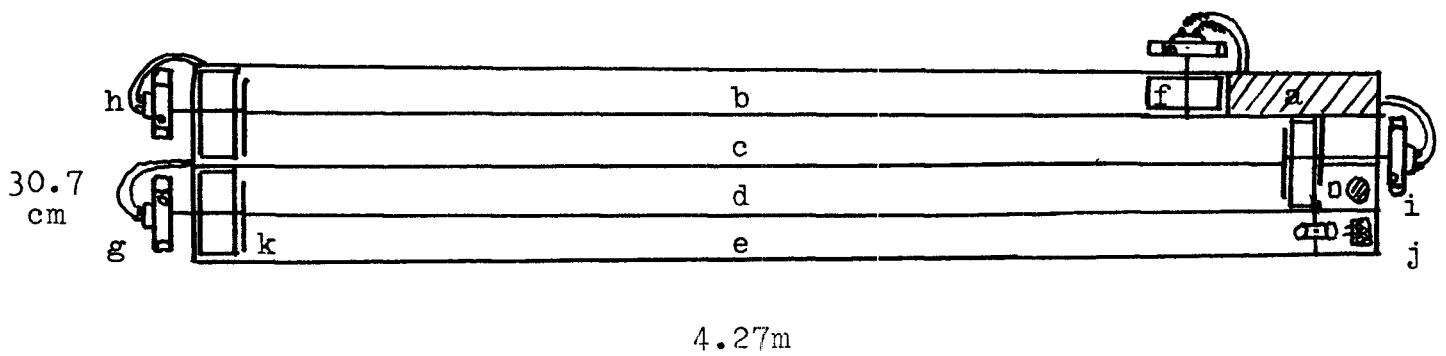
The design and measurements of the run were as follows:

A box was constructed 30.5 cm. wide and 4.27 m. long and with sides 7.6 cm. high. It was divided longitudinally into four lanes each 7.6 cm. wide. In the central partition there was a gap at one end of the run, and there was a gap in each of the two lateral partitions at the other end, which gave a continuous running length of 17.39 m. The food was placed at the end of lane four and the nest box at the beginning of lane one (see Fig. 1a). A Rustrak four pen continuous track recorder was used to monitor entry into and exit from each lane. In the definitive design of the recording unit, each pen was activated by a mercury switch operated by a tipping treadle which an animal had to cross on entering and leaving a given lane.

Each switch was "on" when the lane was occupied and "off" when the lane was vacated. Thus a trace was shown on the recording paper indicating the times of entry and exit from each of the four lanes.

The run as a whole was covered by $\frac{1}{2}$ inch weldmesh held in place by rubber loops to prevent the animal from escaping. The loops were made from $\frac{1}{4}$ inch square catapult rubber and protected underneath by 2 inch wide metal strips to stop the animal gnawing the rubber. The run was painted inside and out with black gloss polyurethane paint for ease of cleaning and to protect the mild steel from rust. The paint lasted very satisfactorily, being unaffected by prolonged urination. The nest box was provided with bedding material. Soon after

Fig. 1a. Diagram of Automatic Activity Monitoring Unit
(Top View)



- a nest box
- b lane 1
- c lane 2
- d lane 3
- e lane 4
- f perspex treadle
- g glass tube and ball-bearing
- h mercury switch
- i water point
- j grain point
- k shield to prevent vole getting under treadle

the first animal was introduced into the run, it became obvious that the test animal was not comfortable on the hard floor of the run. The animals paws became damaged through continual contact with the steel, so $\frac{1}{2}$ an inch deep sawdust was scattered in the run. The sawdust prevented such damage and also made it possible to observe territory marking since urination on the sawdust produced a yellowish stain which could easily be seen.

Design of Treadles and Associated Switches

A system of photocells was considered initially for this purpose, but it was decided that not only were they needlessly complex, but also that more information could be gained by the use of a mechanical system, which could be designed to switch either on or off according to which direction the animal was moving. It was then necessary to design a see-saw or tipping treadle system which was both sensitive enough to react to the small weight of the animal crossing it, and would also remain in either the up or down position after the animal had passed.

Various designs were tried out initially. The first treadles were made of aluminium but problems in fixing the centre spindle made it difficult to make the treadles balance properly. Mild steel sheet was then tried: spindles made of piano wire were easy to solder into position, but the treadle was then prohibitively heavy. This problem was overcome by substituting $\frac{1}{8}$ inch perspex for the steel sheet.

The piano wire spindles were heat-melted into the perspex and it was possible to obtain an exact balance while at the same time the overall weight was not excessive.

A device was then needed which would hold the treadle in either the "on" or "off" (up or down) position except when the animal crossed it. The first device tested consisted of small magnets attached to each end of the treadles. Corrosion due to urination coupled with the action of this device being hampered by becoming blocked with sawdust in the treadle compartment prevented this method proving successful. A second and more successful device tested was a glass tube attached to the side of each treadle containing a small steel ball-bearing and sealed at both ends. The ball-bearing ran down the tube when the treadle tipped and was effective in holding it in position. Various weights of ball-bearings were tried and a series appropriate for each treadle and each animal was determined.

The first switches tried were two simple contacts placed on the floor of the treadle compartment, a copper bar on the edge of the treadle completed the circuit as the treadle fell. This system worked well for some time but the contacts eventually became corroded by arcing and also became contaminated with sawdust, faeces and urine.

External switches were then devised which used the ball-bearing as the contact. These worked for some time but were not reliable, due again to spark corrosion.

Finally, mercury switches were tried which were found to be excellent, and operated without breakdown for the duration of the experiment. This type of switch uses tungsten electrodes and mercury as the contact, and work in a vacuum. They were ideal since they switch on and off by tipping.

A final problem was to devise a means of preventing the animal crawling under the treadle instead of over it, and thus reversing the trace. To do this the animal needed either to lift the treadle from the front or crawl underneath from the side. Both were prevented by placing guards at the entry and exit sides of the treadle, which fitted tightly against the sides of the run.

All the systems were designed so that they could be easily removed. This was made necessary, partly to ensure ease of replacement, but mainly to permit easy cleaning. The treadles quickly became fouled with urine and faeces as the animals used them as territory marking points.

Automatic Monitoring Feeding and Drinking

A method of recording feeding and drinking was devised which utilised the fact that a momentary break in the circuit from the treadle to the recorder would produce a single line "tick" on the trace which recorded the entry and exit into the run.

A small diameter perspex tube was placed at the end of lane four in such a position that the animal had to go

through it to reach the food container. The latter was designed to carry corn and deliver only one or two grains at a time by means of a simple gravity feed system with a grain-sized hole.

As the animal went through the tube it stepped on a pedal which, when carrying its full weight, activated a micro-switch which broke the current to the pen recording the presence of the animal in the lane in which the food container was placed. Since this occurred as the animal entered and left the container, the frequency with which each animal visited the food was given by halving the number of ticks on the trace. Visits to the water bottle were monitored in the same way in lane three. The drinking tube from the water bottle was inserted into the perspex tube which also contained a pedal operated micro-switch.

Difficulty was experienced in obtaining switches which were sensitive enough to register when the animal stepped on the pedal. This problem was overcome by counter-weighting the switch on the trigger. The size of the counter-weight used was adjusted to correspond with the weight of each animal. At first the activating pedal was placed close to the grain silo and the water tube. This resulted in the animal sitting on the pedal when eating and drinking, which caused confusion since the resulting trace on the record tape strongly resembled a short visit to the lane. This problem was overcome by increasing the distance

between the pedal and the tube. Problems also arose from material such as bedding and faeces becoming lodged under the pedal.

Investigation of the effects of disturbance and cover

The automatic unit described above was in operation from January to August 1967. Early test runs showed that a quite regular four-hourly rhythm in the degree of activity appeared in individuals kept in the unit. It seemed possible that this short-term rhythm was artificially produced by the voles reacting to the unusually uniform conditions in the unit and might be absent in nature. It was decided to test this hypothesis by simulating some aspects of a more natural habitat.

Firstly, in the wild, voles must be subjected to many different stimuli, most of them irregular in their timing sequence. In order to give the animals an environment which approximated more closely to nature, a form of disturbance was arranged. The stimulus was a current of air simulating a strong wind which blew for two minutes at a time down the length of the run. This was produced by an electric fan, which, because of its age, also supplied a certain amount of noise. This disturbance was given every three hours. It was therefore a regular stimulus lasting for two minutes. A disturbance at random intervals would have been more natural, but this could not be arranged with the facilities available at the beginning of the series of experiments. The three-

hourly periodicity was chosen to prevent the vole from relating the pre-existing four-hourly rhythm to that of the new stimuli. The effect of introducing and subsequently removing this form of disturbance was tested from January to April 1967 inclusive.

Another aspect of the normal environment of Clethrionomys that was not taken account of in the studies on activity by previous workers or in the initial experiments with the present run was the strong preference of a vole for moving under cover. In fact areas of open ground are usually avoided by this animal while providing excellent living space for Apodemus sylvaticus. Trapping in Houghall Wood just outside Durham (Ashby 1967) showed this clearly. The bare open run may have been rather a hostile environment for an animal which would normally move under dense ground vegetation.

A critical appraisal of the layout of the run and earlier records was made, coupled with a study of the degree of ground cover present in an area in Houghall Wood in which the density of C. glareolus was high. The percentage cover there was estimated using random quadrats in each of the two 25 metre square trapping grids and was estimated to be 65%. It was decided to place strips of brown paper over parts of each lane so as to give this degree of cover for the run as a whole. The opacity of the brown paper was such as to allow the penetration of roughly the same proportion

of the light falling on it as did the leaves of the ground vegetation in the wood. If time had permitted, this experiment would have been elaborated by changing the percentage cover as occurs in nature in spring and autumn to see the resulting effect on activity.

This experiment began in May 1967 and ran through to August of that year. Four voles were used in this series of experiments.

Preparation of Animals for testing in the Automatic Activity Monitoring Unit

Preliminary trials showed that considerable initial disturbance to an individual's activity rhythm occurred on its removal from the very constant environmental conditions of the animal house to those of the experimental unit in the laboratory. A small cage was prepared in a quiet corner of the laboratory, and the animal to be investigated was put in this transitional unit in an attempt to effect some acclimatisation to the laboratory conditions. The longest transitional period necessary was found to be two weeks before introduction to the automatic recording unit. This period was determined by checking results from animals placed in the run immediately on removal from the animal house.

Most animals during the initial series of pilot experiments found it difficult to operate the tipping treadle systems. They reacted to the closed treadle by trying to dig underneath it or by treating it as a closed entrance.

It therefore became necessary to introduce each animal to the treadle system before placing it in the run. A treadle with mercury-switch and ball-bearing tube closing mechanism was set up in the acclimatisation cage between the feeding area and the nesting box. The vole was encouraged to cross the treadle several times to show the animal that the unit would tip under its weight. This introduction to the treadle was also used to determine the size of the counterweights to be used in the run.

Since the run was a much larger area than the animals were used to in the standard laboratory cage, it was initially considered necessary to give each animal a day to acclimatise to the run, but it became clear from direct observations that the animals required only a short time to get used to the unit after acclimatisation to laboratory conditions in general had occurred. There was intense exploratory activity as in the smaller cages often lasting for 5 - 10 minutes. This did not show very strongly on the automatic recorder since the minimum discrete period noted on the recording tape was five minutes. An intense bout of activity for fifteen minutes will show the same trace as if the animal moves through the run three times, once every five minutes. The vole could make many trips through the run in each five minute period and only a single record be indicated on the tape. The five minute recording unit was chosen because of the large number of records involved, e.g.

for the whole eight month series about 70,000 individual five minute units had to be checked for the presence or absence of activity. Had a smaller time interval been chosen, e.g. one minute, then computer analysis would have probably been necessary. The author would like to emphasise that while the unit was running, other experiments were being undertaken at the same time, some of which do not come into this study and the tapes were not analysed after each diel cycle due to lack of time.

Each animal was introduced at twelve midnight to standardise the time that each experiment began. The first experiment was begun at this time and it was considered advisable to continue the same procedure.

Direct Observation of Total Activity

The main requirement was to make a unit in which the animal could be watched while it was unaware of the observer's presence. A cage measuring 46 x 32 x 32 cm. was constructed consisting of a wooden box with one side replaced by glass, illuminated from above through a small wire mesh lid by either white (tungsten) or red light.

A large expanded polystyrene box measuring 1.8 x 0.9 x 0.9 metres was built to act as light-proof container to the cage since it was not practical to black out the whole laboratory. The box was open at one end which rested over-hanging the edge of the bench. Its long axis was horizontal, and the cage was placed at the closed end. A roughly semi-circular

section was cut away from the bottom side at the open end to accommodate the upper part of the observer's body. A thick, black curtain was fastened to the top and sides of the open end of the box, loosely, so that the observer could tuck it round him to exclude extraneous light. Ventilation holes were cut in the top of the box and shielded to prevent light entering. Thus, the observer sat, with the upper half of his body in the box, in the dark, with the cage illuminated from the inside. Under these conditions the observer could watch the animal through the glass side of its cage without being seen by it. The cage contained sawdust 2.5 cm. deep, an exercise wheel, various small branches about 0.5 cm. in diameter and a water point. Food was scattered in the cage at random thus providing the animal with an incentive to collect it together into a store.

It was suspected at the beginning of these experiments that C. glareolus might be primarily nocturnal in its activity. It was therefore decided to try to reverse the diel cycle of the animal so that it would be active during the observer's day. This was done by giving the animal a continuously dark period of twenty-four hours following which alternating twelve hour light and twelve hour dark periods were begun. The vole was then left undisturbed for two weeks to settle down to its new light/dark cycle. The time switch used was of a simple on/off type, and it was not possible to incorporate a dawn and dusk effect in the

diel cycle. When observations were commenced, the cage was illuminated by red light during the "dark" period of the diel cycle on the assumption based on observations by Cleminson (unpublished) and Southern (1954, 1964) on the feeding of C. glareolus that voles are insensitive to the deeper red end of the light spectrum. Hence it was assumed that the experimental animal behaved in red light as it did in the dark. This made it possible to study behaviour over the whole of the diel cycle.

Initially, observations were hampered by the animal's habit of building an elaborate nest and hiding in it for most of the time. To overcome this problem, all the nesting material was removed and a small bottle approximately 7.6 cm. long with a neck of 2.5 cm. diameter was placed in the cage. A small amount of nesting material which the vole had already used, was placed in the bottle. The vole then readily nested in the bottle close to the glass front of the cage and was quite easy to observe within it at close quarters from outside the cage. The maximum length of time that continuous observation could be maintained with an adequate degree of concentration was about five hours. Many such periods exceeded two hours.

It soon became clear that total activity would have to be analysed into its various components to enable an organised written record to be made. Experience in watching individuals in the unit and in the field indicated that the

division of activity into the following twelve types could be observed and recorded competently by the observer using a written record sheet.

(a) Sleep

In this state the eyes are shut, the ears are folded down, the whiskers lie flat along the muzzle, and respiration is noticeably deeper and slower than normal. The animal is resistant to disturbance, responding only to quite strong stimuli such as loud taps on the cage, bangs outside and the observer sneezing.

(b) Doze

This is light sleep with ears erect, whiskers raised, but with respiration still fairly slow and the eyes closed. The animal can be awakened quickly by slight disturbance such as whistles, heavy breathing and even the act of writing with a fountain pen. It was found preferable to use a ball-point pen when recording activity as this seemed to cause the least disturbance. When dozing, the vole often moves its legs as if walking and occasionally makes grooming movements. It is tempting to suggest that during sleep like this the vole may be showing the equivalent to dreaming, i.e. R.E.M. sleep in man. This may indicate that during doze the animal is, at times, much more deeply asleep than at others, since in man and other mammals R.E.M. sleep is marked by a lowering of sensitivity to external stimuli.

(c) Resting

The eyes are open, ears are folded down (as opposed to erected in doze), whiskers usually half erect, respiration is normal. The animal is inactive and usually rests in the nest.

(d) Alert

In this attitude the eyes are wide open and prominent, ears and whiskers are fully erect, the animal stands high on front toes, breathes quickly and sniffs.

(e) Grooming

This includes washing, re-arranging fur and hunting for parasites. It usually occurred in the nest, often following sleep. The animal tended to return to the nest even for short grooming periods. All voles were observed to have parasites. Fleas could be seen moving about in the fur and occasionally mites were found attached behind the ears. The characteristic method of hunting for ectoparasites is to use both front paws to part the fur in a shallow V-shape and expose the parasite. Fleas were not always caught, but were always eaten when captured.

(f) Refecation

This consists of eating faeces. It was seen to occur only in the nest and usually occurred just after waking. The action was quite distinct from normal defaecation. The faeces were taken directly from the anus, chewed and swallowed. They were lighter in colour than

normal faeces and seemed softer. The animal was occasionally observed to drop the pellet and pick it up again.

(g) Defaecation

The animal, when defaecating when in the nest, removed each pellet of faeces from the anus as it emerged and threw it forwards away from the nest with a characteristic flicking upward movement of the head. The vole often defaecated in this manner outside the nest.

(h) Exploration

Each animal's initial exploration of a new cage was very pronounced and took between twenty to thirty minutes. The animal then gradually began to settle down and followed well-used routes to different parts of the cage, often going much further than necessary to reach an objective. The animal preferred to move close to the side of the cage under the branches provided. The vole was indifferent to the exercise wheel provided perhaps due to the large size of the cage.

(i) Drinking

The animal soon learned to drink from a glass tube attached to a bottle. It also took condensation from the glass or water droplets on the branches. Most of the food offered was dry, hence drinking may have been more pronounced than in the wild.

(j) Eating

Food was picked up with the teeth, transferred to

the front paws and then chewed. During the whole time of observation no animal was ever observed to use its fore-paws to pick up food and then transfer it to the mouth for chewing.

(k) Urination

It was done in a typical crouching attitude, tail slightly raised, hind feet apart. In males marking territories, the genital region was often rubbed in the area to be marked. This was also observed in the wild.

(l) Nesting

This activity consists of arranging and collecting nesting material. The material is collected in the mouth and carried to the nest where it is arranged by the animal placing the material in a pile, then sitting on top of the pile, turning round on it and making a hollow. More material is then collected from around the nest and pulled towards the animal. Males make rather perfunctory nests, often mere scrapes in the material. Females make complex ones using coarse material on the outer layers with softer material, e.g. cotton wool, in the centre. These often have a roof and two or three entrances and are constructed by pregnant females. The juveniles which are about to be weaned show typical nest-building activity, often adding to their mothers nest and improving it.

RESULTSAutomatic Activity Monitoring Unit

Eight voles were used in these experiments, which were divided into two series each of four months duration. In the first series, lasting from January to April, an attempt was made to discover the effect of disturbance on any rhythm which may have developed under normal laboratory conditions. Each experiment lasted four weeks. During the first week the animal was left undisturbed and in each case a four-hourly rhythm appeared.

During the next two weeks of each experiment a three-hourly disturbance was used, consisting of an air current produced by a fan as described on Page 17. The stimulus was removed during the final week to see if the short-term activity rhythm would be re-instated. Figs. 1 - 4 show the effect of this disturbance on the short term activity and of its removal. Figs. 30 - 33 give the numerical results for this series.

In the second series of experiments, from May to August, the effect of the absence and presence of cover was investigated using the technique described on Page 18. During the first two weeks a bare run was used with no cover and fixed food and water points. This gave ample time for a short-term rhythm to be developed. During the second two weeks the run was provided with 65% ground cover by using brown paper strips as described on Page 18, and food was

scattered randomly in the run to make foraging necessary to locate it. Figs. 5 - 8 show the effect of providing cover on the short-term rhythm and Figs. 34 - 37 give the numerical results for this series.

Fig. 9 shows the summated results for both series. Those for all the undisturbed weeks have been combined, which shows the four-hourly rhythm to its best advantage. The weeks concerned are week 1 during January to April and weeks 1 and 2 in May and June. The data for weeks 2 and 3 from January to April have been combined to show the effect of disturbance. The data for weeks 3 and 4 of May to August have been combined to show the effect of cover.

No animal was re-used for a second experiment.

Series 1 - Effect of Disturbance

1. JANUARY

The animal used was a male which had been kept for two months in constant conditions in the animal house. It was then given two weeks to become used to the laboratory in the acclimatisation cage and introduced to the automatic activity recording unit at 12.00 midnight on 1st January.

(a) Undisturbed Phase

The main characteristics during the first 24 hours were as follows: For the first five minutes, no activity was recorded then a long period of activity followed which, with two intermissions of 20 and 10 minutes respectively, lasted until 1.40 (see Page 141). Activity then ceased until 3.55

When another session of activity of eight periods of five minutes occurred finishing at 4.35. Activity began again at 7.25 and lasted until 9.30. There were two short breaks adding up to six five-minute periods giving a total of nineteen active periods between these two times. Activity next occurred from 11.30 till 12.00 and from 12.10 till 12.30. During the afternoon activity occurred from 13.45 to 14.15, 15.00 to 15.30, 15.45 to 16.25 and then continued with short rest periods until 18.15. The next and final activity period of the first 24 hours began at 20.25 and ended at 20.55. An indication of a four-hourly rhythm was already appearing, as can be seen from the diel cycle diagrams in the appendix (Page. 141).

The second day commenced with activity from 00.00 to 00.20 (see Page 141). Further activity periods occurred from 1.20 to 1.25, 2.10 to 3.30 and 4.15 to 4.45. There was a quiescent period until 7.00 following which there was a total of 15 five-minute activity periods in the next two hours. As on the first day, the vole was again active at midday, this time for a total of nine five-minute periods, but during the afternoon activity was less intense than on the first day, being recorded from 13.00 to 13.15, 14.40 to 15.05, 16.00 to 16.30 and 17.35 to 18.05. A rest of one and a half hours then occurred followed by activity from 19.40 to 20.20 and then a long rest of 3 hrs. 25 mins. until 23.45 when three active periods were recorded.

On the 3rd January, total activity increased slightly from 91 five minute periods on the 2nd to 102 activity periods, with activity centring around 3.00 to 4.00, 8.00 to 9.30, and 12.00 to 13.00. Then there followed a period of prolonged activity from 14.30 to 21.05 (see Page 142). A similar lengthy activity period occurred on the 1st. At this time, the vole seemed to be preferring to be active during the evening period, but overall this can be seen on the graph in Fig. 1.

On the 4th the four-hourly rhythm can be seen well in the diel cycle diagram (see Page 142), activity centring around 00.00, 4.00 to 5.00, 7.00 to 9.00, 11.00 to 12.45, 16.00 to 18.00, and 20.00 to 21.00. There is still evidence here of more activity in the evening but this was diminishing in extent; there were 29 active periods on the 4th between 16.00 and 21.00 as compared with 35 periods on the 3rd.

The 5th and the 6th day also show the short-term rhythm well, suggesting that the animal was becoming well adjusted to the laboratory environment and the unit. The overall rhythm can be seen best in the graph on Fig. 1 which shows the percentage of time in each hour that the animal was active (solid line) for 1st to 7th January. Well marked peaks at midnight, 4.00, 8.00, 12.00 and 16.00 are present. The increased activity of the animal during the evening period shows the peak at 18.00 hrs. flattening and extending to 17.00. The percentage time active also does not fall as low

during the troughs at 15.00, 18.00 and 19.00 hrs. as it did during the morning. The midnight peak is also followed by higher percentage activity during the trough from 1.00 to 3.00 hrs. than the troughs occurring during the day. This does show that this vole showed a preference for dusk and nocturnal activity under the conditions in the laboratory at that time.

(b) Disturbed Phase

The three-hourly disturbance was begun on the 7th of the month, the first such period being applied at midnight (00.00 hrs). No activity occurred until 1.25, and then nine 5-minute periods followed during the period up to 2.20. No further activity then occurred until 6.10. This represents a large drop in activity (over 50%) in comparison with the previous undisturbed morning, e.g. on the 6th 20 5-minute activity periods were recorded from 00.00 to 6.00 hrs. The four-hourly rhythm is no longer evident in the diel cycle diagram for 7th January (see appendix), activity subsequently occurring at 6.10 - 6.20, 7.20 - 7.59, 9.20 - 10.20, 12.00, 13.15 - 15.20 and 18.20 - 20.00 hrs. No period of activity exceeded four 5-minute units and none of them occurred at the times during which the stimulus was applied. The total number of 5-minute activity periods on the 7th were 40 as compared with 78 activity periods on the 6th. This indicates that the stimulus strongly affected the amount of activity as well as its distribution over the diel cycle.

On the 8th, 42 5-minute activity periods were recorded and these were again grouped in a manner which showed no short-term rhythm. They centre around 1.00 - 2.00, 5.00, 7.00 - 9.00 hrs. and then four short periods of activity totalling 19 5-minute units during the period from 14.00 - 19.00 hrs. At 18.00 hrs. the vole was out in the run when the fan started blowing. It stayed in the run for three 5-minute units in the same lane and then returned to the next box and did not emerge again until 1.40 on the 9th. The total amount of activity per diel cycle began to increase back to the normal level on the 9th with 57 activity units being recorded on that day. This tendency continued with occasional lapses until the end of the disturbed phase. Indeed, on the 16th, for example, a total of 74 activity periods were recorded.

The graph of the disturbed phase in Fig. 1 shows quite clearly that the well established four-hourly rhythm was disrupted during this phase as a whole, although on the 16th there were signs of such a periodicity with activity maxima about 24.00, 4.00, 8.00, 12.00, 16.00 and 20.00 hrs. Though there seems to be little rhythmical activity at all in this series, the vole may have been becoming used to the disturbance during the later stages, shown by the results for the 16th.

(c) Recovery Phase

On the 19th, the disturbance ceased at 00.00 hrs. The immediate effect of its removal can be seen by referring

to the diel cycle diagram for this day. There were 80 5-minute activity periods here, but they show a different distribution than for the 18th. Long periods of inactivity occurred between 5.00 and 7.00, 9.00 and 13.00, and 14.00 and 16.00 hrs.

Throughout this week activity gradually increased, e.g. on the 25th there were 82 5-minute activity periods and on the 26th 80 5-minute activity periods. The four-hourly rhythm also began to re-appear with peaks centring around 24.00 - 1.00, 3.00 - 4.00, 7.20 - 10.00, 12.00 - 13.00, 16.00 - 18.00 and 19.00 - 20.00 hrs. On the graph of $\frac{1}{6}$ time active in each hour (Fig. 1, dotted line) the four-hourly rhythm is not so definite as in the undisturbed phase but shows definite signs of returning. The peak at 4.00 hrs. is shifted back to 3.00 hrs. however, and the 12.00 and 20.00 hrs. peaks are rather low.

Recording of vole 1 was ended on the 29th and a new animal introduced to the unit on February 1st.

2. FEBRUARY

A female was used which proved to be pregnant although the fact was not known at the time of introduction to the run. The elaborate nest building activity produced by this animal towards the end of the experiment led to an investigation into her condition, and she subsequently produced a litter. This was most unexpected since, at this time of year females are not usually pregnant.

On 21st February a power failure to the recorder due to a faulty connection occurred for almost the whole diel cycle making this day's tapes useless.

(a) Undisturbed Phase

After two weeks acclimatisation to the laboratory, the vole was introduced to the run on February 1st at midnight (00.00 hrs.). In this individual's case the primary short-term rhythm of four-hourly duration was not so clearly established before the disturbed periods began as in the case of the individuals tested in January, March and April. The tapes were not analysed until the end of the month and it was only then that the effect of its pregnancy was noted. On the graph in Fig. 2, this can be seen as a shift of emphasis in activity from four-hourly periods, seen in the male during the undisturbed phase in January (see Fig. 2) and likewise in March and April (see Figs. 3 - 4), to a series of roughly three-hourly ones and then back to a four-hourly period, e.g. activity peaks at 00.00, 4.00, 7.00 - 8.00, 11.00 - 12.00, 15.00 and 20.00 hrs. giving a periodicity of 4 hrs., 3 hrs., 3 hrs., 3 hrs., 5 hrs., and 4 hrs. The time between 15.00 and 20.00 hrs. shows a relatively high level of crepuscular and nocturnal activity in each hour.

The diel cycle diagrams for the undisturbed period show that the emphasis on evening activity was not constant for each day. For example, on the 1st, four-hourly periodicity occurred from 00.00 - 1.30 hrs., 4.00 - 5.00, 7.00 - 8.20, and 11.00 - 12.20 hrs. There was then quite extensive activity from 14.15 - 20.20 hrs. totalling 35 5-minute periods.

On the 5th, however, a four-hourly rhythm is beginning to appear throughout the 24 hours and from 14.00 - 20.00 hrs. only 15 activity periods were recorded. On the 6th, 22 activity periods were recorded during the same part of the diel cycle and the trend towards a four-hourly periodicity continued though there was still no clear minimum at 18.00 hrs.

(b) Disturbed Phase

Disturbance began on the 7th and the vole showed a very clear reaction to this. The number of active periods dropped to a mere 28 compared with 70 active periods for the previous 24 hours.

On the 8th the number of activity periods began to increase again totalling 50 on that day and reaching 80 by the 13th (only four diel cycles later) thus exceeding on that day the number for the 6th, the last undisturbed diel cycle. An interesting pattern of activity periods began to appear on the 17th, they are arranged in approximately three-hourly groups with the peaks of activity falling at or just before the time of the disturbance. On the 19th this is shown particularly well. It may be that the vole was beginning to use the disturbance as a timing device, but if the results from 17th to 22nd are grouped together there is no definite evidence of a three-hourly rhythm, so these may be isolated instances of rhythmical activity.

The graph showing the % time active per hour (Fig. 2) shows that the short-term rhythm which may have been appearing

was removed during the disturbed phase. One peak stands out in this graph at 17.00 hrs., and a smaller one at 24.00 hrs.

(c) Recovery Phase

On the 23rd the disturbance was discontinued. The record suggests that the stimulus may have become an expected event in this particular animal's activity pattern since on the 22nd, 87 activity periods were recorded compared with 61 on the 23rd. This shows a reduction of 26 activity periods in one diel cycle on removal of the stimulus.

Since the four-hourly rhythm had not fully developed in the first part of the experiment, it was perhaps unlikely that one would be set up following the period of disturbance. It can be seen from Fig. 2 and the diel cycles for the 23rd to 28th February that in fact no recognisable rhythm re-appeared.

3. MARCH

(a) Undisturbed Phase

The male used was introduced to the run at midnight (00.00 hrs.) on the 1st of March after two weeks acclimatisation in the laboratory. It showed a good four-hourly rhythm from the 1st to the 6th of the month (see Fig. 3). It was a docile animal, and became used to the run very quickly. In Fig. 3 the percentage of time that this animal was active in each hour of the diel cycle can be seen. The undisturbed phase is shown as a solid line. Peaks at 4.00, 8.00, 12.00, 20.00 and 24.00 hrs. are well shown with a smaller peak at 15.00 - 16.00 hrs.

(b) Disturbed Phase

This phase was begun on March 7th. The introduction of the three-hourly stimulus has a marked effect on short-term activity rhythm of the vole. The four-hourly rhythm broke down (broken line, Fig. 3, Page 44). During this phase activity peaked at 7.00 hrs. with small peaks at 14.00 and 19.00 hrs.

On the 7th total activity dropped from 85 activity periods in the previous diel cycle to 30 periods (see diel cycle diagrams). On the 8th, activity began to increase to 41 activity periods and on the 9th, 47 periods were recorded. By the 14th March the effect of the stimulus was becoming less evident as activity periods reached 71. During this diel cycle the animal was active in every two-hourly period except between 14.00 and 16.00 hrs., and 22.00 and 24.00 hrs.

By the 22nd of the month, the vole was active for 87 periods, 2 periods more than on the 6th March, the diel cycle before the disturbance began.

(c) Recovery Phase

The three-hourly disturbance was removed on the 23rd. The noticeable drop in activity from 87 periods on the 22nd to 67 on the 23rd shows that the lack of stimulus did have an effect. However, the drop in activity was not as marked as in the January

Activity began to increase steadily reaching 90 periods on 27th and the four-hourly short-term rhythm began to re-appear.

This can be seen as the dotted line in Fig. 3.

4. APRIL

(a) Undisturbed Phase

A male was used as in January and March. It was introduced to the run at midnight (00.00 hrs.) on April 1st after two weeks acclimatisation in the laboratory as described previously. The first weeks results show that a good four-hourly rhythm had developed, (Fig. 4, solid line). This vole had a high activity level with 108 activity periods on its second diel cycle in the run, followed by 103, 95, 96 and 89 5-minute units for the consecutive days.

(b) Disturbed Phase

The disturbance began at 00.00 hrs. on the 7th. As in the previous experiments the initiation of the disturbance caused a strong change in the four-hourly rhythm. Activity dropped from 89 periods on the 6th to 44 periods on the 7th. The following day, on the 8th, there were two periods of activity from 24.00 hrs. on the 7th to 3.00 hrs. totalling ten five-minute units. There were six activity periods from 4.45 to 5.15 hrs. Activity was beginning to increase but not until 18.00 hrs. on the 8th was the animal outside the nest when the fan was blowing. The activity period concerned lasted from 18.00 to 18.05 hrs. From then on until 00.20 hrs. on the 9th the animal stayed in the nest indicating perhaps that it had been frightened by being caught outside the nest during the disturbance with no cover, as in the case of the

January animal on the 8th January (see Page 144). On the 9th the switch controlling the fan did not operate at 09.00 hrs. and gave no disturbance at that time, and then failed to switch off the disturbance commencing at 12.00 hrs. which ran continuously until 15.00 hrs. As can be seen from the diel cycle diagram for the 9th April, this caused considerable modification in activity. There was no activity at all from 12.00 to 19.00 hrs. on that day. The readings from 8.00 to 10.00 hrs. on that day are not reliable since one of the pens in the recorder jammed and indicated a continuous activity. The timing of the disturbances was re-set and the recorder repaired at 18.00 hrs. on the 9th.

On the 10th activity began to increase again after the strong reduction in the previous diel cycle. There was considerable activity from 01.30 until 4.30 hrs., possibly indicating increased foraging in response to the lack of activity in the latter half of the previous diel cycle. On the 11th the animal seemed to be associating its activities around the three-hourly disturbance until 12.00 hrs., when there was a massive drop in activity - none being recorded until 19.30 hrs., and the subsequent activity period consisted of only five 5-minute activity units. This was the only activity recorded between 12.00 and 24.00 hrs. on the 11th. On the 12th, the 5-minute activity periods began to increase; this trend continued for the next five days, e.g. on the 14th there was a total of 85 activity periods.

On the 18th the number of 5-minute activity periods dropped drastically to only 28 - possibly indicating that the animal was unwell, although there may have been an external disturbance which was not recorded.

(c) Recovery Phase

On the 19th the fan was discontinued and the cycle diagram shows a considerable change in activity distribution for that day; possibly in reaction to this but also to the drop in activity during the 18th. A long period of exploration or foraging occurred from 03.05 to 05.05 hrs. on the 19th. The drop in activity which occurred from 05.05 till 24.00 hrs. on the 19th (compared to records like 17th, 16th etc.) was continued into the 20th.

The four-hourly rhythm showed definite signs of re-appearance (dotted line, Fig. 4), but the 20.00 hrs. peak did not return.

FIG. 1 EFFECT OF DISTURBANCE ON SHORT-TERM ACTIVITY RHYTHM (6').

- Undisturbed phase (1st - 6th)
- - - Disturbed phase (two minutes fan stimulus) (7th - 18th)
- Recovery phase (undisturbed) (19th - 24th)
- ↕↕ Sunrise at beginning and end of month
- ↕↕ Sunset at beginning and end of month
- X Two minute disturbance timing

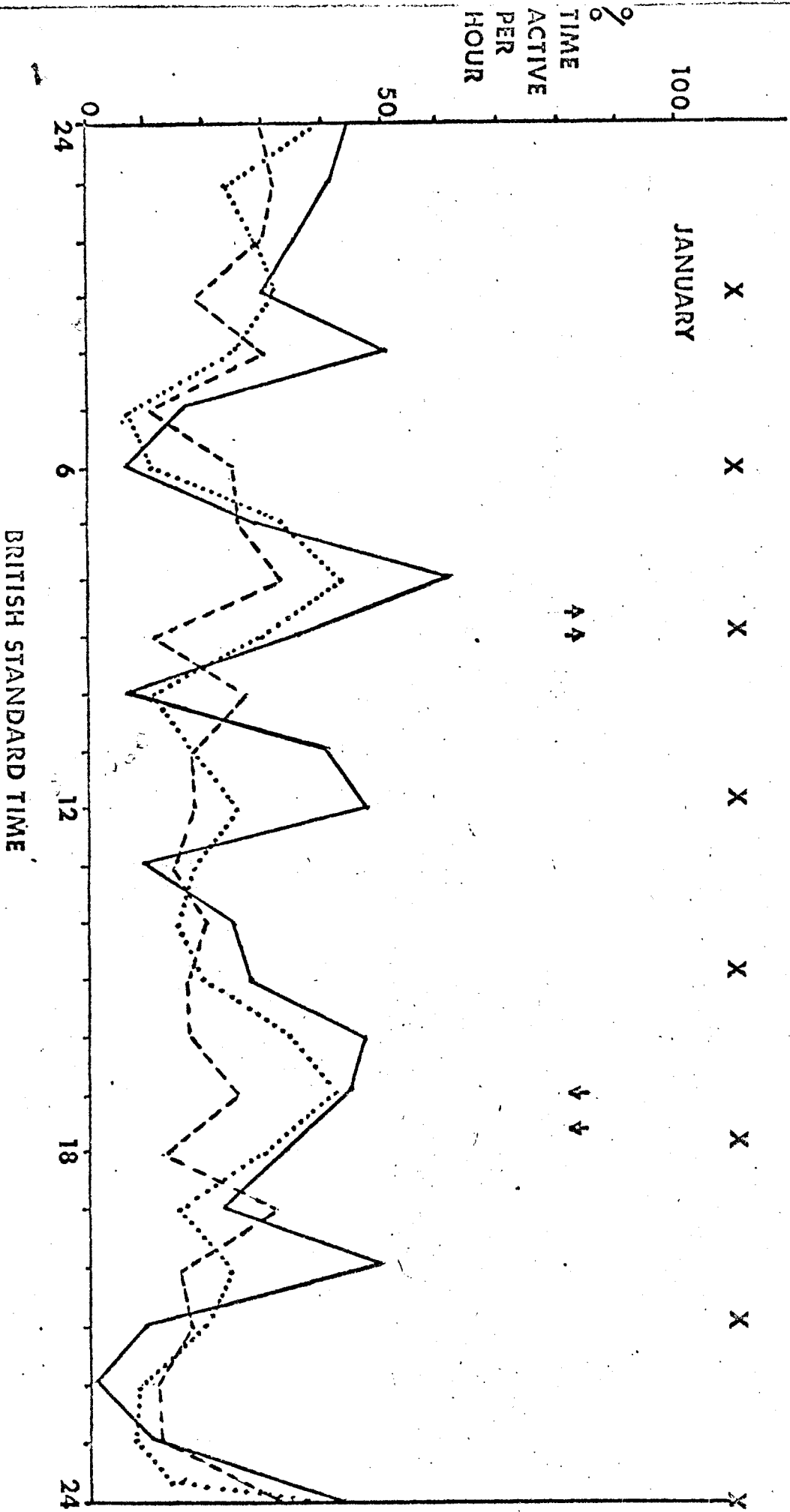


Fig. 2 Effect of disturbance on short-term activity rhythm (22)

- Undisturbed phase (1st - 6th)
- - - - Disturbed phase (two minutes fan stimulus) (7th - 22nd)
- Recovery phase (undisturbed) (25th - 28th)
- ↑ ↑ Sunrise at beginning and end of month
- ↓ ↓ Sunset at beginning and end of month
- X Two minute disturbance timing

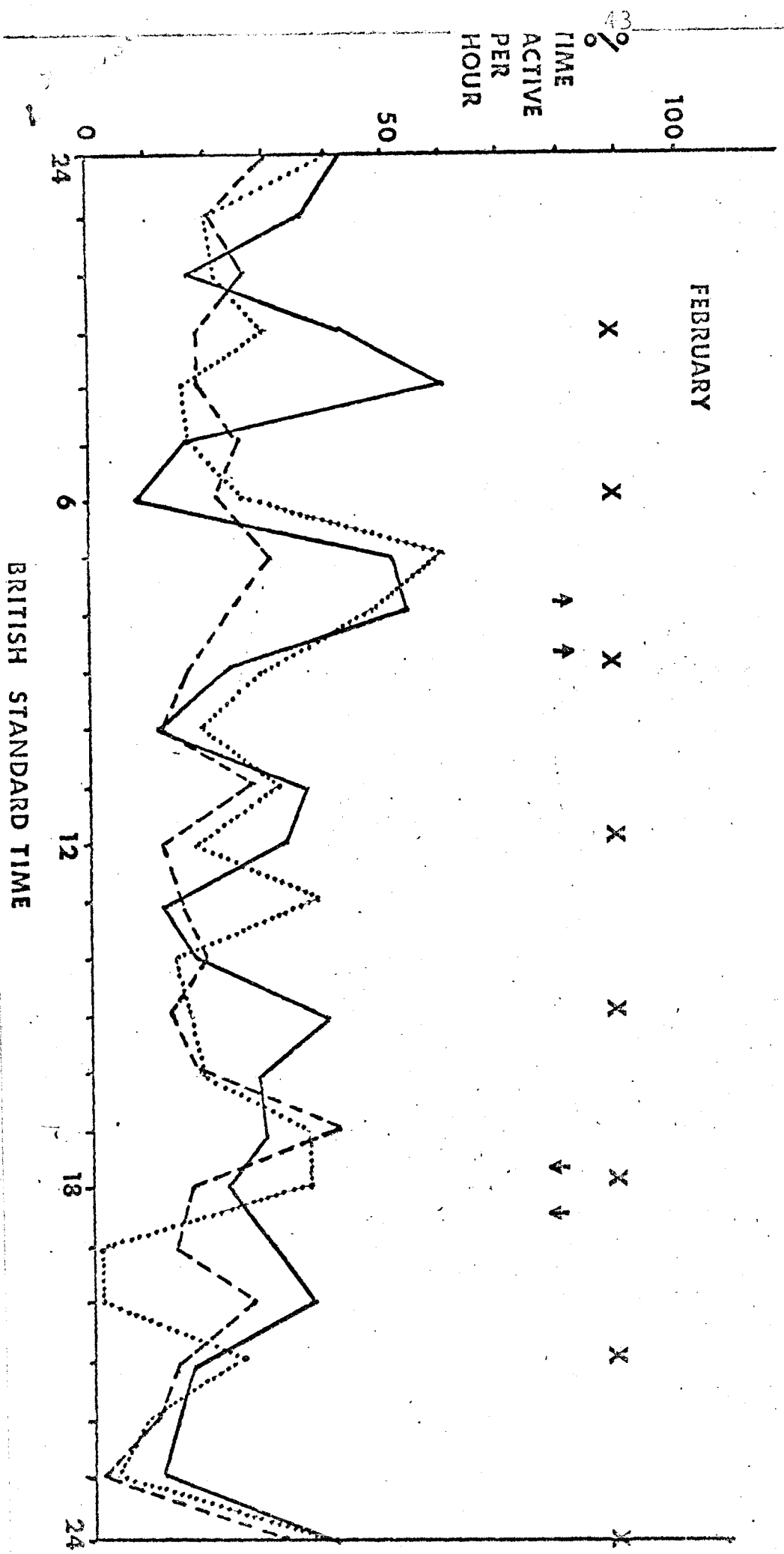


Fig. 3 Effect of disturbance on short-term activity rhythm (6)

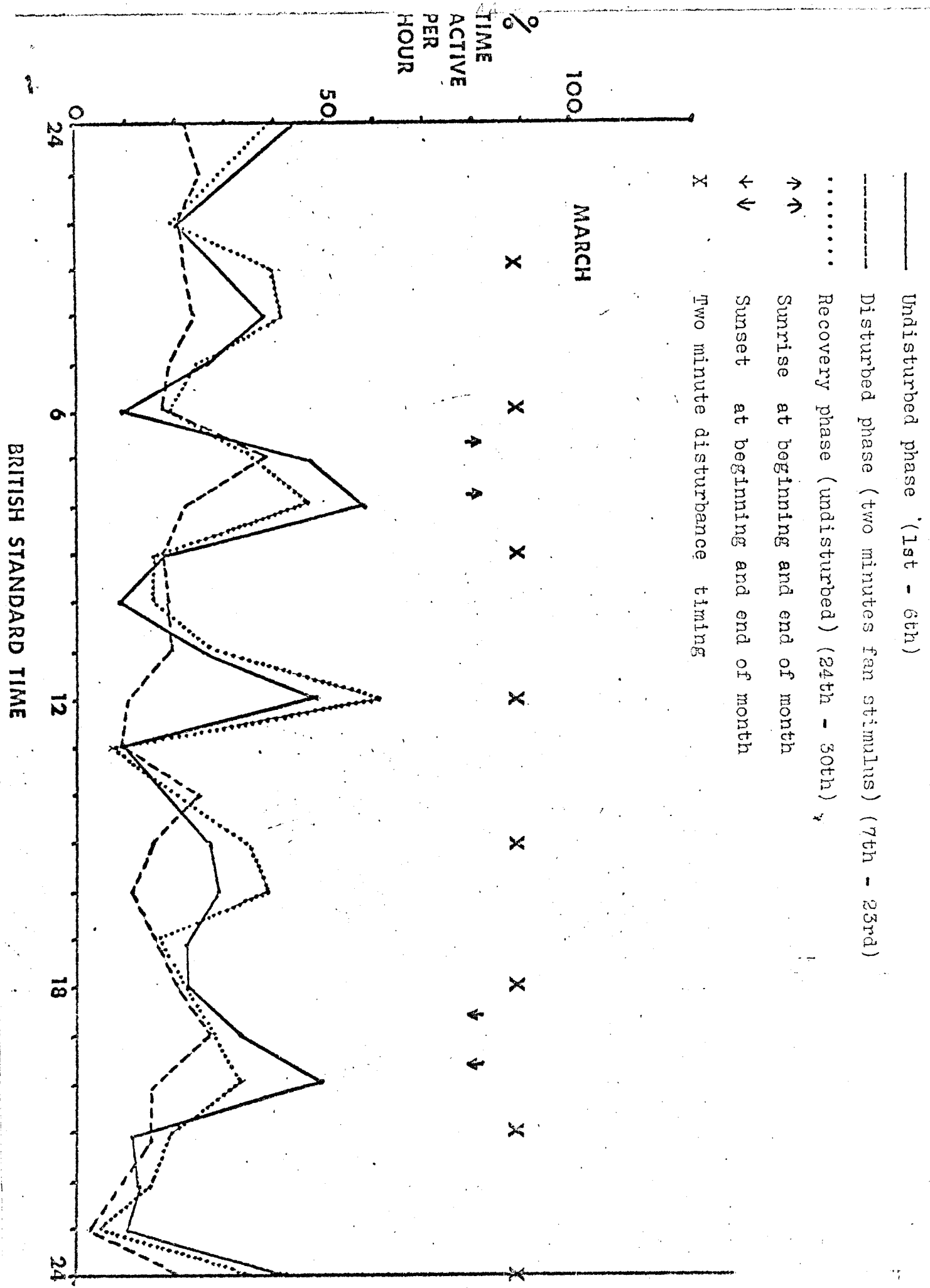
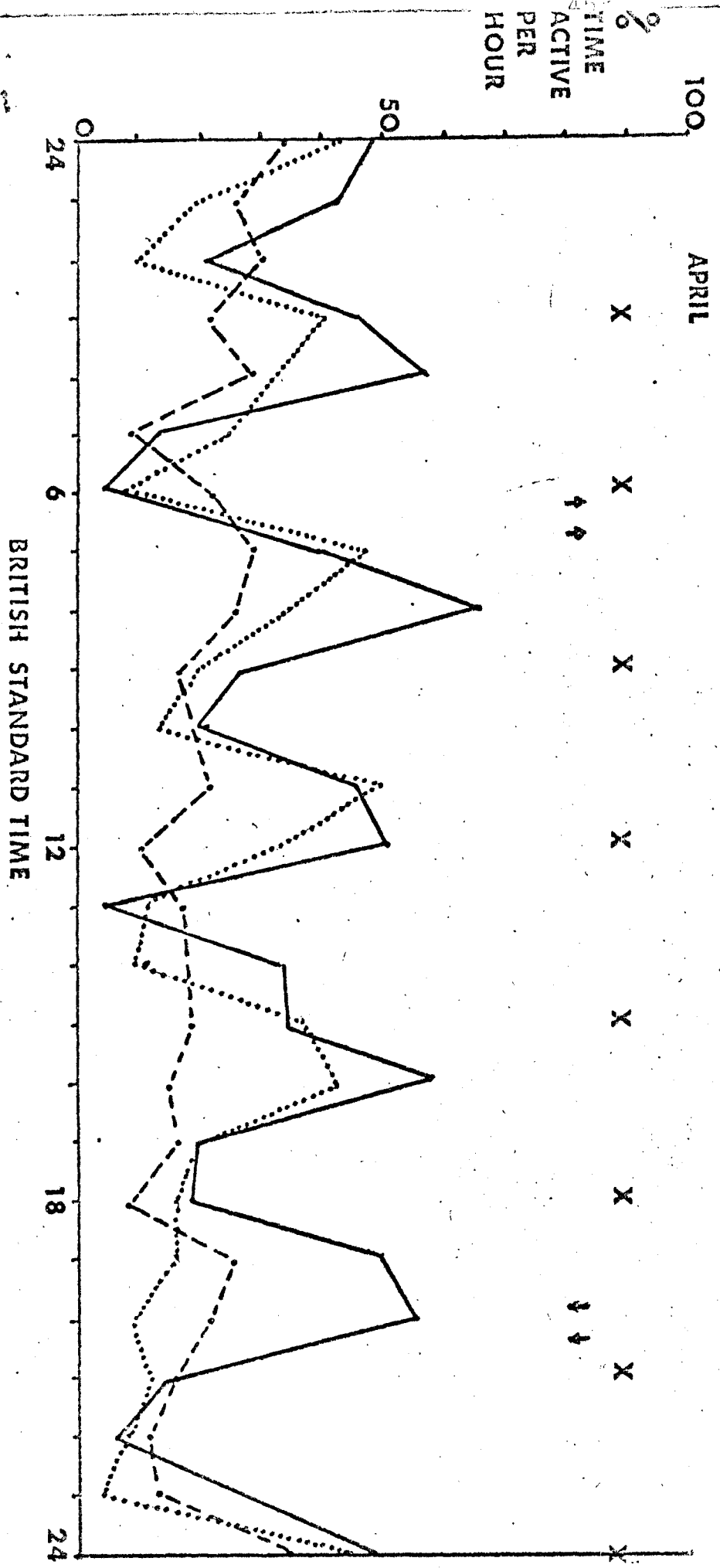


Fig. 4 Effect of disturbance on short-term activity rhythm (♂)

- Undisturbed phase (1st - 6th)
- - - Disturbed phase (two minutes fan stimulus) (7th - 20th)
- Recovery phase (undisturbed) (21st - 29th)
- ↑↑ Sunrise at beginning and end of month
- ↓↓ Sunset at beginning and end of month
- X Two minute disturbance timing



Effect of Disturbance on total amount of activity per day

- A - Undisturbed
- B - Disturbed
- C - Recovery

Fig. 4a

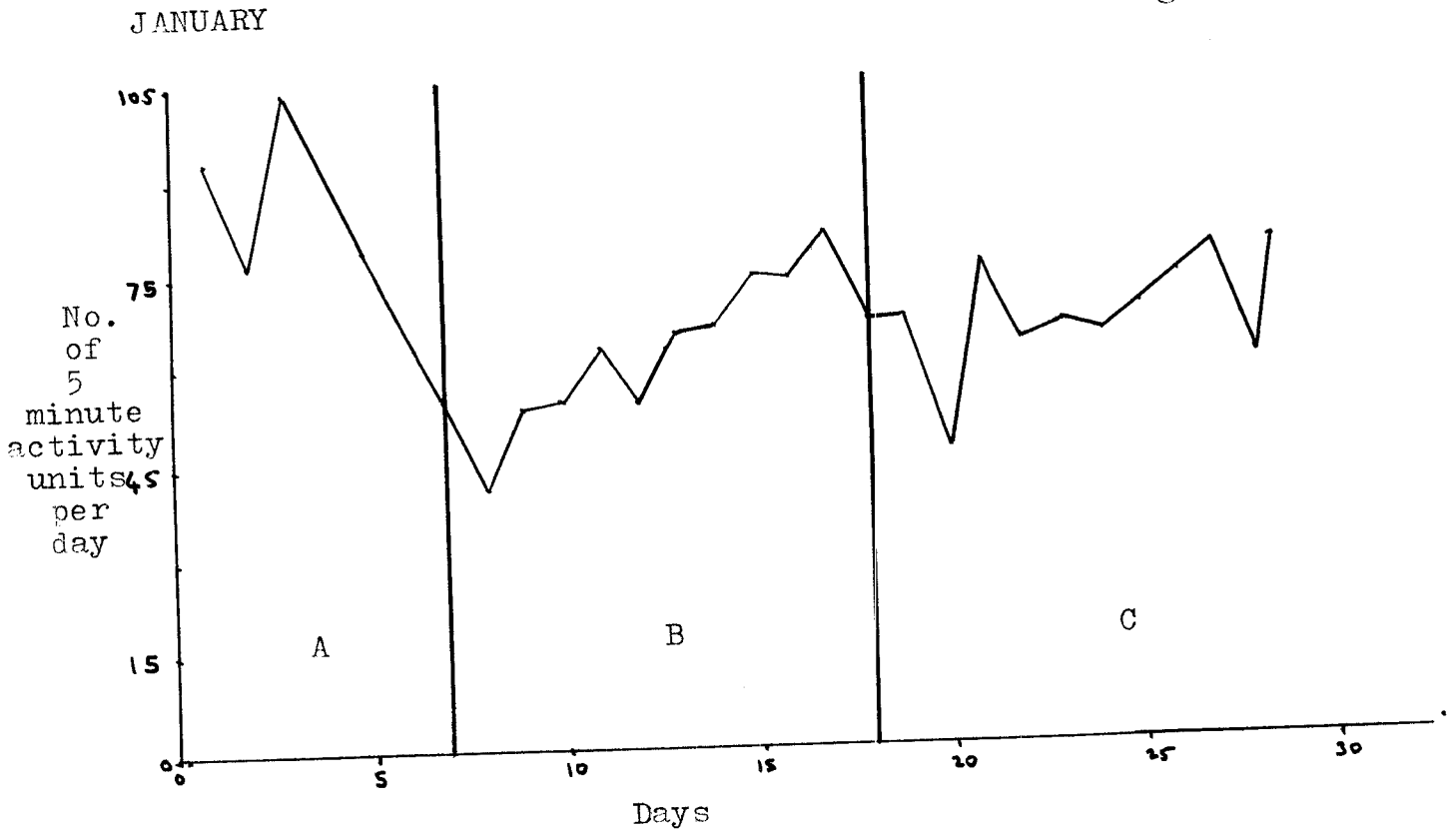
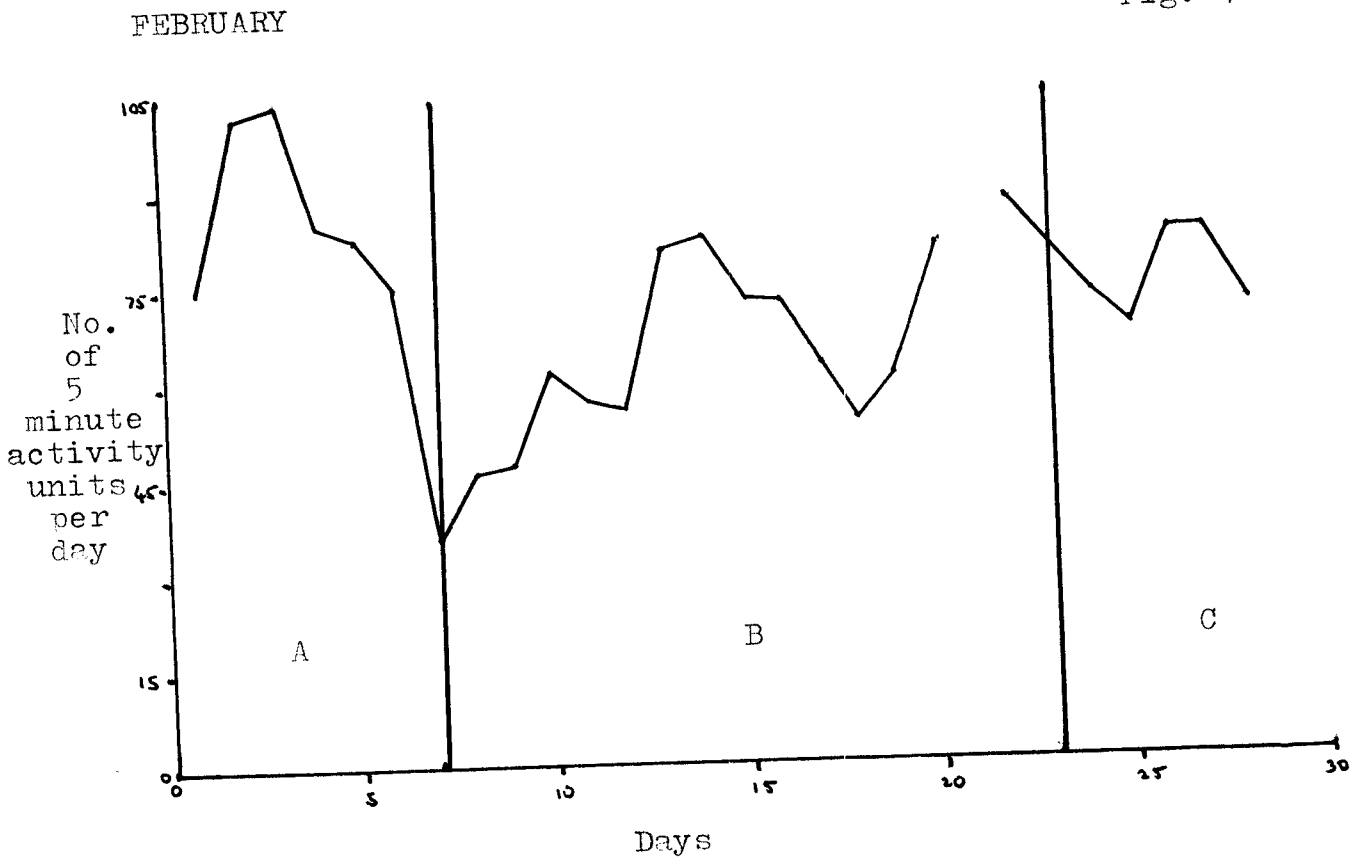


Fig. 4b



Effect of Disturbance on total amount of activity per day

- A - Undisturbed
- B - Disturbed
- C - Recovery

Fig. 4c

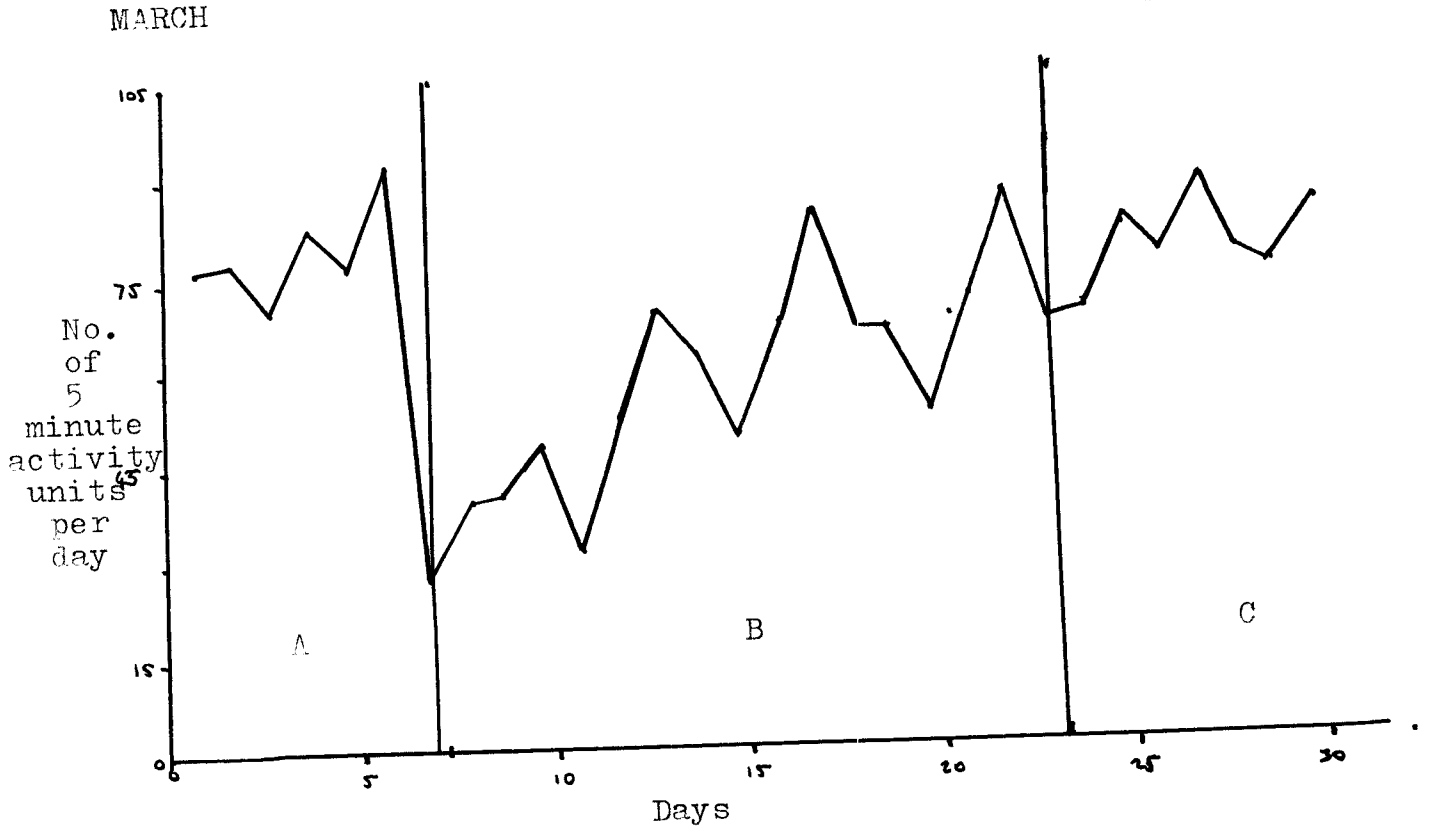
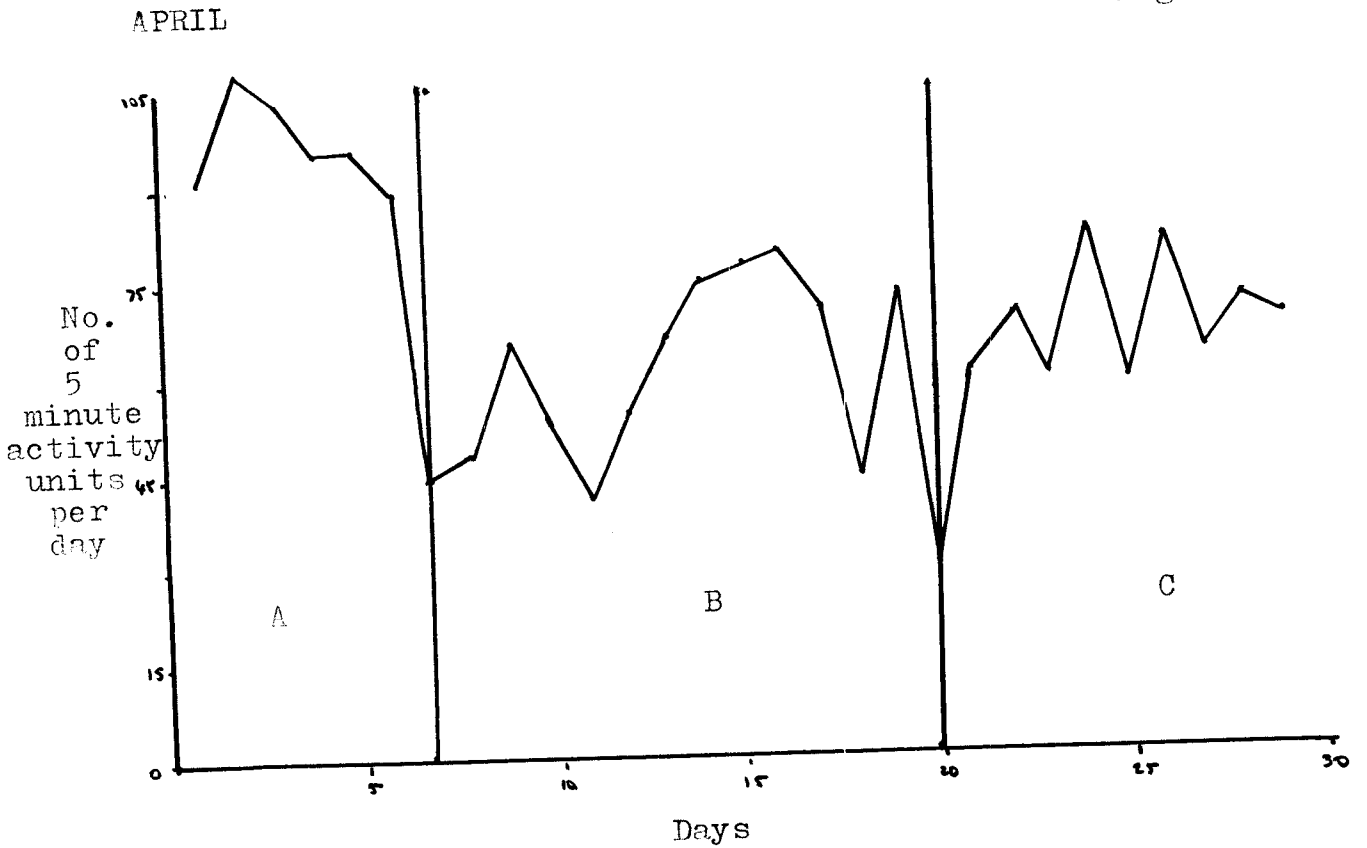


Fig. 4d



Series 2 - Effect of Increasing Cover

This series of experiments, carried out from May to August inclusive, was intended to determine the effects of cover and the need to search for food, on the short-term rhythm. At this stage no attempt was made to differentiate between these two factors, for example, by scattering the food in the run with no cover provided, since this was an attempt to make the situation in the run approximate more closely to natural conditions.

Four voles were used in this series of experiments, one animal for each month. Each animal was given two weeks (14 days in May and July and 15 days in June and August) to allow short-term rhythms to become well established. In June and August an extra day was added to the uncovered phase by mistake. Cover, in the form of brown paper strips laid along the run, was then provided for the remaining days of each month and food was scattered as randomly as possible at irregular intervals in the uncovered portions of the run.

1. MAY

(a) Uncovered Phase

The first animal in this series was a male and was introduced to the run at midnight on 1st May, 1967, after two weeks in the acclimatisation cage. During the uncovered phase a good four-hourly rhythm appeared which can be seen well in Fig. 5 (solid line), and in the diel cycle diagrams for May in the appendix.

(b) Covered Phase

The run was covered for this phase as described in the Methods on Page 18, on the 15th May. The short-term rhythm began to break down and eventually vanished (see Fig. 5, dotted line). During the first week of the covered phase overall activity increased, for example, there were 422 activity periods in the last week of the uncovered phase and 629 activity periods in the first week of the covered phase. In fact, this vole showed a consistent increase in activity during the covered phase, 1,395 activity periods compared with 922 for the uncovered phase. The difference is exaggerated since the covered phase lasted three diel cycles longer than the uncovered, but it is still marked, i.e. to make up the difference in activity periods the vole would have had to have been active for about 157 periods each day for three uncovered days. The numerical results for May can be seen in Fig. 34.

During the first week of the covered phase the vole began to build subsidiary nests in the lanes of the run and during the second week it began to spend all its time in the run and virtually abandoned the nest box. This made interpretation of the record tapes difficult since previously the end of an activity period could be traced back to track 1 on the tape as the animal returned to the nest box. The problem was overcome by frequently checking which lane contained the main nest area. This was done as carefully as

possible in order not to disturb the vole.

2. JUNE

(a) Uncovered Phase

In June a female was used. This animal was not pregnant. It was introduced to the run at midnight on June 1st after two weeks in the acclimatisation cage. A good four-hourly rhythm appeared during the first fifteen days as can be seen in Fig. 6 (solid line). The build up of this rhythm can be seen from the diel cycle diagrams for June in the appendix and also from the numerical results for June (Fig. 35). For example, on the 1st activity peaked at 00.00 hrs., 3.00 hrs., 8.00 hrs., 12.00 hrs., 16.00 hrs., and 20.00 hrs. During the uncovered phase there was a small additional activity peak at 10.00 hrs.

(b) Covered Phase

As in the previous experiment during this phase, the four-hourly rhythm eventually disappeared (see Fig. 6, dotted line), for example, on 16th (the first covered diel cycle), activity peaks were at 00.00 hrs., 4.00 hrs., 7.00 hrs., 11.00 - 13.00 hrs., 16.00 hrs., and 19.00 hrs. By the 30th the vole was most active at 1.00 hrs., 5.00 hrs., 11.00 hrs., and 16.00 hrs. (see Fig. 35 and diel cycle diagrams), showing no definite rhythmical activity.

During the covered phase overall activity increased during the early morning and at mid-day, and was reduced in the afternoon, i.e. from 3.00 hrs. to 6.00 hrs during the

uncovered phase 187 activity periods were recorded, compared with 266 activity periods for the same period during the covered phase. At mid-day, from 11.00 hrs. to 13.00 hrs., there were 128 activity periods during the uncovered phase and 199 during the covered phase. Both these sets of figures show a definite increase in activity at these times during the covered phase. The reason for the increase is difficult to deduce from the evidence available. However, in the last two weeks of June, a period of hot weather caused the overall temperature in the laboratory to increase during the afternoon which may have caused a drop in the vole's activity at this time.

As in the first experiment (May) of this series, overall activity increased in the covered phase to 1376 activity periods from 1045 in the uncovered phase.

3. JULY

(a) Uncovered Phase

In July another male was used. The procedure for introduction and acclimatisation was the same as described in the previous experiments. During the uncovered phase an excellent four-hourly rhythm developed as can be seen from Fig. 7 (solid line). Its development can be seen from Fig. 36 and the diel cycle diagrams for July. For example, on the 1st, activity peaked at 00.00 hrs., 4.00 hrs., 10.00 hrs., 12.00 hrs., and 16.00 - 17.00 hrs. By the 14th, the last day of the uncovered phase activity peaked at 00.00 hrs.,

Effect of Increasing Cover on total amount of activity per day

E - Uncovered
F - Covered

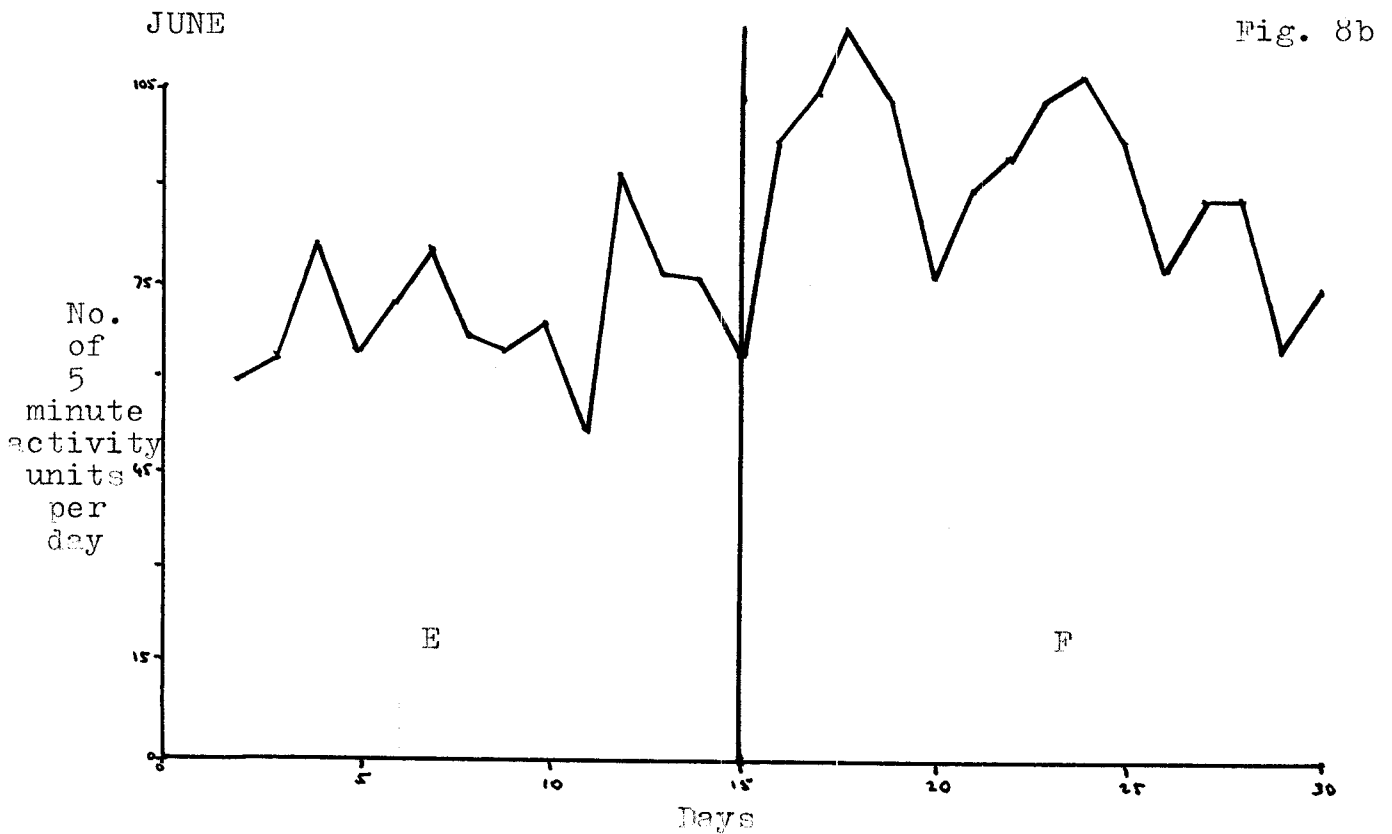
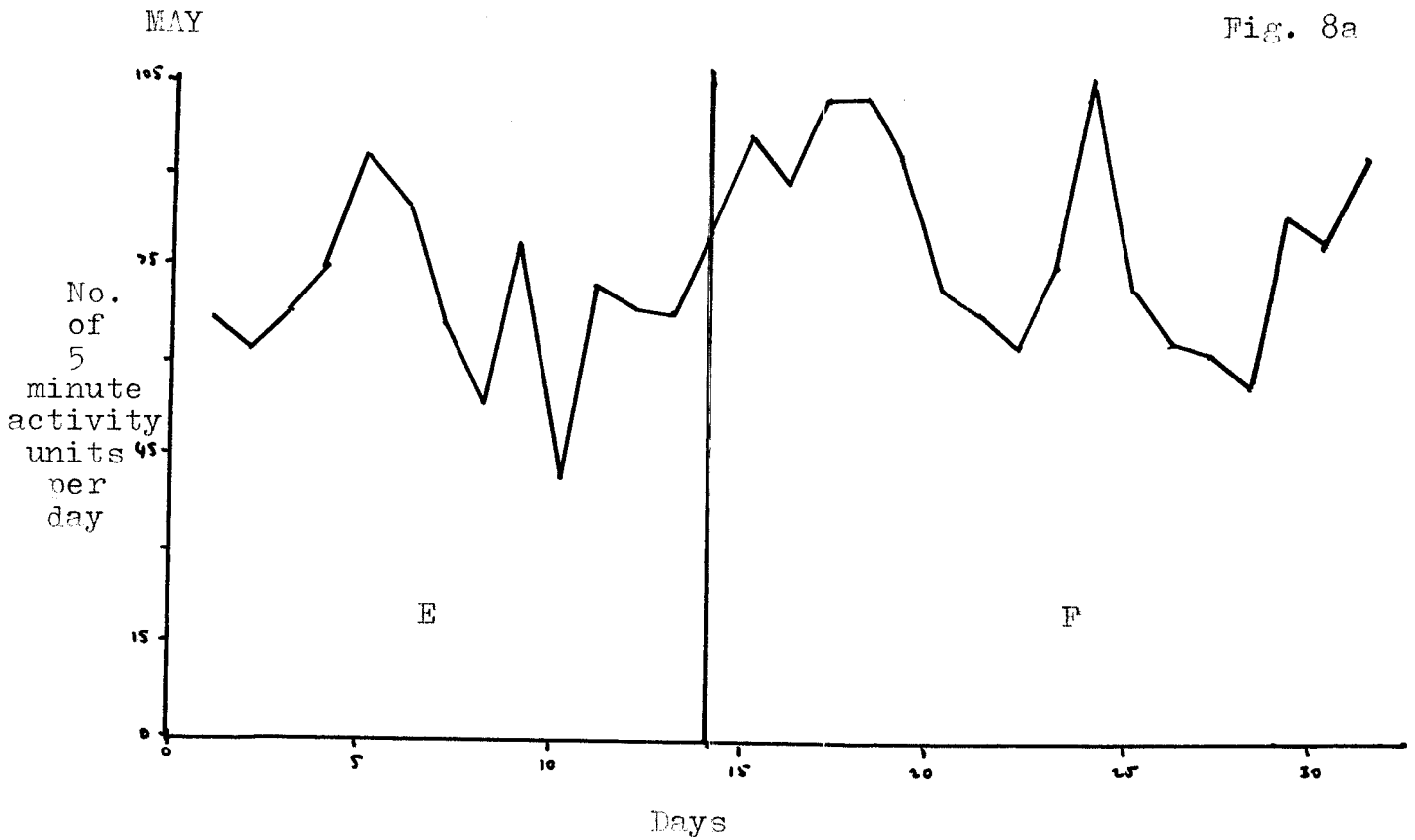


Fig. 5 Effect of cover on short-term rhythm (81)

- Uncovered unit (first two weeks) (1st - 14th)
- 65% ground cover provided (second two weeks) (15th - 31st)
- ↑ ↑ Sunrise at beginning and end of month
- ↓ ↓ Sunset at beginning and end of month

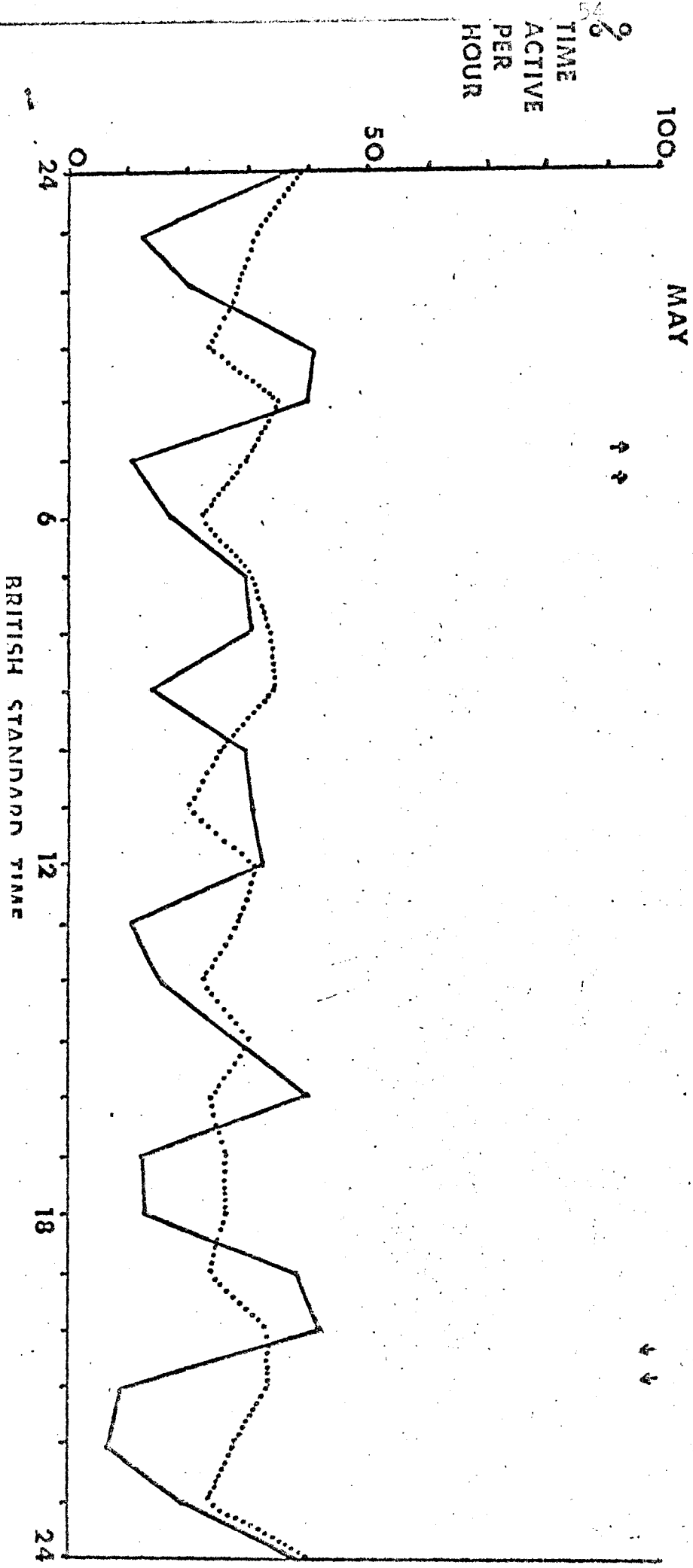


Fig. 6 Effect of cover on short-term rhythm (2)

- Uncovered unit (first two weeks) (1st - 15th)
- 65% ground cover provided (second two weeks) (16th - 30th)
- ↑ ↑ Sunrise at beginning and end of month
- ↓ ↓ Sunset at beginning and end of month

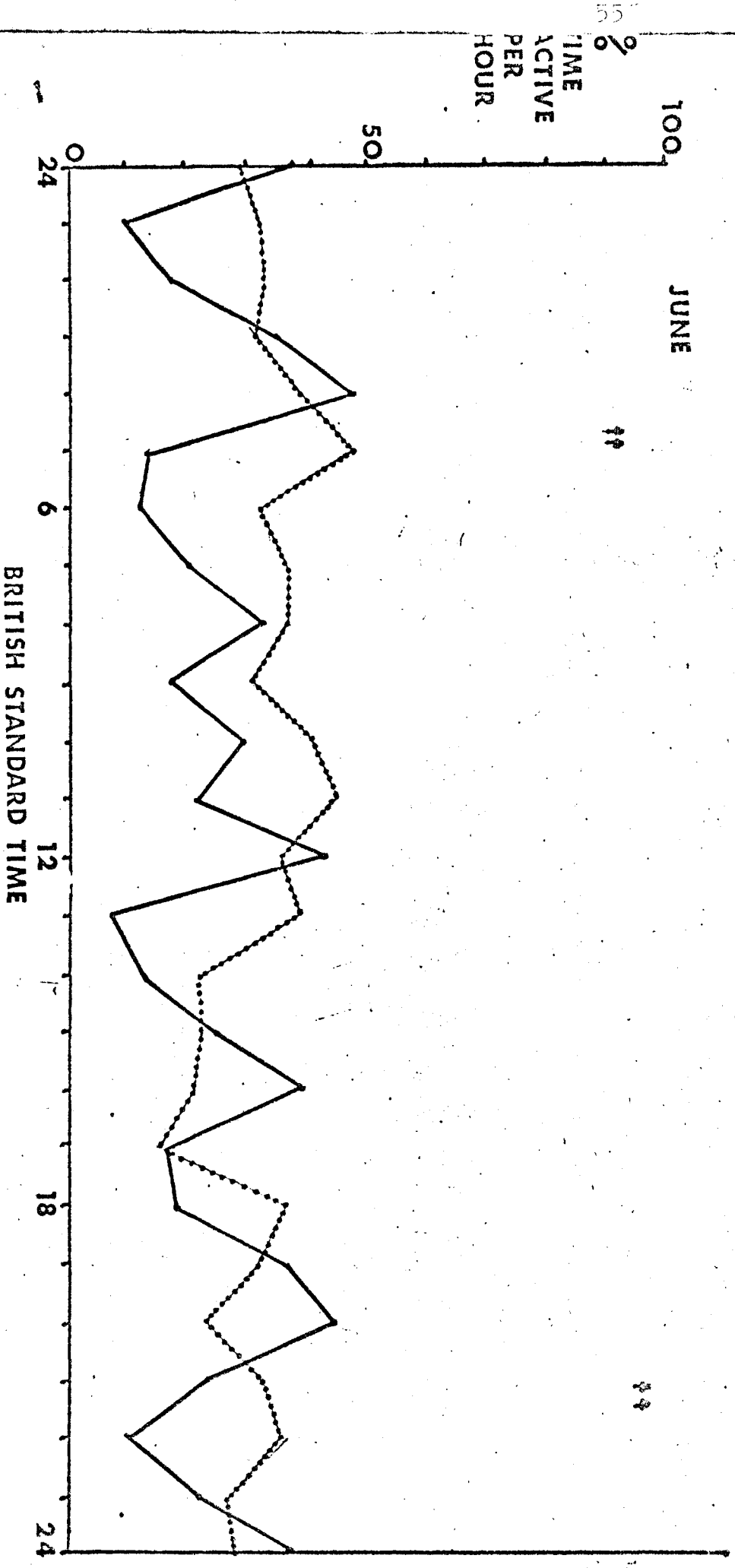


Fig. 7 Effect of cover on short-term rhythm (87)

- Uncovered unit (first two weeks) (1st - 14th)
- 65% ground cover provided (second two weeks) (15th - 30th)
- ↑ ↑ Sunrise at beginning and end of month
- ↓ ↓ Sunset at beginning and end of month

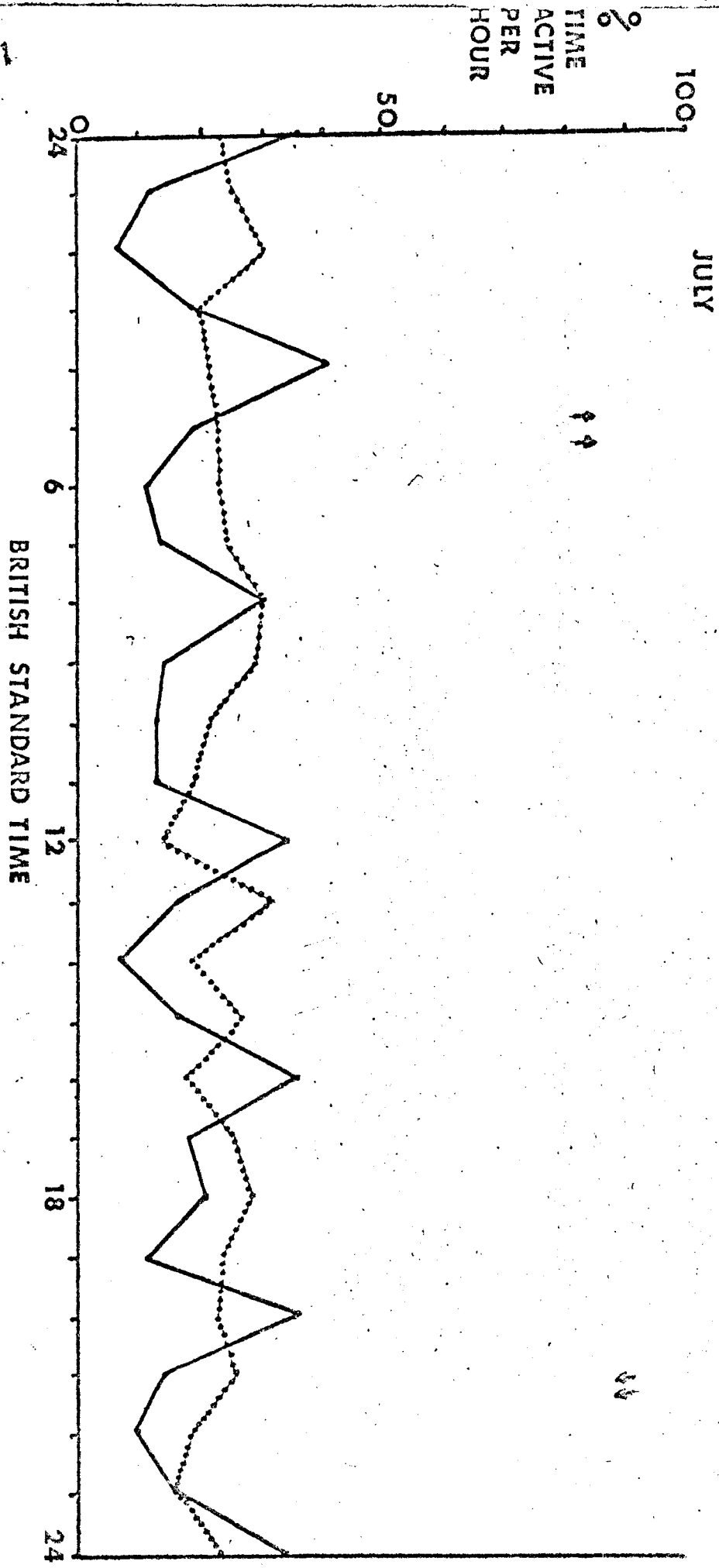
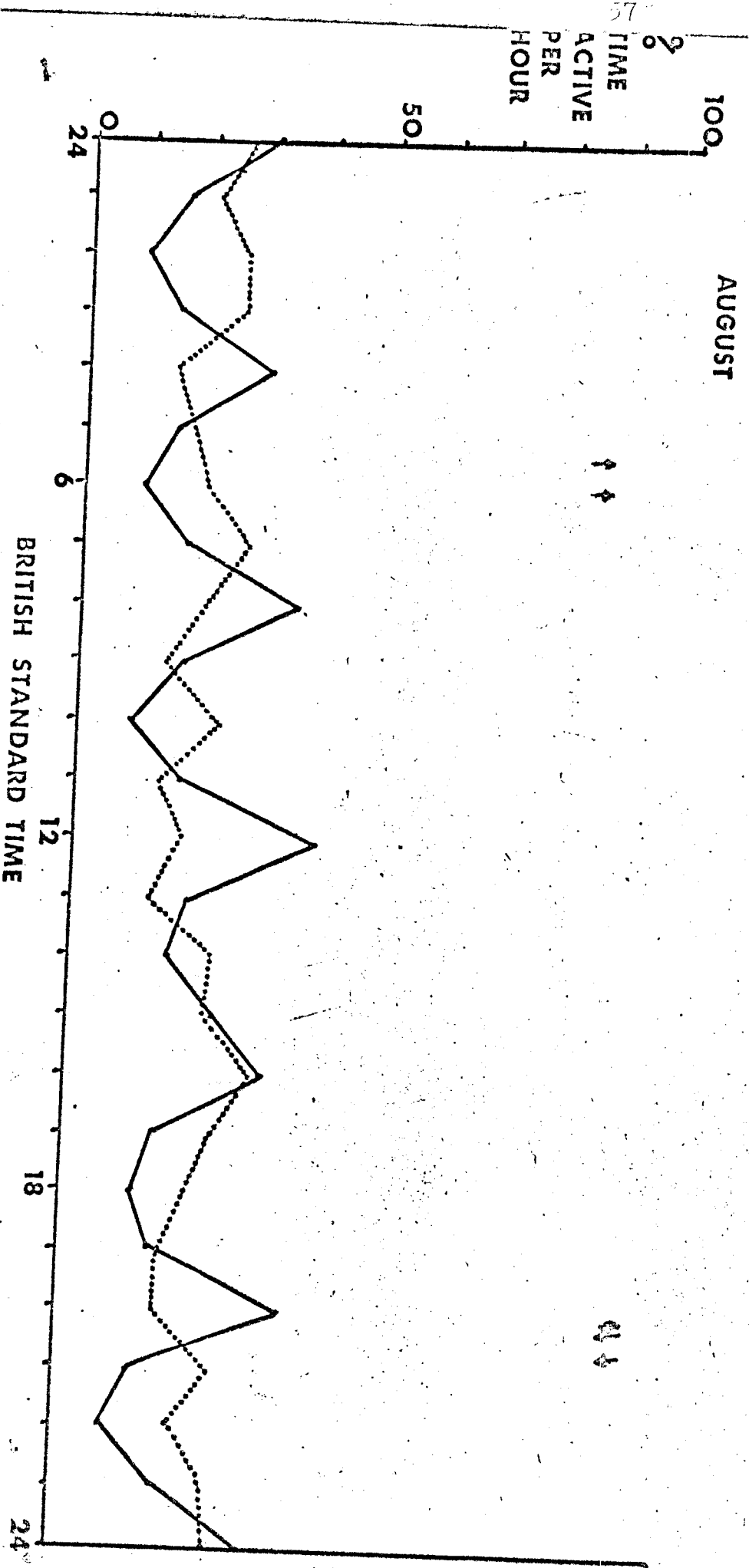


Fig. 8 Effect of cover on short-term rhythm *C. 89*

- Uncovered unit (first two weeks) (1st - 15th)
- 65% ground cover provided (second two weeks) (16th - 30th)
- ↖ ↗ Sunrise at beginning and end of month
- ↘ ↙ Sunset at beginning and end of month

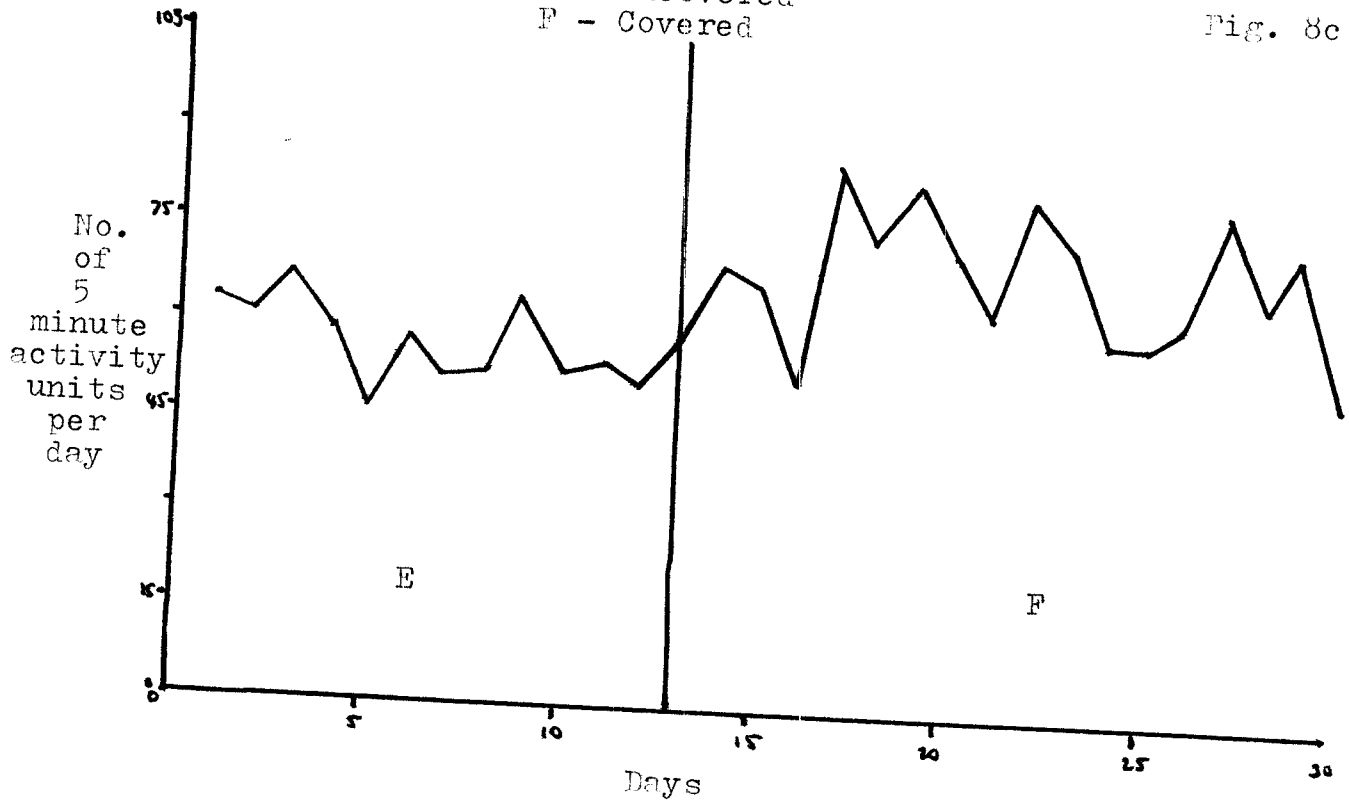


Effect of Increasing Cover on total amount of activity per day

JULY

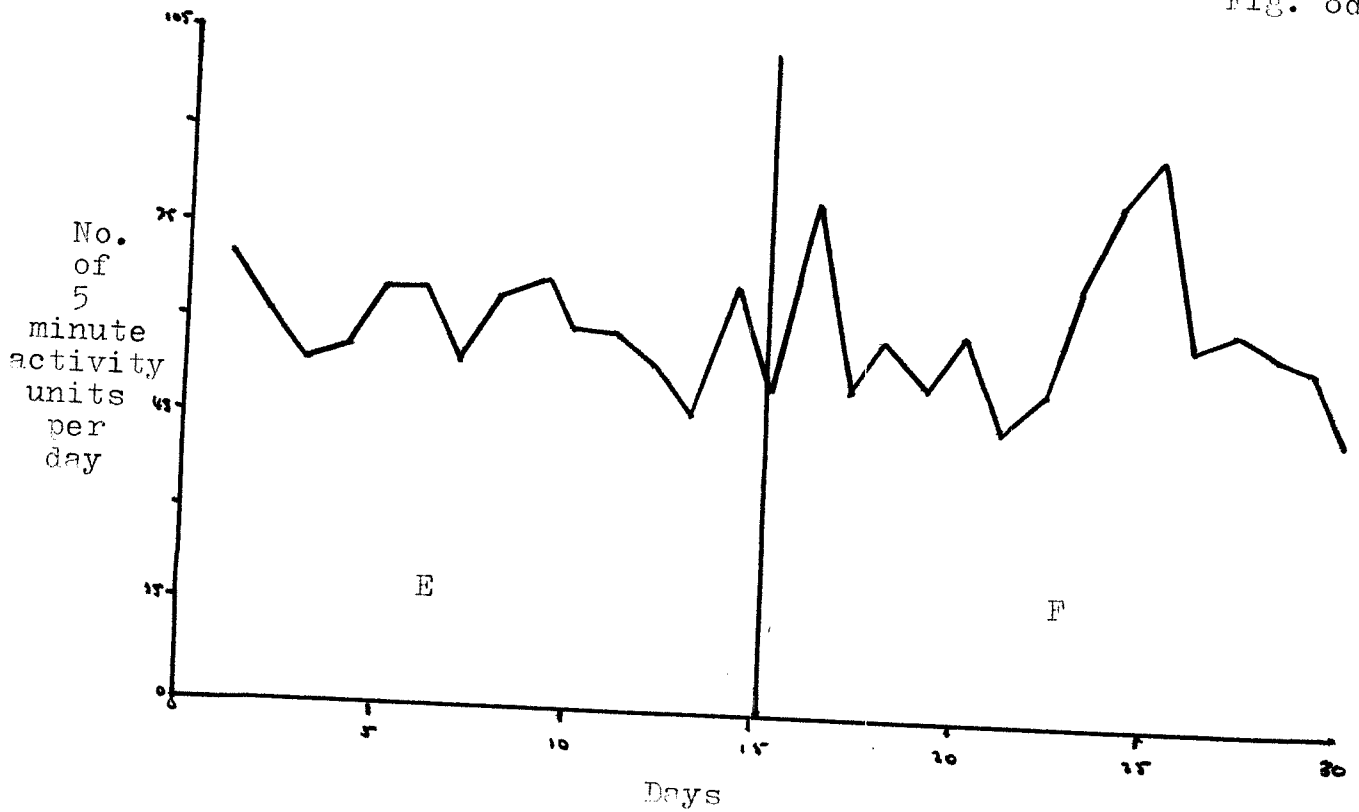
E - Uncovered
F - Covered

Fig. 8c



AUGUST

Fig. 8d



Summated Results for Automatic Recordings

In Fig. 9 the summated results of the whole eight months' recordings are shown. The solid line shows the four-hourly rhythm for all the eight animals from January to August. The broken line is the total of the four months' recording (January to April) showing the effect of the three-hourly disturbances. The dotted line is the summated results from the covered phases from May to August.

From Fig. 9 it can be seen that, while the four-hourly rhythm is well-marked in the undisturbed phase it is not shown at all clearly in the disturbed phase, although in the latter series there is a suggestion of three peaks at midnight, 7.00 to 8.00 hrs., and 17.00 hrs. respectively. It might be suggested that the last two results may indicate a dawn and dusk activity peak during the disturbed phase, but the short-term rhythm did not change with the photo-period or the time of dawn and dusk. This lack of effect is most interesting and will be discussed more fully in the Discussion on Page 115.

During the disturbed phases as shown in Figs. 1 - 4, the four-hourly rhythm did not appear. However, in the graph of the summated results, Fig. 9, there may be a suggestion that it was damped down rather than removed completely. Co-incident peaks in Fig. 9 are at 00.00 hrs., 7.00 to 8.00 hrs., and 16.00 to 17.00 hrs., small peaks can be seen also at 4.00 hrs., 11.00 hrs., and 20.00 hrs.

in the graph of the disturbed phase. Thus the short-term rhythm may have been modified by the disturbances which occurred every three hours.

For example, after the 00.00 hrs. disturbance, activity dropped to a low point at 1.00 hrs. and began to rise at 2.00 hrs. The graph is lowered again at 3.00 hrs. in association with the disturbance. At 4.00 hrs. activity rose a little (by 2%) but did not reach the same level of activity as the 4.00 hrs. peak during the undisturbed phase. Activity continued to rise at 5.00 hrs. and was not affected by the 6.00 hrs. disturbance as much as that at 3.00 hrs. Possibly dawn acted as a stronger stimulus to increase activity than the dampening effect of the disturbance. At 7.00 hrs. activity began to fall again and the drop continued at 8.00 hrs., missing the 8.00 hrs. peak seen in the undisturbed phase. The 9.00 hrs. disturbance is associated with a drop in activity. At 10.00 hrs. activity began to increase again and then dropped again at 11.00 hrs. Despite the disturbance at 12.00 hrs. the graph begins to rise again, activity increased possibly because it had been reduced so much previously that the animals were forced to leave the nest to feed and drink more often. Activity slowly increased between 13.00 and 17.00 hrs., but the 16.00 hrs. peak (equivalent to that of the undisturbed phase) did not appear, it was moved to 17.00 hrs., and overall activity was definitely lower. After 17.00 hrs. there is

another drop in activity to 18.00 hrs. where the disturbance probably reduced the rise in activity which would have occurred in the undisturbed phase by 5%. Activity at 20.00 hrs. was much lower in the disturbed phase by a factor of 17% and began to drop again. The 21.00 hrs. disturbance pushed activity down again and it reached its lowest point at 23.00 hrs. During 23.00 to 00.00 hrs. activity increased again possibly a feeding response to the lack of activity at 20.00 hrs.

In addition to changing the short-term rhythm, the disturbances caused an actual depression in the total activity during the disturbed phase. During this phase the animal was only 87.5% as active as in the undisturbed phase.

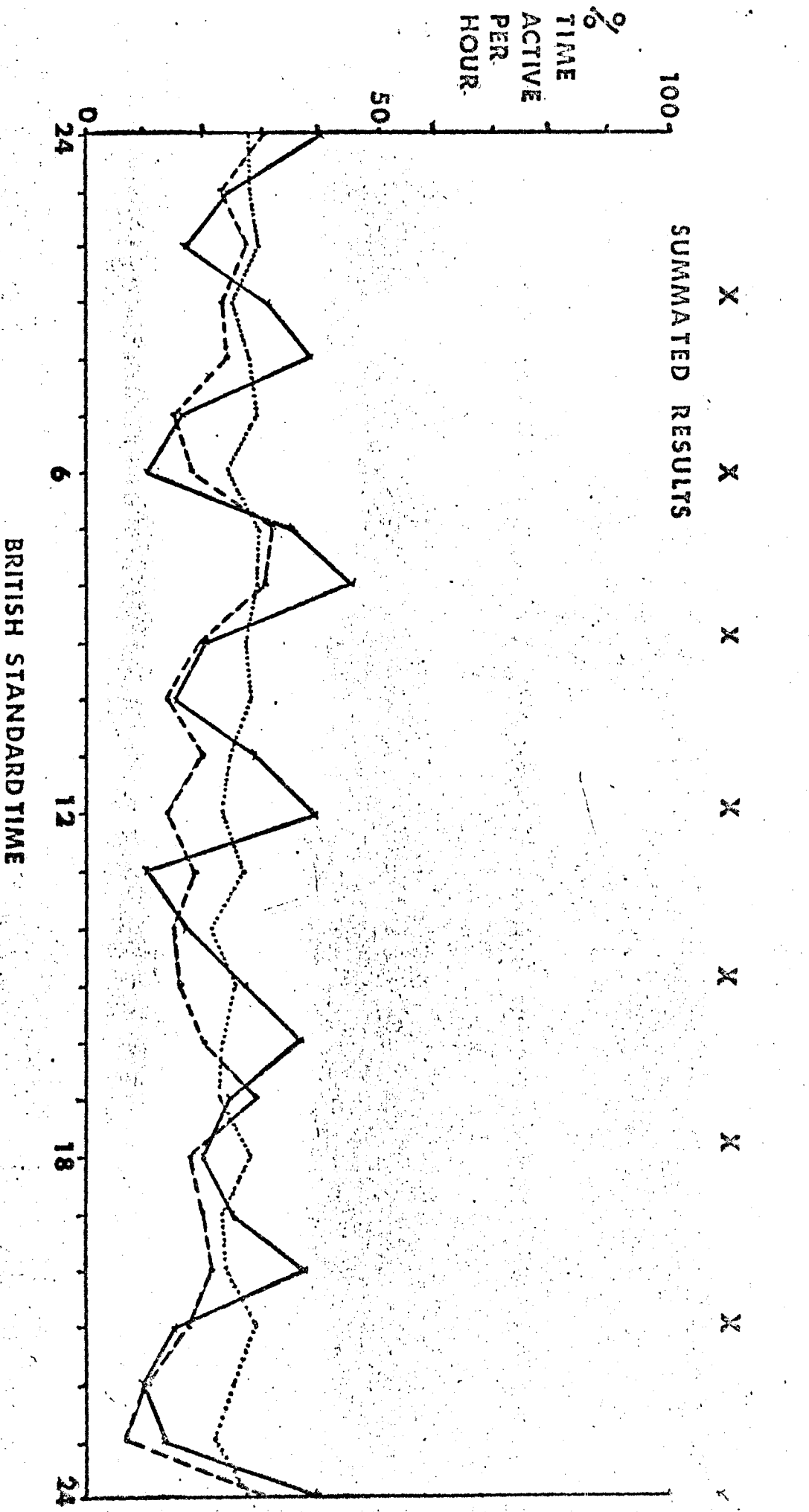
In view of the effect of the disturbances it might be suggested the regular four-hourly rhythm shown in the undisturbed phases was, in fact, a feeding rhythm which showed a "hunting" periodicity, i.e. the animal was forced out to feed and drink in the "hostile" environment of the uncovered run at regular intervals associated with hunger and thirst.

This interpretation of the first series of experiments is supported by the results of the second series using a covered run. Here the "environment" in the run approximated more closely to that found under natural conditions. The summated results of the covered phases are shown as the dotted line in Fig. 9. From this graph it can be seen that

activity in the covered run seems to have been uniform over the whole diel cycle. Overall activity varied by only 8% per hour. The highest percentage time active per hour was 30% at 7.00 hrs. while the lowest was 22% at 14.00 hrs. No short-term rhythm is immediately discernible from this series.

Fig. 9 Summated Results of 8 experiments

- Undisturbed phases January to August
- Covered phases May to August
- - - - Disturbed phases January to April
- X Two minute disturbance timing



Direct Observation Experiments

In this series, three male voles were used. Two of these animals were used only in initial trials designed to test the apparatus and to work out the series of activities which would be possible for a single observer to handle using a written record sheet. The results given are from the third animal which was observed in light and dark periods of twelve hours duration.

Each activity was, of necessity, a widely based one and could have been further divided into several aspects. For example, grooming could have been divided into washing, scratching, fur arranging and parasite catching. In fact, the inactive phase of resting in the nest was further subdivided into three separate phases, sleep, doze and rest. These phases were chosen because they obviously described different states of resting in all three animals. Each state played an important part in the total activity and showed a significant percentage time spent in the nest.

The vole was observed in the light on nine separate occasions making a total of 21 hrs. 55 minutes observation between May 4th 1967 and May 26th 1967. The animal was observed in the dark also on nine separate occasions for a total of 24 hrs. 50.5 minutes between May 28th 1967 and June 14th 1967. The numerical results for this series of experiments can be seen in Fig. 38.

Length of Continuous periods engaged in one activity

The graphs in Figs. 10 - 16 (Pages 71 - 77) show the distribution of the length of observed activity periods. The modal value for the length of time that any given activity lasted was one to two minutes, in all cases except sleep and doze where a second peak occurred at six minutes. A combined graph of these two activities is given in Fig. 12. The peaks are much flatter than in doze or sleep and the height of the main peak is much lower which could be an indication that deep and light sleep alternate.

Rest (Fig. 13) has a peak at one minute and the graph shows a small peak at four minutes. Alert, as might be expected, is a short-term activity and lasted usually for only one minute, the tail of the curve (Fig. 14) is very short. Grooming also tended to be a short-term activity of one to two minutes. Explore usually took between one to two minutes, but the animal was in such a restricted environment that the results cannot really be used as an indication of normal behaviour patterns. Drink, eat and nest were also short-term sequences lasting between one and two minutes.

The longest period for any activity was recorded during sleep, a period of 10 minutes. The longest periods for each activity were as follows: doze 8 minutes, rest 9 minutes, alert 4 minutes, groom 6 minutes, explore 3 minutes, eat 3 minutes and nest 2 minutes.

Drink, urination, defaecation and refection were such

short activities that lengths of time for them would have been measured in seconds rather than minutes and were noted simply as events, for example, the percentage total time spent in these activities were as follows: drink 1.21%, urination 1.97%, defaecate 2.58%, and refection 2.31%. The numerical results for this series of direct observation experiments is given in Fig. 38.

A statistical treatment of the results of the direct observation experiments is given in the appendix (Page 128) which strongly indicates that the figures given above are not due to chance. Therefore it would seem valid to assume that C. glareolus tends to show short bursts of activity rather than prolonged periods of activity.

The greater part of each period of observation showed the vole either asleep or resting, no difference between light and dark was observed. Overall percentage breakdown of activities was as follows:

Deep sleep (much slowed respiration, vibrissae and ears flat)	29%
Light sleep (slowed respiration, vibrissae and ears erect)	14%
Resting (eyes open, respiration normal)	19%
Alert	10%
Grooming	13%
Feeding, exploration	15%

It can be seen from the above results that activities

which could be recorded above ground made up only 38% of the total activity spectrum. 62% of the total activity studied occurred in the nest, e.g. sleeping and resting. Indeed, grooming which took up 13% of the total often occurred in the nest also, thus, the total percentage of possible above-ground activities may have been lower.

Relationship of Activities to one another (Figs.17 - 28)

Using the results from direct observation, it is possible to produce a picture of relationships between each activity. Figs. 17 - 28 show the percentage frequency that other activities followed a given activity. It must be emphasised that this data was obtained from one animal watched on 18 separate occasions for different lengths of time, in light and dark from 4th May 1967 to 14th June 1967. The author would hesitate to suggest that these figures are typical for the species as a whole, but personal observation of small mammal activity by the author supports their validity.

After sleeping (Fig. 17), grooming occurred most often followed by alert and doze which were slightly less usual.

After doze (Fig.18) the animal was most likely to sleep, then either alert or groom followed by rest.

After resting (Fig. 19), it might be expected that sleep/doze would be the most frequent activity. In fact, grooming was most frequent with alert and explore following closely in that order, sleep coming only fourth in the series.

After alert (Fig. 20) sleep was most common followed by

doze and groom.

After grooming (Fig. 21) activities were evenly distributed. Alert was most frequent by 1% only, followed by eat, sleep, doze and rest, all at the same frequency.

After defaecation (Fig. 22) refection occurred most often with doze, alert, sleep and nest following in that order.

After explore (Fig. 23) rest was most common followed by groom, then sleep.

Drinking (Fig. 24) was followed by rest, then alert, and then doze and groom equally.

After eating (Fig. 25) sleep was most common followed by rest then alert, groom and explore.

The pattern after urination (Fig. 26) was most interesting. Rest was most frequent with sleep a close second. There is then a large drop to doze and groom at 10%, while explore comes next.

Nesting (Fig. 27) was followed by alert, sleep and groom on the same frequency, with rest, eat and explore only 2% below these.

As might be expected grooming was the most frequent activity after refection (Fig. 28) with alert, sleep and nest an equal third.

Comparison of Behaviour in Light and Dark

In Fig. 29 the relative total time spent in each activity in light and dark periods is shown. The numerical

results from this experiment can be seen in Fig. 3^a. As can be seen from both these figures activity in light and dark seems virtually the same. A statistical treatment of these results is given on Page 138 in the appendix and indicates that there is no significant difference between the two results.

The times during which this vole was observed had to be chosen to fit in with other work which was being undertaken at the time and, therefore, no attempt could have been made to make regular observations. However, the observations were arranged, as far as was possible, to cover all parts of the light and dark periods, at some time. It is impossible to relate these results to dawn and dusk since no provision for this effect was incorporated in the equipment.

Fig. 10

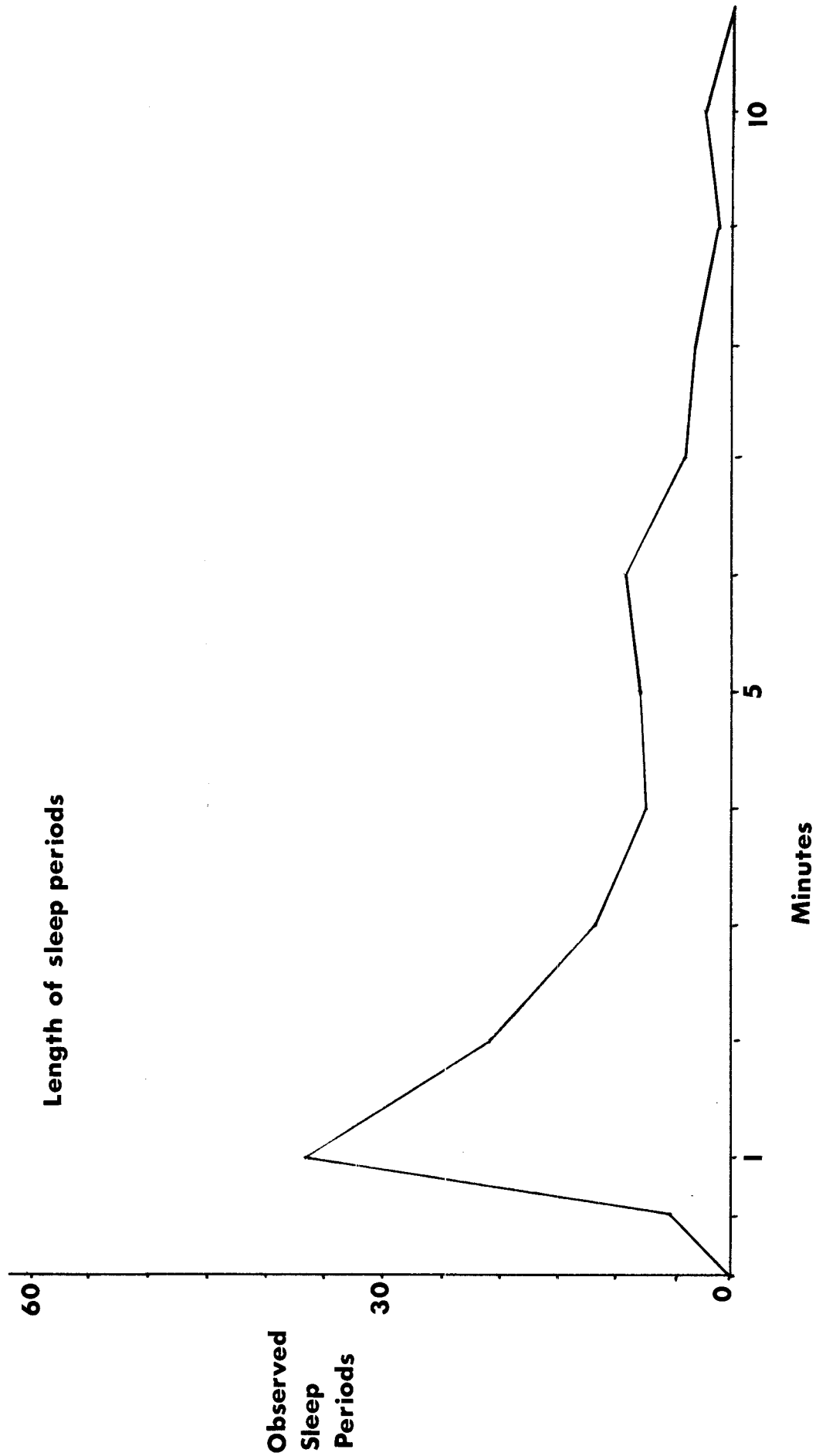


Fig. 11

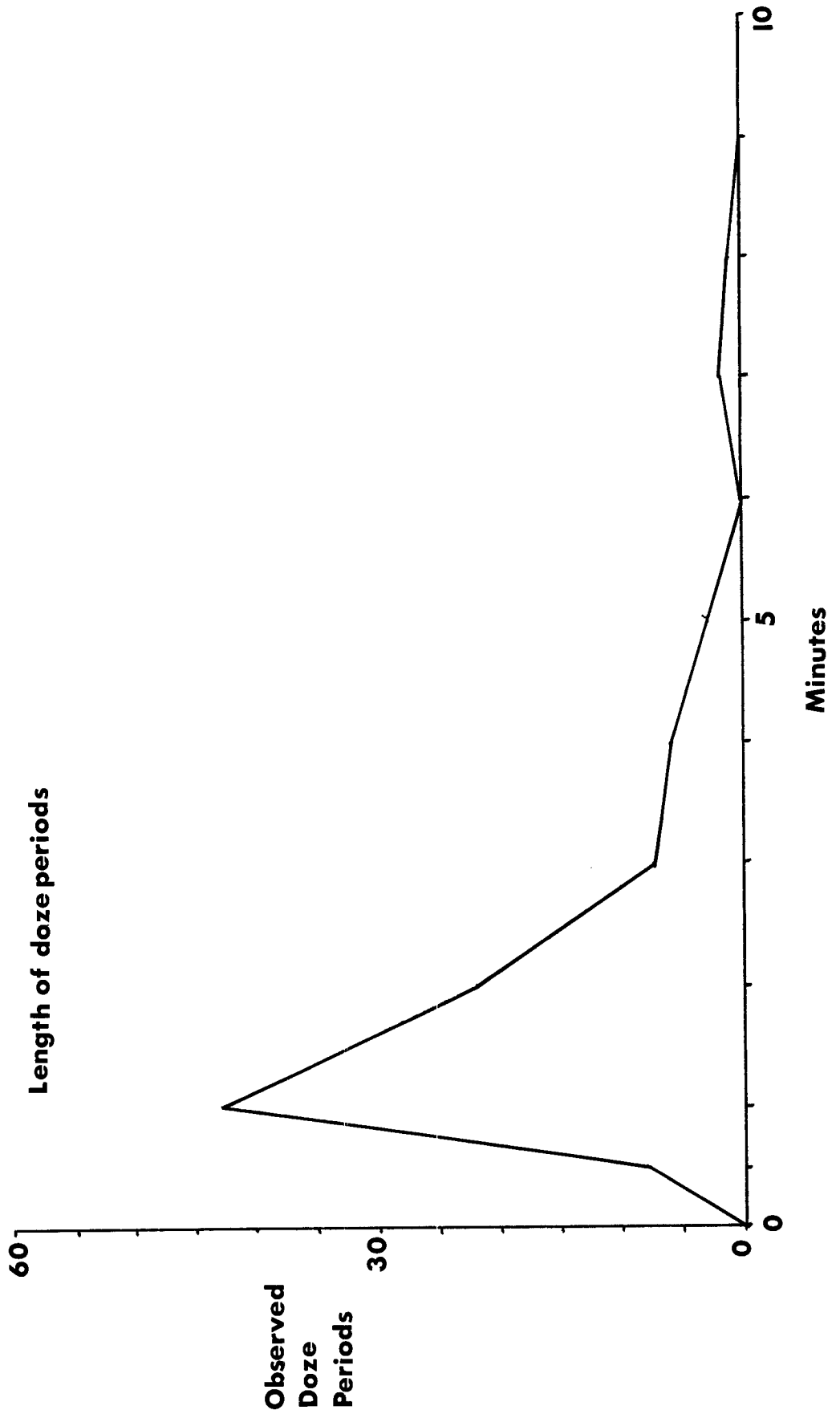


Fig. 12

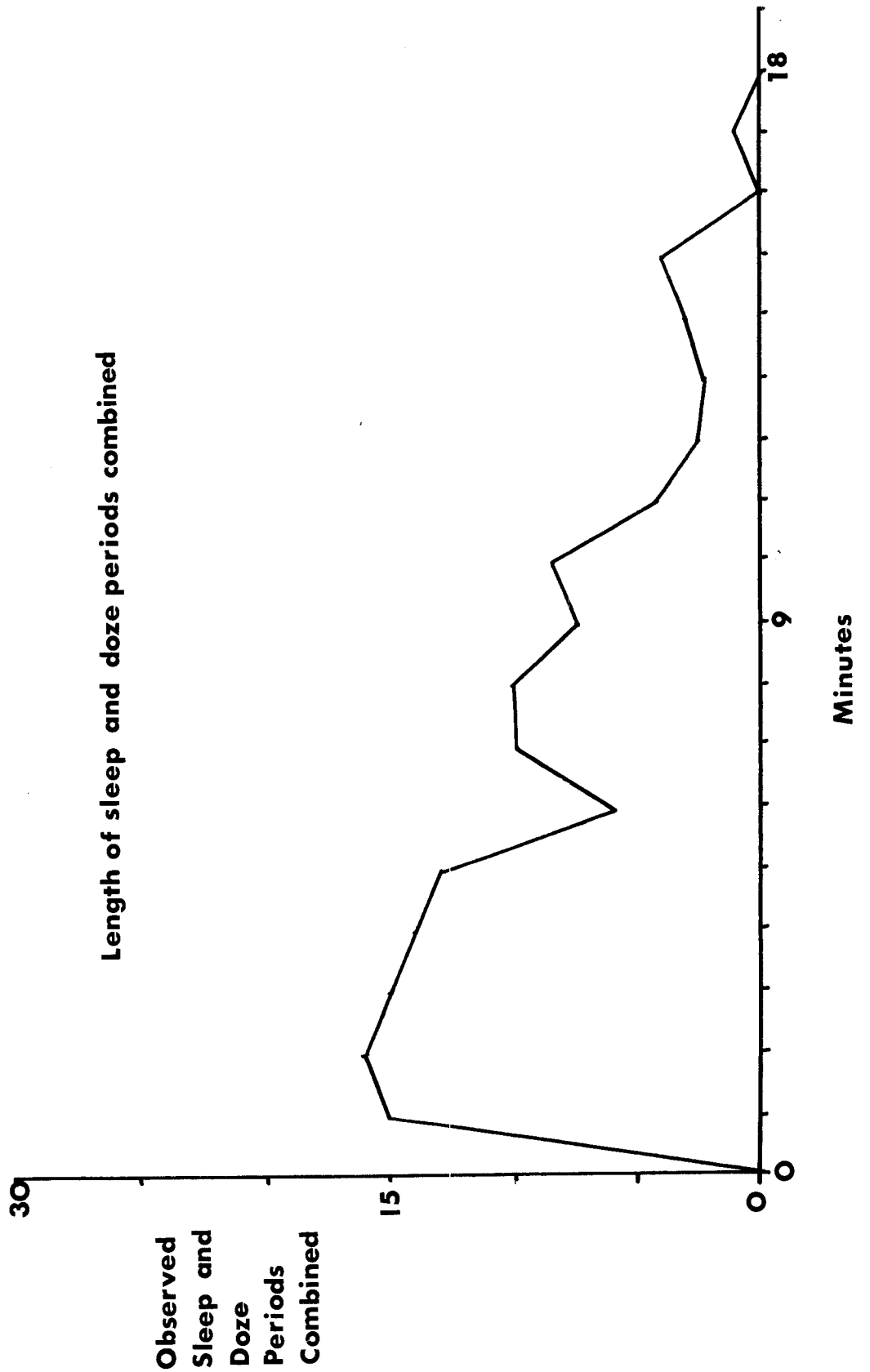


Fig. 13

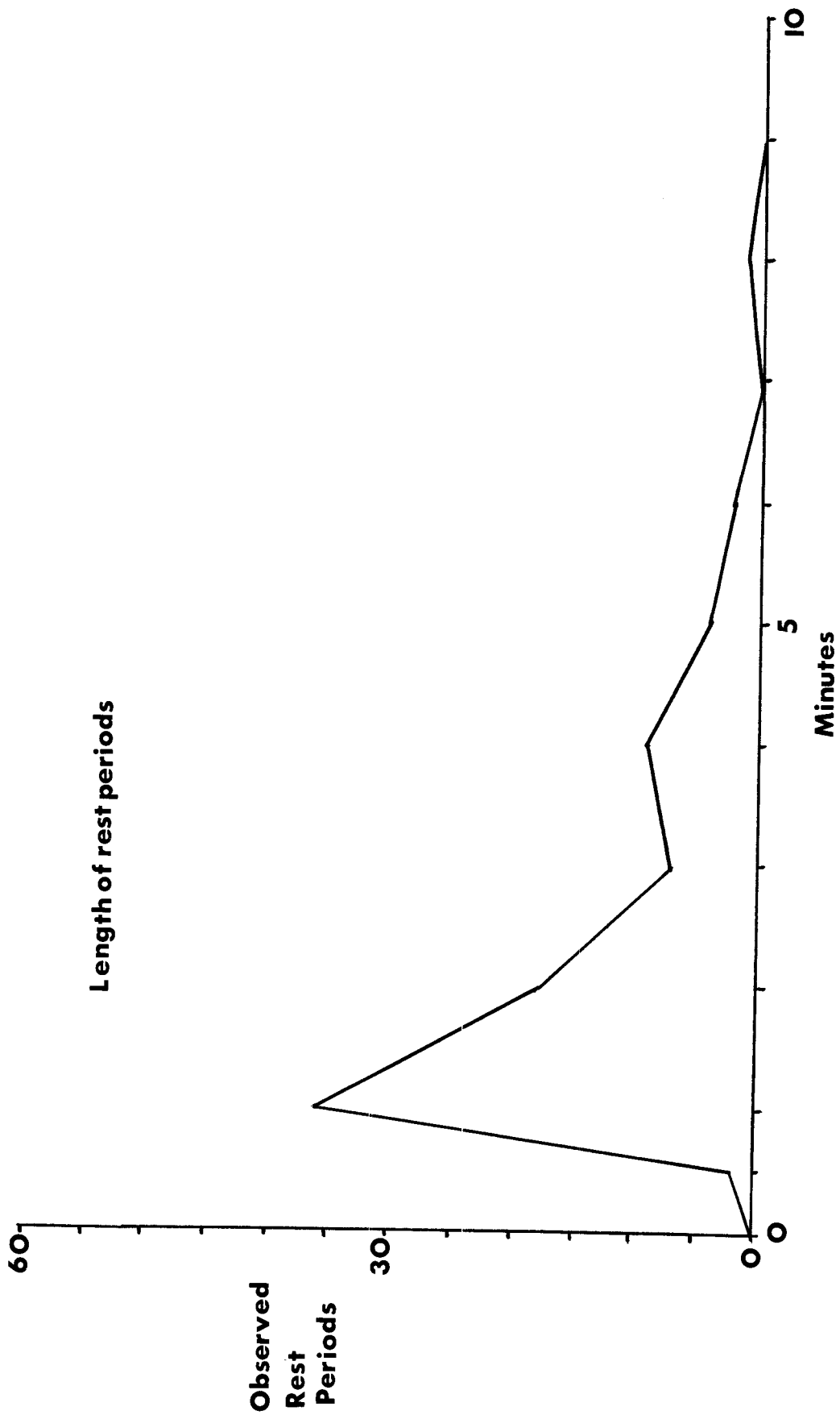


Fig. 14

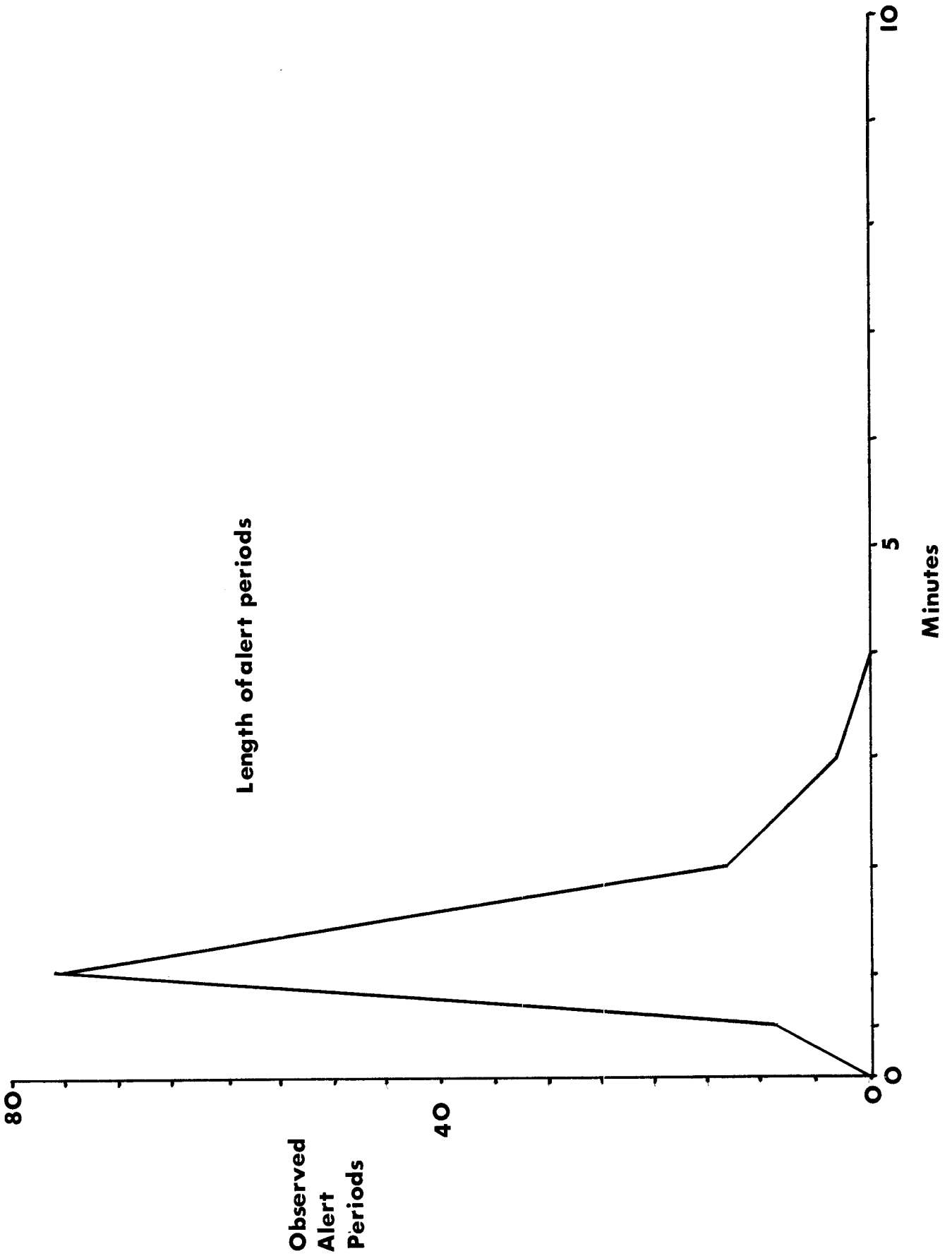


Fig. 15

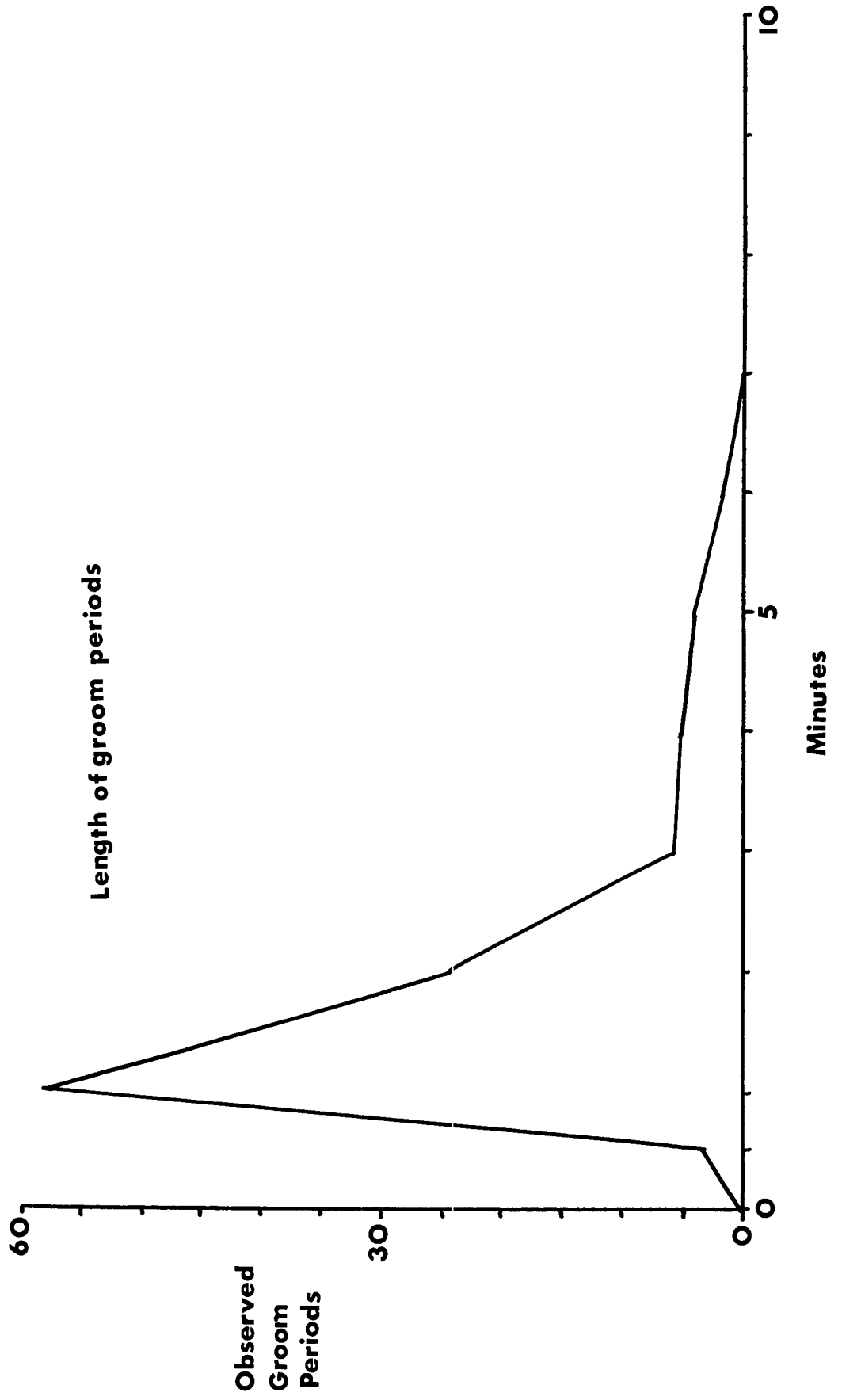


Fig. 16

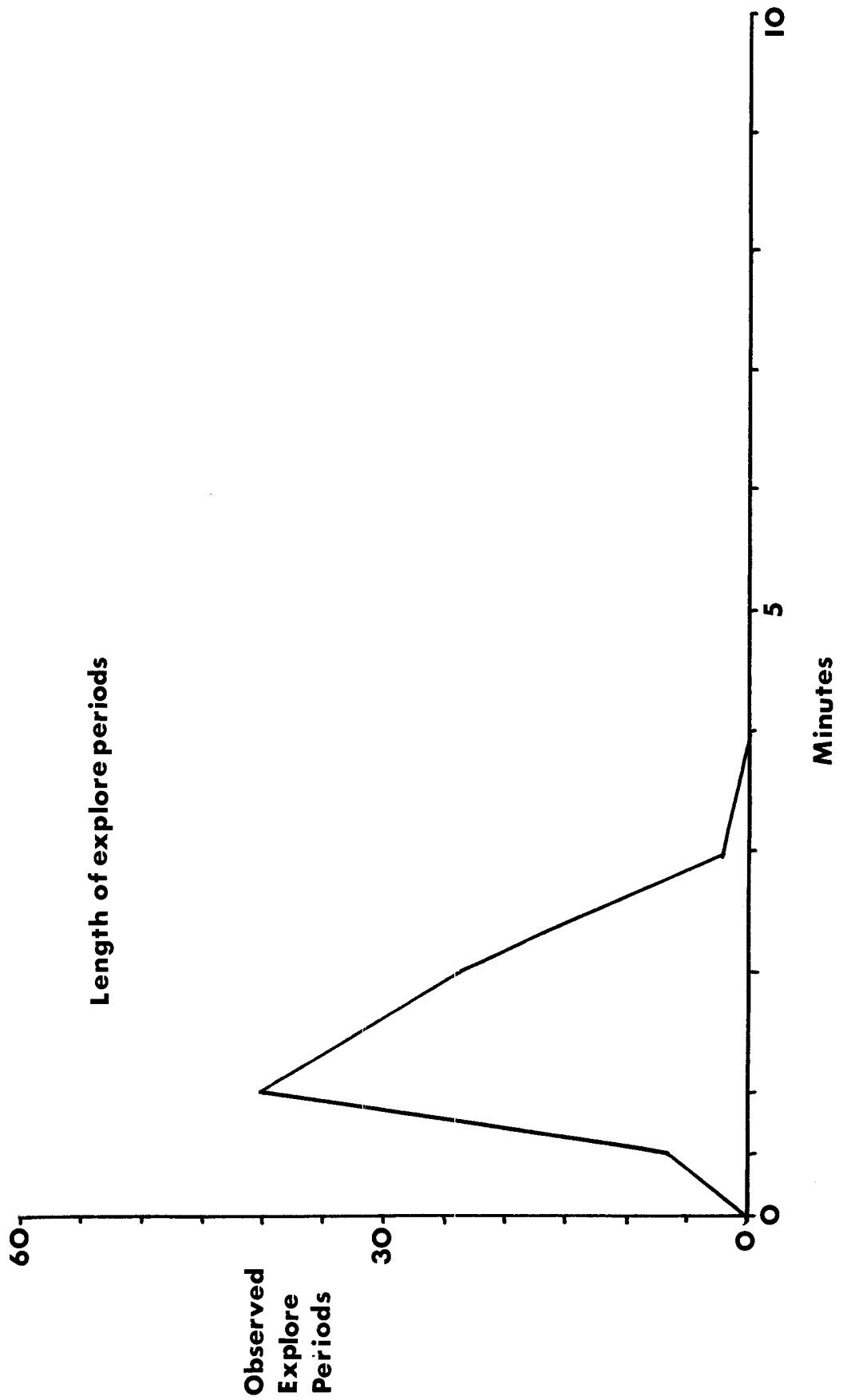


Fig. 17

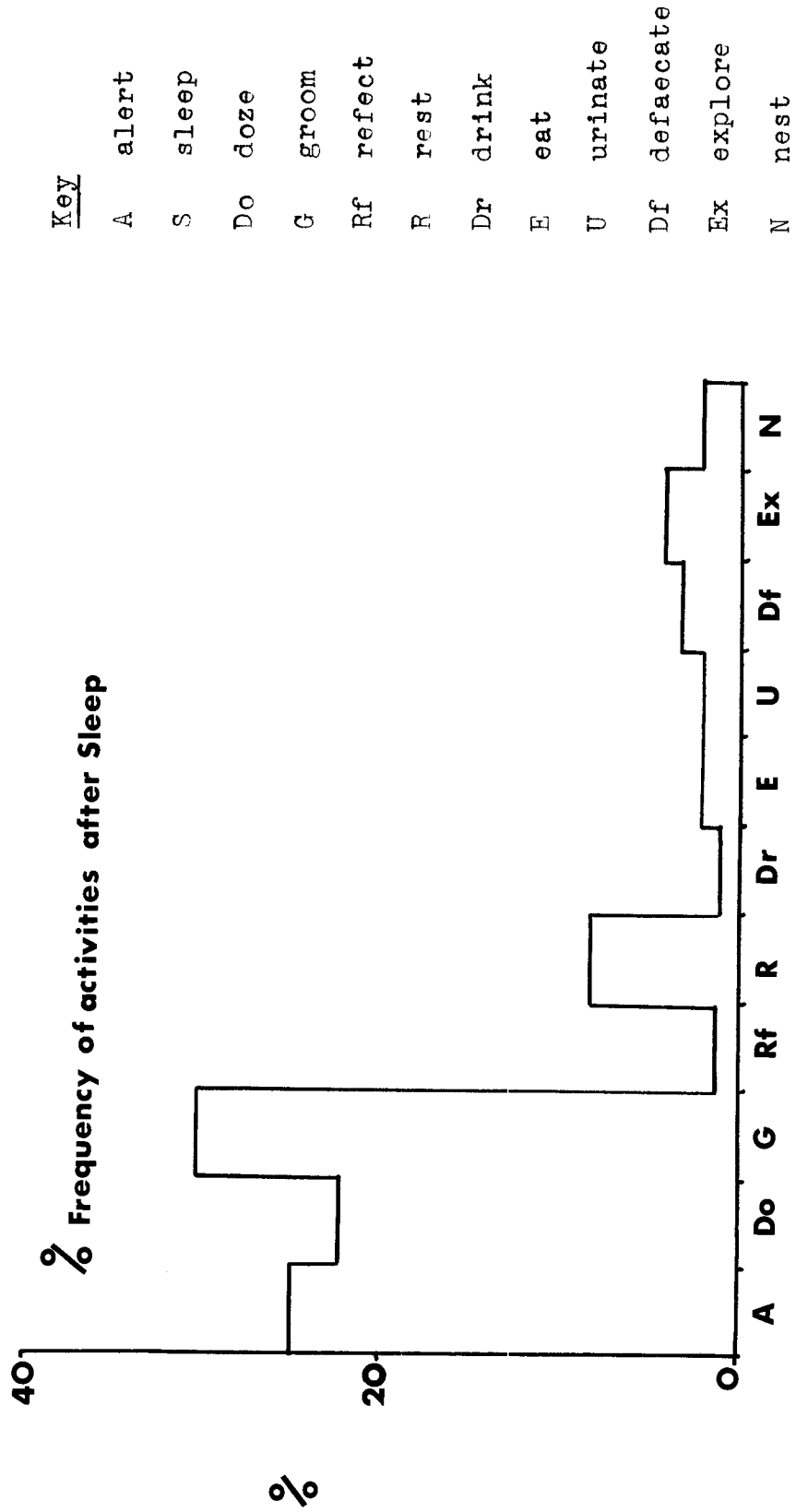


Fig. 18

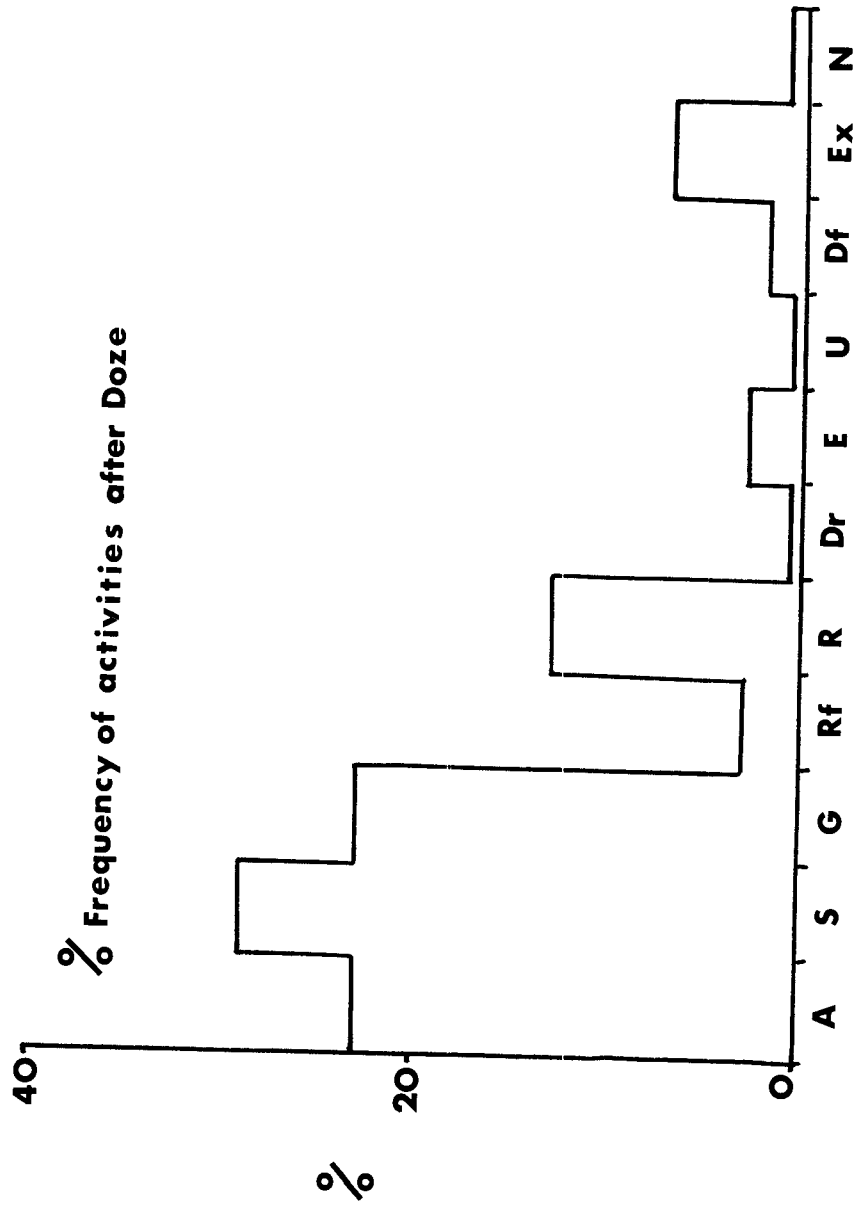


Fig. 19

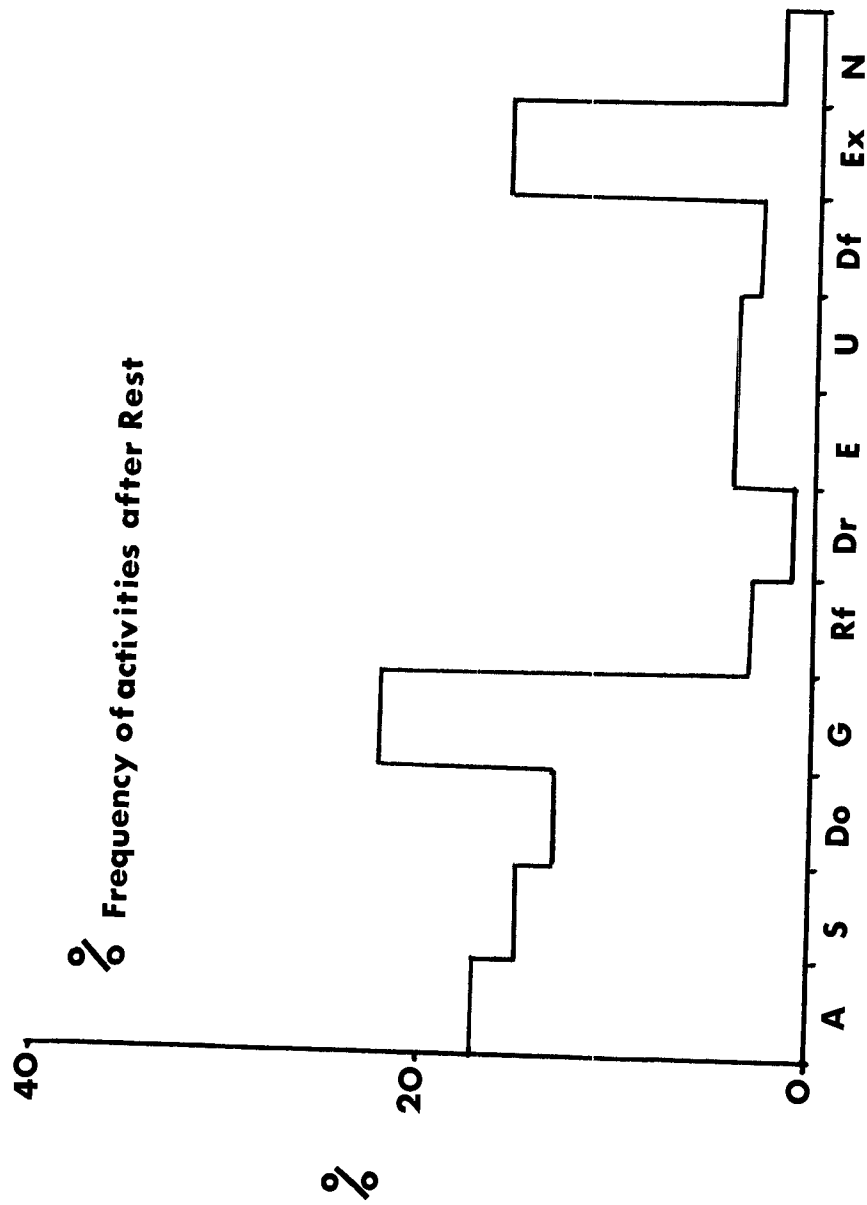


Fig. 20

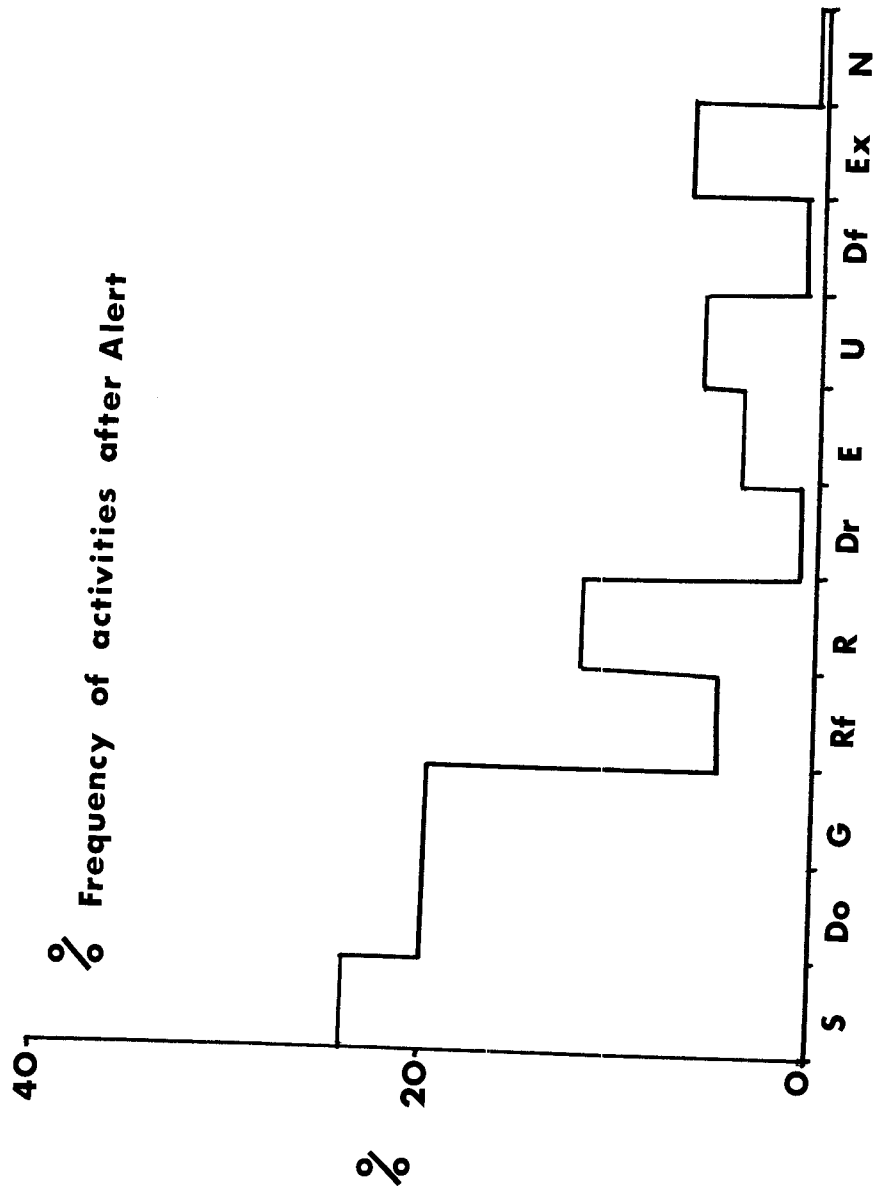


Fig. 21

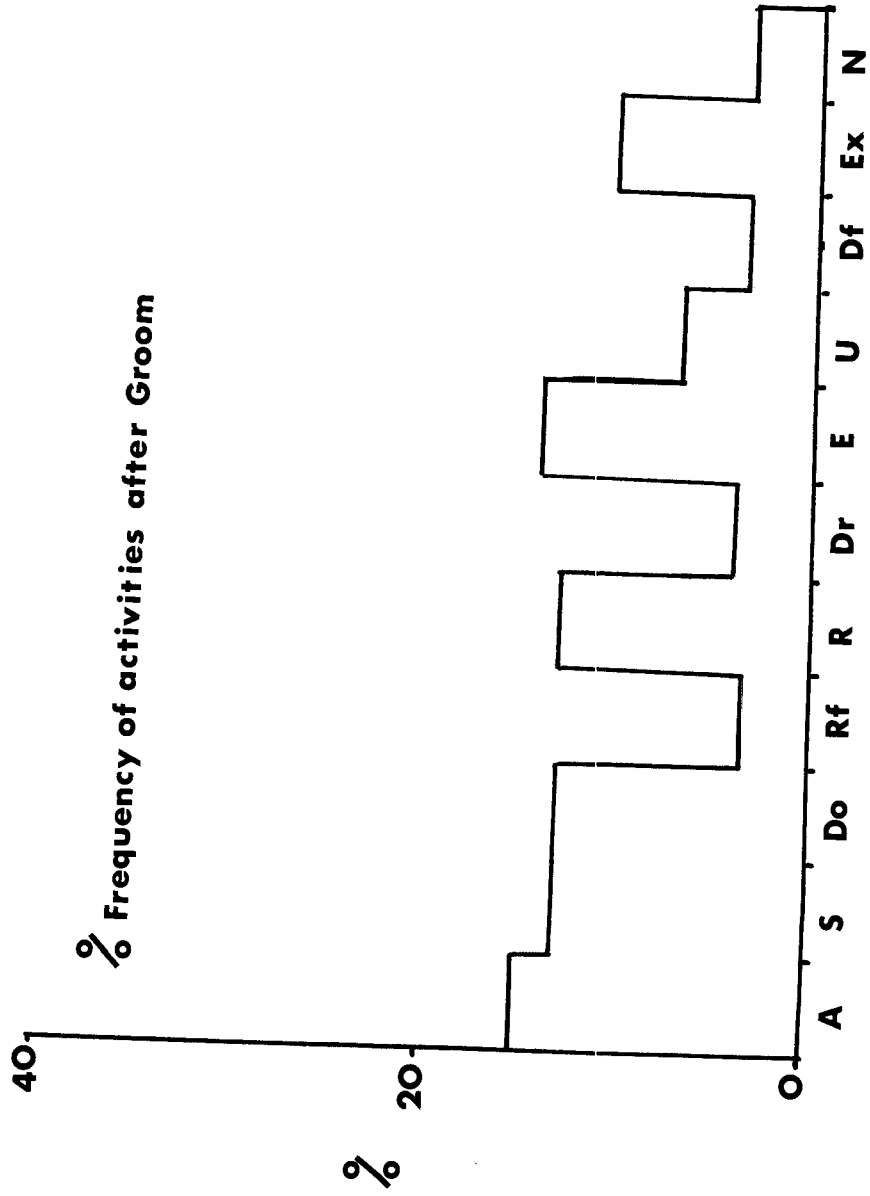


Fig. 22

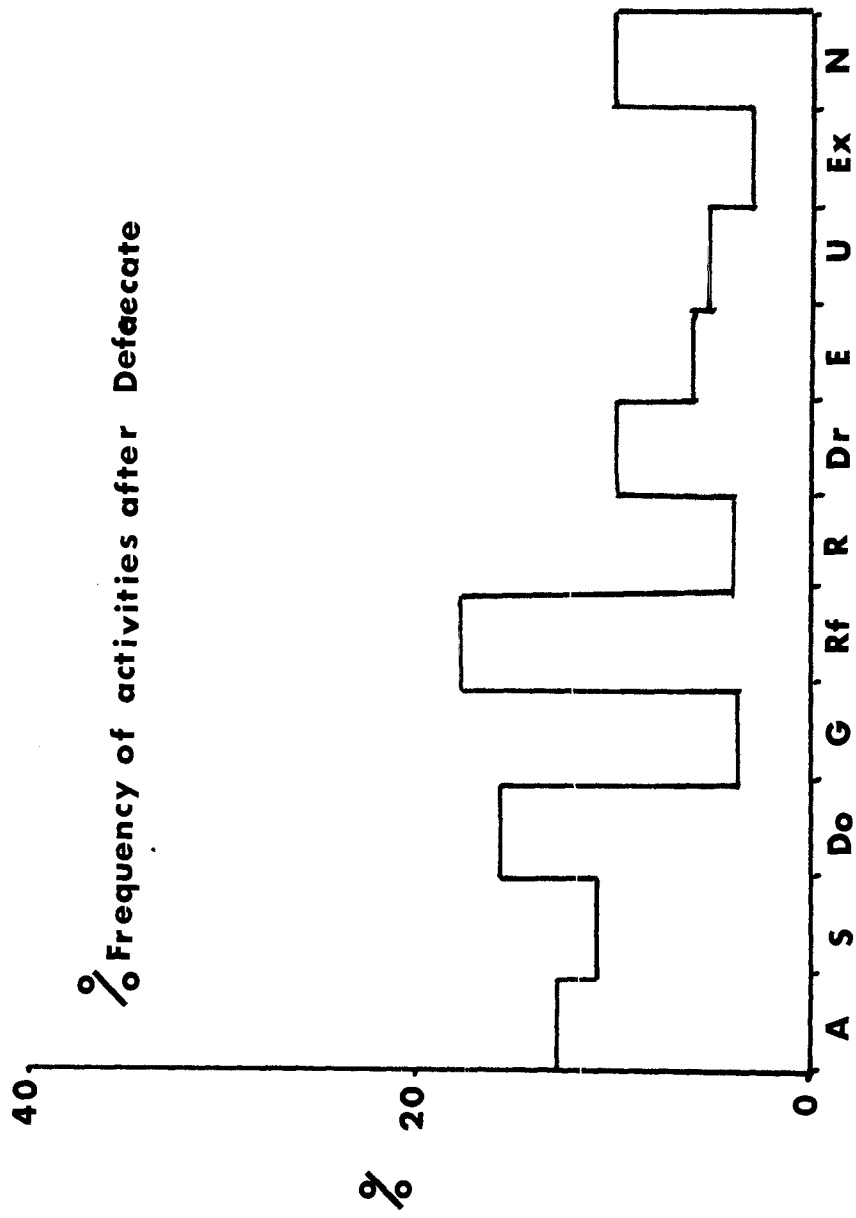


Fig. 23

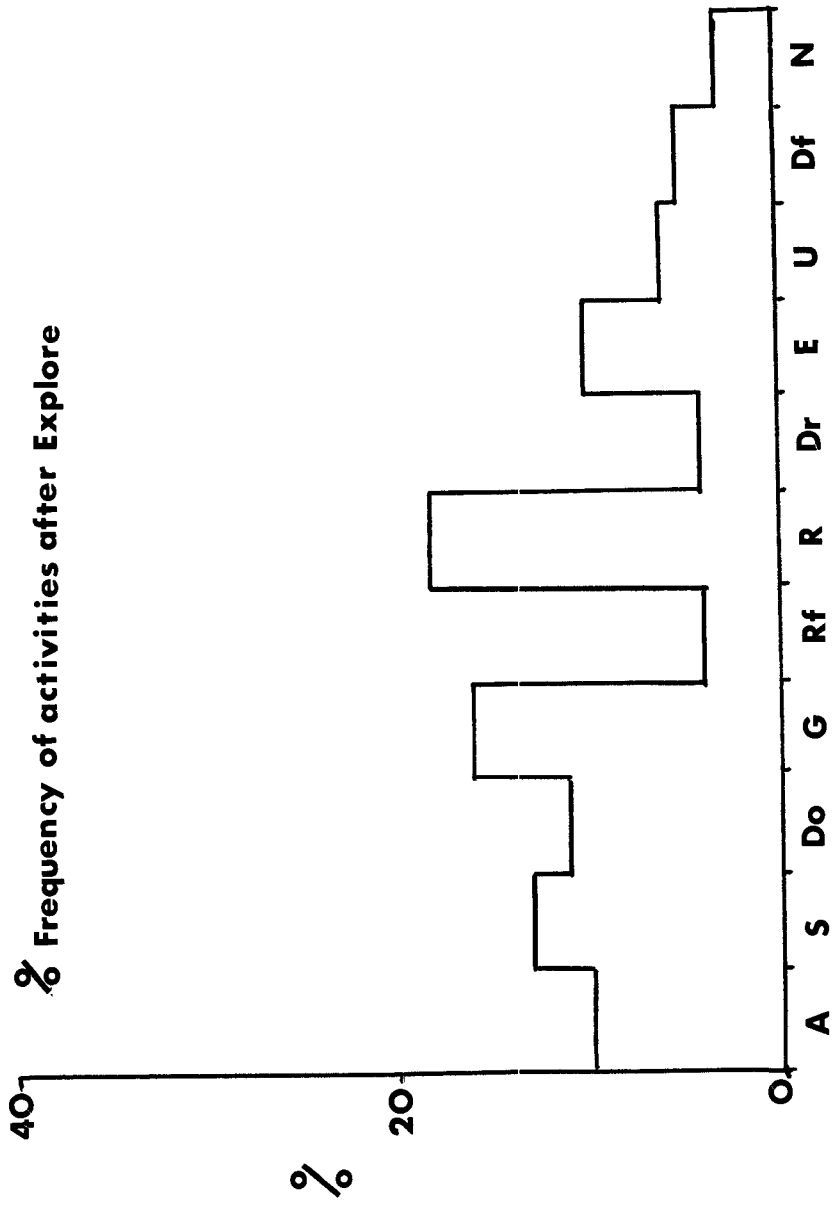


Fig. 24

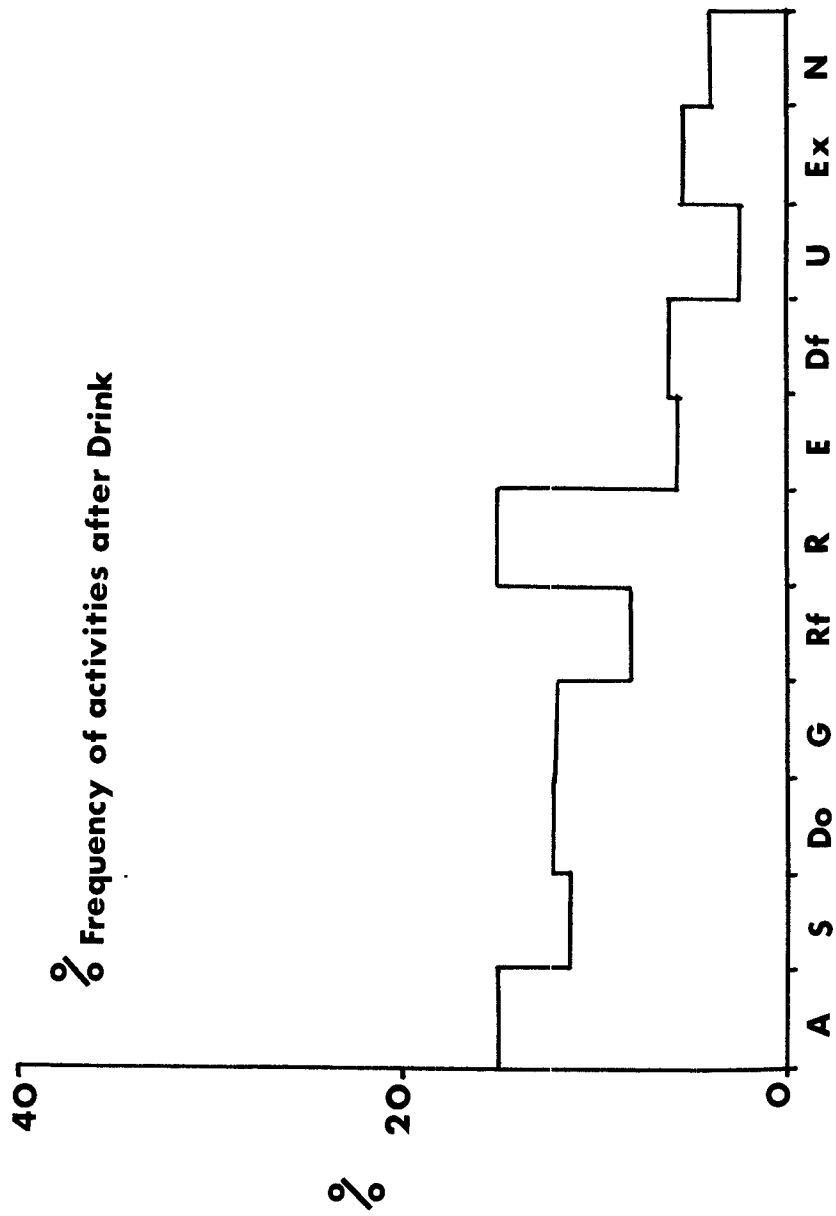


Fig. 25

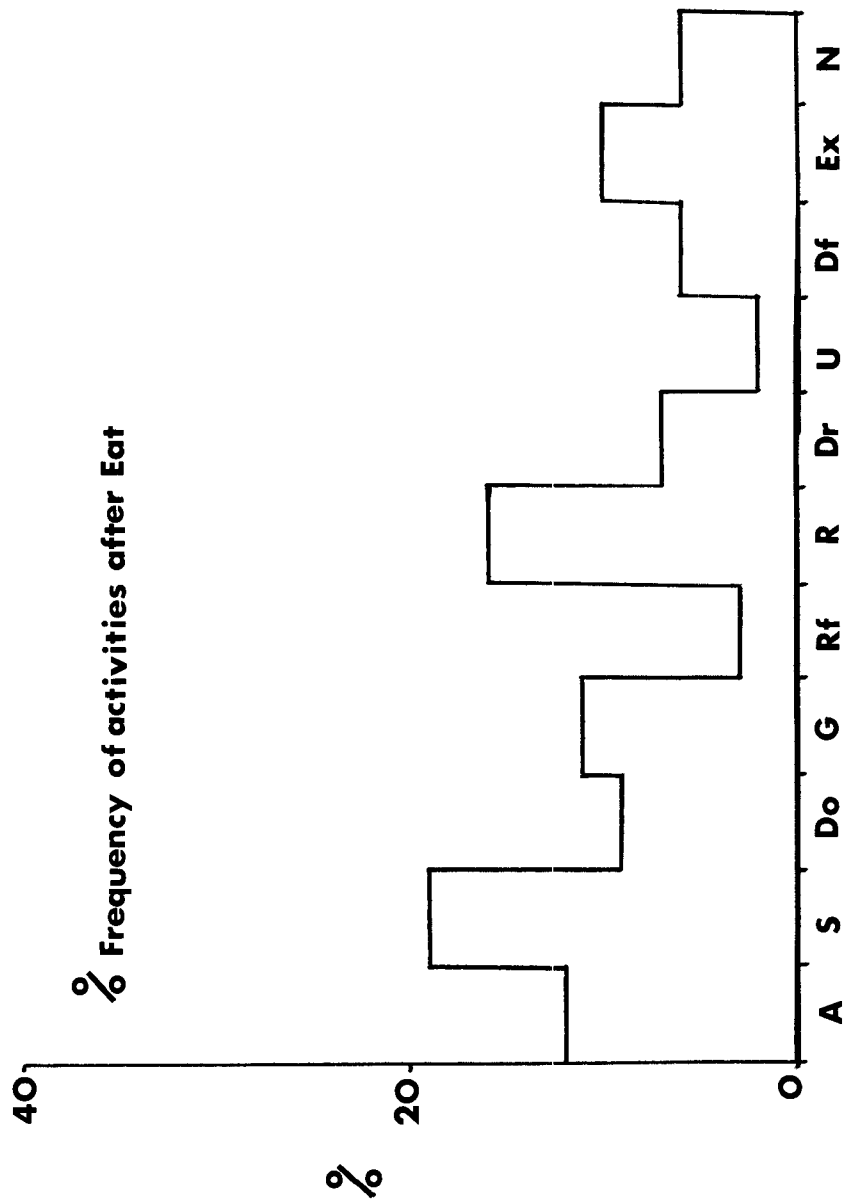


Fig. 26

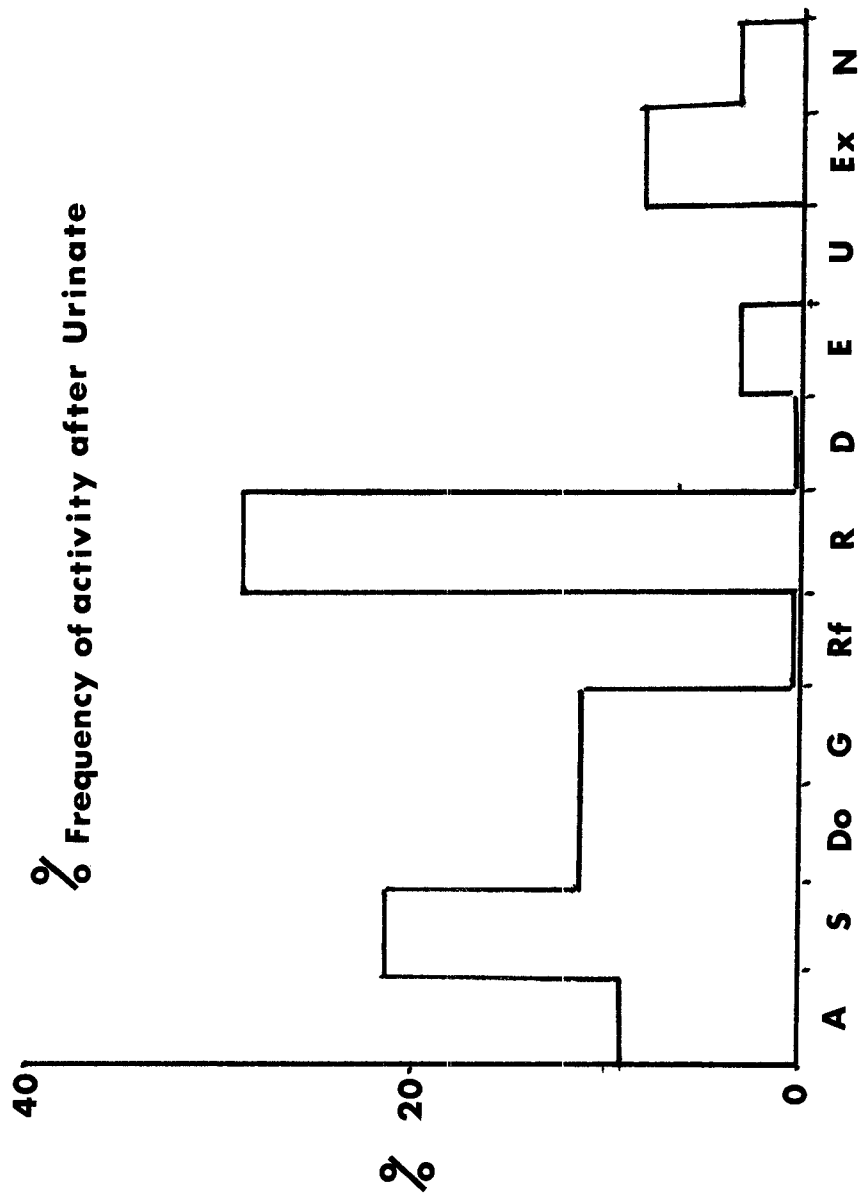


Fig. 27

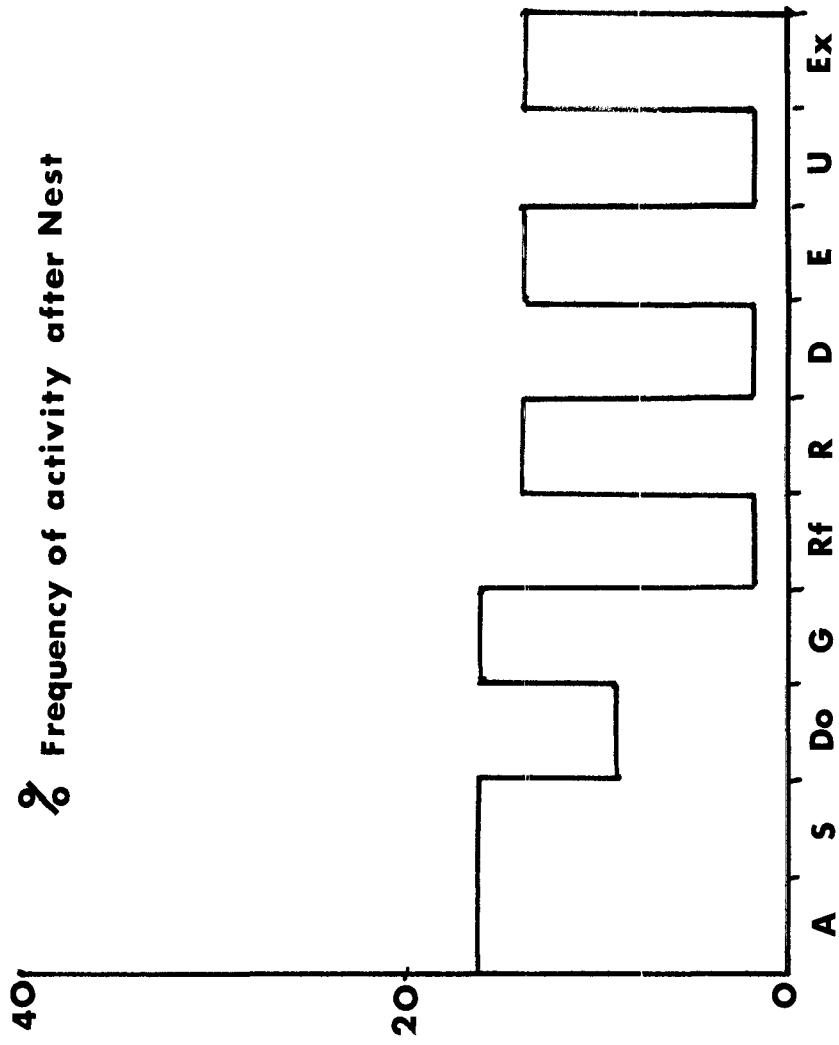


Fig. 28

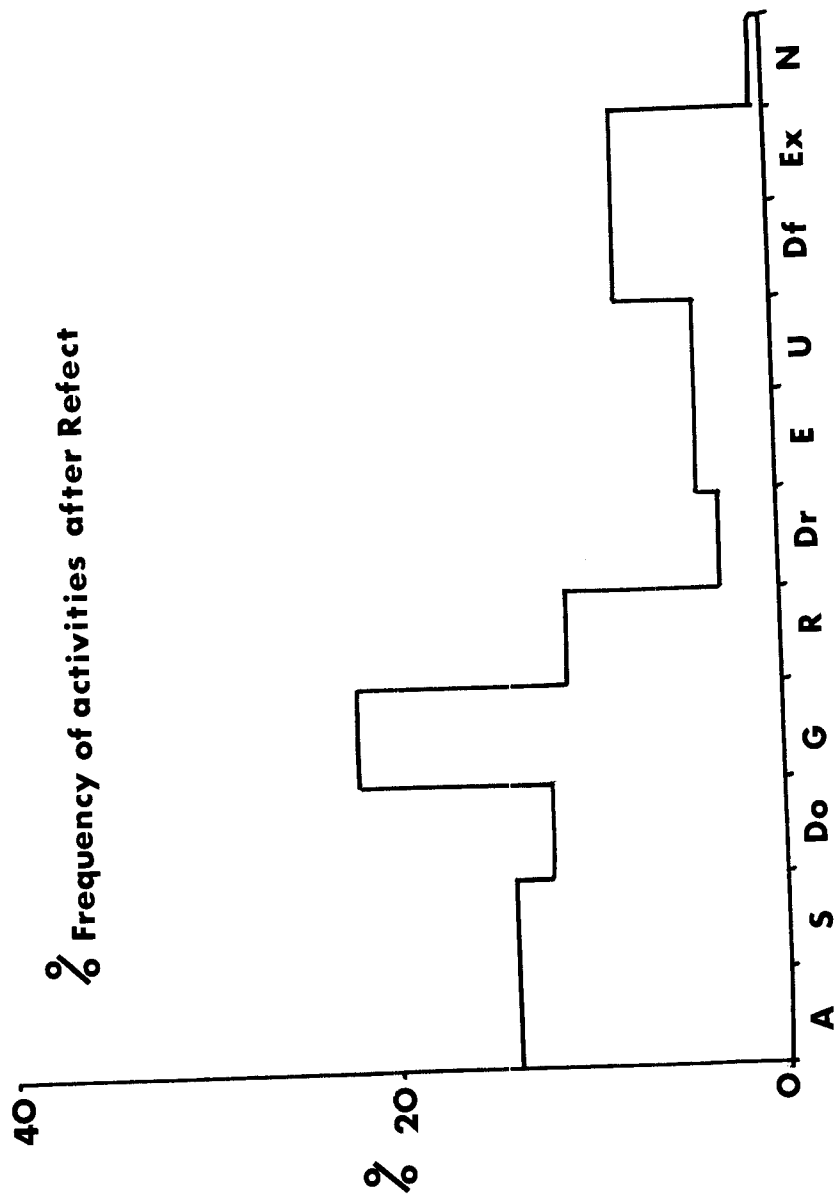
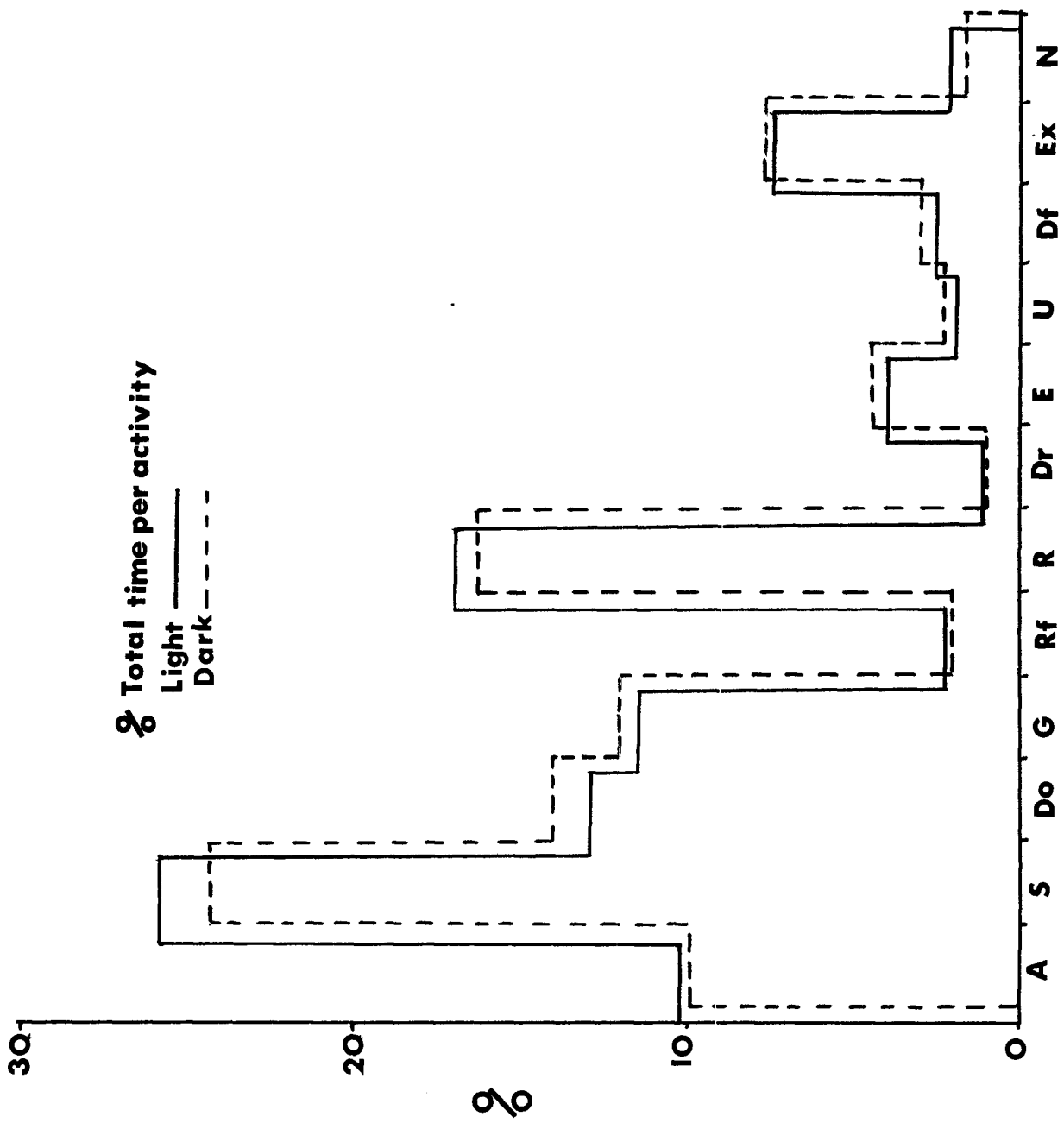


Fig. 29



JANUARY

HOURS B.S.T.

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FEBRUARY

HOURS B.S.T.

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MARCH

HOURS D.S.F.

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9	3	3	3	0	2	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41
10	0	4	0	3	4	0	0	7	2	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	46
11	0	4	0	3	4	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49
12	0	0	3	0	4	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52
13	0	0	3	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52
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16	0	4	0	5	5	4	0	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60
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18	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	57
19	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52
20	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51
21	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51
22	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51
23	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51
24	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	67
25	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	82
26	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	77
27	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	82
28	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	79
29	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	76
30	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	85
31	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	6

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DATE	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	TOTAL
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2	9	9	1	9	9	0	3	8	8	0	0	6	6	3	5	1	7	4	5	5	4	3	3	2	108
3	1	4	0	10	3	0	0	10	3	4	4	4	8	0	3	4	9	5	3	9	10	1	0	5	103
4	4	4	6	5	12	2	0	6	8	0	4	4	6	0	3	4	6	0	4	8	9	0	0	0	95
5	10	7	0	9	6	5	0	2	12	3	4	4	2	0	7	8	3	0	0	0	9	3	0	3	96
6	4	0	8	9	6	0	0	0	8	8	2	2	11	0	2	2	8	2	0	8	5	4	0	2	89
7	35	31	15	33	42	10	3	29	48	19	14	33	37	3	24	25	42	15	13	36	40	11	5	19	
8	0	6	4	0	0	0	0	9	0	6	0	0	0	3	2	3	0	0	5	6	0	0	0	0	44
9	0	5	5	0	3	3	3	6	4	0	0	3	0	0	4	0	3	0	1	0	0	0	0	0	48
10	5	4	4	4	3	2	0	3	12	12	3	0	0	0	0	0	0	0	0	3	4	0	0	0	65
11	0	4	7	4	3	0	4	0	3	5	3	0	3	0	3	0	0	3	0	2	1	0	0	0	52
12	3	3	0	3	3	0	6	0	0	0	6	9	0	0	0	4	0	0	0	5	0	0	0	0	40
13	4	4	5	0	4	0	4	0	2	0	4	3	2	3	0	1	0	4	0	6	3	0	3	0	54
14	6	0	9	4	4	3	3	3	3	2	5	4	1	3	3	3	3	3	2	5	1	4	0	2	66
15	6	2	3	1	3	0	4	0	3	0	5	4	1	8	0	6	0	5	0	6	4	4	0	5	75
16	8	3	0	4	3	3	4	9	5	0	0	9	0	0	1	6	4	0	3	3	5	1	0	0	79
17	8	4	2	4	6	2	0	3	3	0	5	4	5	0	0	6	3	0	4	6	9	4	0	0	70
18	3	3	1	2	3	1	2	2	3	0	3	4	3	0	1	0	4	0	0	5	2	0	0	0	43
19	4	0	8	11	0	0	0	4	0	0	0	0	0	4	0	0	4	1	0	1	0	11	11	0	73
20	0	3	0	0	0	0	0	4	0	0	0	0	0	5	0	0	6	4	0	0	6	0	0	2	32
21	58	43	51	37	50	15	37	49	44	78	34	38	17	31	18	32	26	28	15	45	38	28	21	23	
22	5	2	4	3	3	2	0	4	6	0	0	7	4	0	0	8	5	0	0	0	0	4	4	4	61
23	3	3	0	4	6	0	3	7	2	0	10	6	4	0	3	8	3	4	3	0	0	0	4	0	69
24	3	2	0	4	0	7	0	5	3	0	0	6	4	0	3	7	3	6	0	0	4	3	0	0	60
25	8	2	0	6	4	9	0	8	3	5	4	6	4	0	0	3	5	4	0	6	3	2	1	0	82
26	4	1	0	4	9	3	0	7	2	7	0	4	6	0	0	5	5	0	3	3	0	1	0	0	59
27	7	2	2	7	2	2	2	2	6	3	0	5	10	0	3	6	4	3	6	2	2	4	0	0	80
28	9	1	3	6	1	2	1	9	8	1	0	6	3	1	1	2	6	0	2	4	3	0	0	0	62
29	4	5	1	5	5	2	2	9	7	5	3	9	2	9	0	0	8	3	2	0	0	0	0	0	71
48	22	10	45	35	27	8	51	37	23	14	53	36	12	12	10	39	47	22	18	18	10	14	8	5	68

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HOURS B.S.T.

DATE	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	TOTAL
1	5	2	1	6	0	0	2	0	9	4	0	4	5	0	0	2	5	2	1	3	7	2	1	2	68
2	5	1	1	6	0	0	1	0	0	0	0	4	5	0	0	4	3	4	0	2	9	3	0	0	63
3	7	0	2	4	0	0	0	5	4	0	3	7	1	0	2	6	4	0	4	7	2	0	2	0	69
4	6	2	0	8	4	2	1	4	6	0	8	4	7	0	2	4	6	1	1	4	7	0	2	0	76
5	7	0	3	0	0	0	0	3	9	0	1	5	7	0	0	4	8	1	0	7	8	0	3	0	94
6	8	0	0	0	0	0	0	4	2	0	3	6	5	0	0	6	7	0	0	9	7	0	2	0	85
7	3	3	0	0	0	0	5	0	3	6	5	0	4	0	4	2	4	0	0	4	0	0	1	0	67
8	3	0	0	8	0	0	6	4	0	3	6	0	0	0	0	4	2	0	0	6	0	0	2	0	54
9	7	0	3	0	0	0	4	0	3	1	3	0	4	0	0	4	2	0	0	4	0	3	1	0	80
10	3	0	0	4	0	0	3	5	1	0	5	4	0	0	0	4	10	0	0	4	0	4	0	0	43
11	0	4	3	4	0	0	4	5	0	3	6	0	7	0	0	4	2	3	2	0	4	0	0	1	73
12	4	3	8	5	9	3	5	0	1	0	4	1	7	0	0	3	7	3	2	0	6	0	0	0	69
13	0	2	5	2	9	3	2	4	3	3	7	6	1	2	3	3	0	5	1	7	9	3	0	0	81
14	5	2	1	2	9	3	1	4	5	2	0	7	5	1	1	3	6	1	3	0	9	1	1	4	81
15	6	0	4	4	7	3	0	6	7	3	4	5	2	4	0	6	4	2	2	5	4	0	3	2	97
16	8	3	4	5	7	2	4	5	7	6	3	6	4	4	0	4	4	5	2	5	9	3	4	3	90
17	6	3	5	3	4	4	4	5	5	4	5	6	4	3	0	6	3	5	5	4	3	5	3	1	103
18	4	5	3	5	4	5	6	7	4	4	4	4	4	4	2	3	3	4	5	4	4	4	0	4	103
19	7	6	3	3	4	3	0	6	4	8	2	3	2	2	2	4	4	4	5	2	4	4	4	2	94
20	3	3	4	2	4	1	7	7	0	6	2	2	3	3	0	3	3	5	2	4	2	2	0	4	72
21	3	5	4	5	4	5	0	7	4	6	1	0	6	0	3	4	0	4	4	2	3	1	0	2	70
22	2	0	2	2	0	6	2	0	0	4	6	0	3	3	0	3	3	2	6	0	2	6	8	3	64
23	4	3	0	1	4	1	5	0	3	5	1	4	2	4	4	0	3	2	1	2	3	1	0	2	76
24	3	2	6	2	0	3	4	1	0	9	0	3	9	2	2	3	2	2	0	7	6	6	4	0	106
25	4	3	4	0	7	7	1	4	5	4	4	0	4	0	4	4	4	0	7	0	4	0	1	0	72
26	3	2	0	7	4	6	4	3	2	5	0	3	2	0	2	4	2	0	3	0	6	0	4	0	65
27	2	0	0	4	5	6	1	7	2	9	4	0	4	0	0	4	4	7	0	4	4	2	1	0	63
28	0	3	6	0	6	6	2	4	2	4	0	5	0	0	4	4	5	0	7	0	0	3	1	0	59
29	3	5	5	3	4	0	4	3	2	0	4	0	0	5	3	4	0	3	0	4	0	3	0	0	85
30	0	7	7	1	3	6	2	4	3	2	6	0	5	5	6	5	0	8	4	0	0	4	10	0	81
31	5	7	4	3	5	2	0	3	5	2	4	4	4	3	3	0	3	4	0	4	5	4	4	1	95
71	66	59	49	75	61	47	64	70	71	55	42	66	58	47	62	49	54	54	48	69	68	56	46		

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HOURS 3.S.T.

DATE	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	TOTAL
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2	6	1	2	4	5	0	1	0	4	0	4	2	6	0	2	3	4	0	1	2	7	1	0	3	60
3	6	1	2	3	4	0	2	0	4	0	4	5	7	0	2	4	5	1	2	6	8	2	0	4	63
4	7	1	2	4	5	0	2	0	3	0	4	6	8	0	2	4	6	0	2	6	7	4	0	4	85
5	5	2	3	2	4	0	1	2	6	1	2	3	5	0	1	2	3	0	0	4	5	4	1	5	71
6	7	2	3	6	5	0	2	2	7	0	3	2	8	0	2	5	7	0	2	8	5	3	1	2	80
7	4	3	1	5	8	2	4	4	3	3	3	2	6	3	3	6	4	3	0	4	5	1	0	3	67
8	3	0	2	4	7	1	2	4	2	2	1	2	8	0	1	7	2	7	0	5	3	1	2	0	65
9	6	1	0	5	6	0	4	4	6	3	5	4	2	1	1	0	1	0	2	5	5	0	3	0	69
10	6	1	0	5	6	0	4	4	6	3	5	4	2	1	1	0	1	0	2	5	5	0	3	0	65
11	1	2	5	8	9	0	1	4	4	2	1	2	3	0	1	3	2	7	0	3	5	4	2	4	69
12	2	1	8	7	4	2	0	2	4	2	1	0	3	1	3	2	1	0	3	6	5	5	2	6	52
13	4	3	1	8	7	0	2	4	4	2	1	0	3	1	3	2	1	0	3	6	5	5	2	6	69
14	3	0	2	7	4	6	1	3	3	2	4	7	5	0	1	7	0	7	0	4	5	4	0	4	67
15	5	0	1	1	6	4	3	2	4	0	1	5	4	0	1	0	1	0	7	5	3	1	0	3	65
16	5	1	1	4	6	2	4	4	4	4	4	4	2	1	1	2	1	0	7	5	3	1	0	4	69
17	5	2	2	5	6	6	1	4	4	4	4	4	2	1	1	0	1	0	7	5	3	1	0	3	65
18	7	1	2	4	5	0	2	4	4	4	4	4	2	1	1	3	2	7	0	4	5	4	2	4	69
19	5	1	2	4	5	0	2	3	4	0	1	5	4	0	1	7	0	7	0	4	5	4	2	4	65
20	6	3	8	5	6	3	1	7	3	2	8	8	2	0	3	2	1	0	3	6	5	4	2	6	69
21	2	0	4	7	0	1	2	3	6	8	7	2	6	0	1	1	0	0	3	4	6	1	0	3	65
22	3	1	5	6	7	0	6	5	7	2	7	3	9	0	1	2	2	0	3	4	6	1	4	5	94
23	2	0	4	3	2	1	2	8	3	2	8	3	9	0	1	7	1	0	3	4	6	1	4	3	94
24	4	1	7	0	3	4	1	2	8	10	7	3	9	0	1	2	2	0	3	7	0	0	0	2	98
25	3	8	2	2	2	9	2	1	5	9	3	6	5	0	2	0	4	1	8	7	1	6	7	1	77
26	2	3	0	1	2	7	3	4	6	5	6	1	0	5	0	5	5	0	1	6	7	1	6	7	77
27	4	3	1	7	2	8	2	4	7	7	3	2	3	0	2	0	4	1	9	7	0	2	0	3	88
28	3	4	0	8	1	9	1	4	8	8	2	1	0	6	1	3	7	0	7	1	6	5	0	2	88
29	2	3	5	3	2	7	6	4	5	1	0	0	4	5	2	7	3	1	0	7	0	2	0	4	88
30	1	6	8	7	1	9	7	0	0	5	7	9	8	1	3	2	0	1	2	5	1	3	2	0	64
52	57	58	56	69	85	56	65	65	56	75	82	55	62	40	43	38	29	56	56	43	59	66	47		1376

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HOURS B.S.T.

DATE	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	TOTAL
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2	4	1	0	2	6	3	1	2	5	2	3	2	5	2	0	2	5	3	2	1	4	5	4	2	60
3	5	2	0	3	6	4	0	3	3	1	3	3	2	3	1	3	5	2	6	3	5	1	0	2	66
4	3	1	0	1	7	1	2	4	3	4	1	1	6	6	1	1	3	1	4	6	3	0	2	5	59
5	4	1	0	2	6	1	0	2	1	1	0	2	4	2	0	1	2	1	1	0	3	3	0	2	47
6	5	2	0	3	5	0	1	1	7	1	0	0	3	4	0	4	3	0	2	0	4	2	6	2	57
7	6	0	1	1	5	2	0	0	8	0	2	1	5	1	0	2	6	2	3	1	6	3	5	4	52
8	4	2	1	2	6	1	0	2	1	1	0	1	4	0	0	1	7	1	3	2	4	2	1	0	53
9	5	1	1	2	5	2	0	1	0	0	2	1	2	1	0	0	8	2	3	5	7	3	5	1	65
10	4	2	0	3	4	3	0	0	4	1	1	1	3	2	0	2	7	1	2	4	6	1	2	0	54
11	3	1	0	2	5	4	2	1	3	0	0	2	4	1	0	1	6	2	0	3	5	1	1	0	55
12	4	1	0	3	4	2	2	0	4	1	1	3	3	0	2	3	7	2	1	2	4	2	3	0	50
13	4	1	0	2	5	3	2	1	4	0	0	1	4	1	0	2	8	3	0	2	5	1	2	0	58
14	5	2	1	1	4	4	0	0	3	1	2	1	5	2	0	5	7	2	3	6	6	3	0	1	71
15	6	2	1	2	5	1	2	3	4	1	3	2	6	3	1	6	8	3	5	7	7	0	3	6	51
16	3	2	1	3	4	5	5	3	5	1	0	3	0	8	4	2	3	0	8	2	0	1	7	5	86
17	1	2	1	3	5	2	1	3	1	5	3	2	0	3	1	3	3	5	5	5	1	7	0	2	75
18	2	4	3	2	3	3	4	0	1	2	3	2	3	7	3	2	3	7	5	5	4	0	1	3	84
19	1	2	1	3	2	4	5	1	1	5	1	3	1	6	4	4	3	5	5	1	3	0	1	2	72
20	2	4	2	2	3	0	3	1	1	2	3	2	2	4	3	2	0	7	6	6	0	3	0	1	63
21	1	3	2	3	2	4	4	5	1	1	2	1	2	3	1	4	4	0	7	2	7	0	3	0	81
22	2	1	0	2	3	1	1	2	0	4	0	1	4	1	5	6	5	4	0	7	4	2	1	4	75
23	3	2	0	3	2	6	0	3	9	3	1	5	3	2	3	4	7	1	4	4	7	4	4	3	60
24	2	3	2	3	1	2	4	2	5	2	0	1	4	1	2	2	1	0	7	1	4	1	4	1	59
25	3	1	0	2	0	3	1	0	4	3	1	6	3	2	0	2	7	1	0	0	0	2	2	0	63
26	1	4	0	1	1	3	2	1	3	4	1	1	5	7	0	1	0	0	0	0	0	0	0	1	80
27	2	1	1	0	0	3	0	3	9	2	1	1	4	6	2	1	0	0	3	3	6	1	5	0	66
28	4	8	1	4	7	0	8	3	4	4	5	7	3	0	7	7	0	0	2	5	0	3	4	1	76
29	0	7	3	0	1	4	1	8	2	3	4	3	0	1	0	0	2	6	1	0	3	0	3	0	66
30	7	1	0	2	3	6	2	3	4	2	4	4	0	1	3	7	4	1	5	4	5	6	4	0	52
47	51	58	38	44	45	46	48	59	51	51	41	38	27	62	37	55	35	53	57	48	45	51	36	32	

AUGUST

HOURS B.S.T.

DATE	24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	TOTAL
1	3	2	2	2	5	2	1	1	5	3	2	2	4	5	3	1	6	3	2	2	4	2	2	3	69
2	2	1	3	3	4	4	2	2	2	1	2	3	5	4	0	2	5	2	1	3	3	3	3	1	60
3	1	3	0	2	2	3	1	2	5	0	0	2	7	1	2	2	4	2	2	2	2	2	2	0	53
4	5	2	2	4	2	1	1	3	1	1	0	1	4	1	2	3	4	3	2	3	4	3	4	0	54
5	5	2	1	2	3	2	2	2	3	2	0	2	5	5	5	2	4	2	1	2	4	1	0	2	66
6	3	2	2	1	2	2	0	1	3	2	3	3	1	5	3	2	5	0	2	5	4	0	2	4	53
7	4	2	2	0	4	3	2	4	4	6	2	2	6	2	2	7	3	2	0	2	2	2	2	3	64
8	2	2	0	3	4	5	2	4	7	4	2	2	7	3	0	4	5	0	0	2	6	2	0	2	67
9	4	4	0	2	2	1	0	5	2	4	2	4	7	1	1	3	5	2	2	2	3	3	1	2	59
10	5	5	0	3	4	2	2	2	7	4	1	1	9	2	0	2	5	2	0	2	4	2	0	2	58
11	5	2	1	0	4	1	2	0	4	7	1	0	3	1	1	4	3	2	2	3	2	2	1	2	53
12	6	2	0	1	5	2	2	1	8	4	1	0	3	1	0	2	2	2	3	2	4	4	0	2	47
13	1	1	1	2	3	1	2	1	2	2	1	2	4	1	3	5	2	2	2	0	3	2	0	3	67
14	5	3	1	2	5	1	0	4	2	7	0	2	5	3	0	1	4	2	3	0	0	1	0	2	47
15	5	2	1	2	3	2	2	1	1	0	1	2	4	1	3	5	2	1	3	0	3	2	0	2	52
16	5	2	1	2	2	1	2	4	1	3	1	2	5	3	0	4	6	2	3	0	4	4	0	2	80
17	5	3	2	3	4	2	1	1	6	5	4	4	7	3	2	4	6	5	4	0	1	2	1	4	50
18	2	4	2	3	0	2	7	0	3	1	2	3	0	1	1	2	5	2	6	2	4	5	2	3	60
19	2	3	3	0	4	3	6	4	0	1	2	0	7	0	2	3	4	3	5	3	3	3	0	1	52
20	2	3	7	2	1	1	4	1	3	0	3	2	3	1	2	0	1	3	2	4	2	2	0	4	61
21	3	4	4	3	2	3	2	4	4	1	1	0	3	1	3	0	1	3	3	3	3	2	0	3	45
22	2	3	0	2	0	1	1	1	3	0	1	2	4	1	4	2	3	4	0	4	2	2	4	1	51
23	0	0	4	3	1	3	4	1	3	0	1	2	3	1	1	2	1	3	0	4	3	4	1	4	69
24	0	3	7	3	2	2	4	3	3	0	0	3	4	1	0	4	4	4	2	2	4	5	7	3	82
25	7	2	0	4	1	3	2	1	2	1	8	7	0	2	0	3	4	4	6	4	4	4	2	0	90
26	8	3	8	2	3	4	4	3	10	3	9	2	1	7	0	2	3	4	2	3	3	4	0	2	60
27	3	7	1	1	3	4	2	4	7	2	2	1	1	2	0	3	4	4	3	4	4	4	0	2	63
28	0	6	2	3	2	1	0	5	4	7	5	0	1	3	3	2	4	3	4	3	3	0	1	0	60
29	3	1	1	0	3	4	2	7	1	1	2	2	0	2	2	1	4	4	3	0	4	4	0	4	57
30	0	3	0	3	2	0	0	5	0	1	0	1	3	3	1	0	3	2	1	3	0	2	1	0	45
48	39	47	47	47	27	32	37	49	37	26	42	26	33	25	42	40	54	44	37	30	30	45	35	45	925
56	29	18	27	54	29	21	32	65	31	17	32	75	35	31	44	61	27	23	27	68	22	16	31	931	

TOTAL TIME IN EACH ACTIVITY

LIGHT

MAY	ALERT	SLEEP	DOZE	GROOM	REFT.	REST	DRINK	EAT	URINATE	DEFAECATE	EXPLORE	NEST	TOTAL
4th	8.5	33	2	10.5	2	14	5	6	3	2	7	8	101
9th	11	50	11	9	4	7	1	2	2	3	5	3	108
10th	27	62.5	39	46.5	4	48	0	11	7	12	24	6	287
12th	13	18	16	12.5	3	18	3	5	3	4	12.5	3	111
17th	29	74	33	20	6	14	0	5	1	4	7	1	194
22nd	11.5	31	4	5	2	14	1	4	1	0	3.5	1	78
23rd	11.25	36.5	24	23.25	3	29	4	3	1	4	10	1	150
25th	10.5	18.5	28.5	13.5	4	63.5	1	9	4	3	13.5	3	172
26th	14	19	15.5	13	2.5	17	1	8	4	2	15	3	114
TOTAL	135.75	342.5	173	153.25	30.5	224.5	16	53	26	34	97.5	29	1315
%	10.32	26.04	13.15	11.65	2.31	17.07	1.21	4.03	1.97	2.58	7.41	2.20	

DARK

28th	25	59	31	41	3	56	2	13	6	10	28	7	281
30th	7	29	1	13	2	10	4	5	2	2	6	1	82
JUNE													
2nd	11	20	19	10	2	17	1	7	4	3	8	0	102
4th	21	66	25	12	5	10	1	9	3	4	10	1	167
5th	10.25	25.5	20.25	18	6.5	10	3	8	7	5	12	3	128.5
7th	13	20	16.5	12.5	3	19	3	6	4	5	13	2	117
9th	29	73	32	19	5	13	1	4	1	3	6	1	187
12th	9	17	27	12	3	62	1	8	5	2	12	1	159
14th	26	61	38	45	3	47	0	10	5	9	17	6	267
TOTAL	151.25	370.5	209.75	182.5	32.5	244	16	70	37	43	112	22	1490.5
%	10.14	24.85	14.07	12.24	2.18	16.37	1.07	4.69	2.48	2.88	7.51	1.47	

SUMMATED RESULTS

HOURS B.S.T.

MONTH	24	1	2	3	4	5	6	7	8	9	10	11
JAN	44.4	40.2	19.4	29.1	51.3	16.6	6.9	27.7	61.1	36.1	6.9	41.6
FEB	43	37.5	16.6	43	61	16.6	9.7	52.7	54.1	23.6	12.5	32.5
MARCH	43	31.9	19.4	29.1	38.8	24.1	8.3	47.2	59.7	18	8.3	25
APRIL	48.4	43	20.8	45.8	58.3	13.8	4	40.2	66.6	26.3	19.4	45.8
MAY	38.4	11.5	20.5	41	39.1	10.2	17.3	29.4	30.7	13.4	29.4	30.1
JUNE	38.8	9.4	16.6	33.8	46.6	12.2	11.1	19.4	32.7	16.1	28.8	21.1
JULY	36.3	11.9	6.5	17.8	40.5	19	11.9	13.6	30.3	14.8	13	13.6
AUG	31.1	16.1	10	15	30	16.1	11.6	17.7	36.1	17.2	9.4	17.7
TOTAL	40.4	24.9	17.1	31.2	39.9	17.1	11.9	35.4	45.5	21.4	15.5	29.1

DISTURBED

JAN	37.1	22.7	28.7	30.3	24.2	7.5	10.6	32.5	23.9	28.7	10.6	18.1
FEB	29.4	21.1	27.7	19.4	19.4	26.1	22.7	31.6	52.7	17.7	12.2	28.8
MARCH	22	25	23.2	21.4	23.2	19	17.8	38.8	22	18.4	19.6	10.7
APRIL	34.5	25.5	30.3	22	29.7	8.9	22	29.1	26.1	16.6	20.2	22.6
TOTAL	30.8	23.6	27.5	23.3	24.1	15.4	18.3	33	31.2	20.4	15.7	20.1

GROUND COVER ADDED

MAY	34.8	32.3	28.9	24	36.7	29.9	23	31.3	34.3	34.8	26.9	20.5
JUNE	28.8	31.6	32.2	31.1	38.3	47.2	31.1	36.1	36.1	31.1	41.6	45.5
JULY	24.4	26.5	30.2	19.7	22.9	23.4	23.9	25	30.7	29.6	21.3	19.7
AUG	26.5	21.6	21.6	21.6	15	17.7	20.5	27.2	20.5	14.4	23.3	14.4
TOTAL	28.7	28	29.4	25.2	28.2	29.5	24.6	29.9	30.4	27.5	28.3	25

SUMMATED RESULTS

HOURS B.S.T.

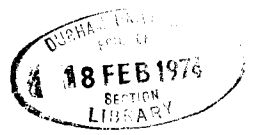
MONTH	12	13	14	15	16	17	18	19	20	21	22	23
JAN	48.6	9.7	25	27.7	47.2	44.4	16.6	23.6	51.3	11.1	1.3	16.6
FEB	25.7	18.1	15.9	19.6	34	43.1	31.	15.9	24.2	21.9	9	9.8
MARCH	33.3	13.8	19.4	41.6	28.8	30.5	23.6	31.9	38.8	18	15.2	13.8
APRIL	18	4.1	15.2	18	20.8	37.5	38.8	2.7	33.3	27.7	16.1	4.1
MAY	51.3	9.7	18	27.1	29.1	22.6	22.2	33.3	51.3	11.1	12.5	9.7
JUNE	60.8	5.8	19.1	35.8	39.1	16.6	23.3	28.3	34.1	20	16.6	5
JULY	51.3	4.1	33.3	34.7	58.3	20.8	18	50	55.5	15.2	6.9	26.3
AUG	33.3	11.1	9.2	36.1	43.5	20.3	16.6	16.6	9.2	12.9	7.4	4.6
TOTAL	39.5	10.9	17.4	27.8	37.5	24.8	21.3	25.3	38.2	15.3	10.2	13.8

DISTURBED

JAN	25.7	18.1	15.9	19.6	34.	43.1	31	15.9	24.2	21.9	9	9.8
FEB	12.7	15.5	20	14.4	19.4	43.3	17.7	15	28.3	15.5	11.6	2.7
MARCH	9.5	25.5	15.4	11.3	17.2	16	20.8	28.5	16	15.4	10.1	2.3
APRIL	10.1	18.4	10.7	19	15.4	16.6	8.9	26.7	22.6	16.6	12.5	13.6
TOTAL	14.5	19.4	15.5	16.1	21.5	29.8	19.6	21.5	22.8	17.4	10.8	7.1

GROUND COVER ADDED

MAY	32.3	28.4	23	30.3	24	26.4	26.4	23.5	33.8	33.3	27.4	22.5
JUNE	30.5	34.4	22.2	23.8	21.1	16.1	36.6	31.1	23.8	32.7	36.6	26.1
JULY	14	32.2	19.2	28.6	18.2	27.6	29.6	25	23.4	26.5	18.7	16.6
AUG	18.3	13.8	23.3	22.2	30	24.4	20.5	16.6	16.6	25	19.4	25
TOTAL	23.8	27.2	21.9	26.2	23.3	23.6	28.3	24	24.4	29.4	25.5	22.5



DISCUSSION

The results from the Automatic Activity Recorder described here show that the C. glareolus used, under normal cage conditions, developed a definite rhythmical behaviour pattern of approximately four-hourly periodicity. The occurrence of short-term rhythmical activity has been reported previously in many species of small mammals. Crowcroft (1954) demonstrated such rhythms in Sorex araneus and Sorex minutus. Among the Cricetidae, Miller (1955), St. Girons (1960, 61) and Stebbins (1968) found that Clethrionomys did show rhythmical behaviour while Davis (1933) and Hadfield (1940) demonstrated the same in Microtus. Southern (1954) working on Mus musculus and Grodzinsky (1963) on Apodemus agrarius were able to demonstrate rhythms in Murids.

The present series of experiments was designed to discover whether the rhythm shown by the test animals in the laboratory was a natural response or whether they were reacting to abnormally uniform laboratory conditions. Having established a well-defined four-hourly rhythm in the automatic recording unit (a rhythm built up over three weeks' laboratory acclimatisation), the short three-hourly disturbance quickly destroyed it.

This would seem to indicate that, in the wild, natural disturbances would quite easily remove any short-term periodic behaviour. For example, occurrences like strong winds, presence of predators, heavy rain and freezing

conditions must affect the behaviour patterns of small mammals. This does not mean that more definite diurnal rhythms geared to dawn and dusk are not present in the wild in some species, but it does indicate that short-term rhythms described from laboratory experiments may not appear in wild populations. The dawn and dusk activity peaks are well shown from trapping and tracking results in, for example, Apodemus and Peromyscus, which rarely seem to come above ground during daylight (Brown 1956, Southern 1964, Falls 1968). In the wild it seems that Apodemus sp. and Peromyscus sp. have a diet richer in protein and fat than Clethrionomys and Microtus, and feed heavily on e.g. insects and other arthropods. It may then be possible for species exploiting such a diet, for example, Mus musculus and Peromyscus maniculatus to survive without food during the hours of daylight; though there is some indication that Apodemus burrows often contain food stores (Cleminson, personal communication). Cleminson also demonstrated using time lapse photography that Apodemus did not emerge from the nest in the laboratory during daylight hours (eight hours light, sixteen hours dark, no dusk or dawn effect), and therefore showed no short-term rhythm associated with feeding.

He presumes that any eating during daylight must be limited to refectation since the individuals studied did not store food in the nest. He did have visual (photographic) evidence of refectation, but could not separate this from grooming. In Clethrionomys, during the direct observation

experiments, the author was able to observe refection closely and it has since been noted in a breeding colony of Apodemus obtained from the South of France. In the past, it has been noted that other species may, as an abnormality, practice coprophagy in captivity, for example gorillas and chimpanzees. However, a growing amount of evidence is appearing which indicates that not only rabbits (Kulwick, Roman, Straglia and Pearson, 1953) but many rodents depend on refection to provide vitamins. Sharkey (1971) compared the effect of feeding rabbits and guinea pigs (both prevented from refeeding) on fresh lucerne. The rabbits survived indefinitely but the guinea pigs survived for short periods only. Earlier experiments by Hintz (1969) showed that the prevention of refection in guinea pigs decreased the apparent digestibility of dry matter, organic matter, crude protein, ether extract and acid detergent fiber when these rodents were fed on alfalfa meal or a semi-purified diet. Faeces from semi-purified diet animals were analysed for eight minerals using mass spectroscopy and showed an increase of minerals in faeces compared with animals allowed to practice coprophagy. Hintz therefore suggests that refection is important in the utilising of nutrients by rodents and should be considered in any digestion trial. Stillings and Hackler (1966) studied the effect of refection on protein utilisation in the laboratory rat. In a metabolic study in which male weanling rats consumed 5 g. daily of diets containing 10% protein, the

prevention of refection decreased nitrogen absorption and increased urinary nitrogen excretion and metabolic faecal nitrogen. In a growth study in which rats were given diets containing 10% protein with no restriction on amount of food provided, prevention of refection gave lower protein efficiency ratios and weight gains, but had little effect on food intake.

It seems, therefore, that refection in Clethrionomys may be present under natural conditions, but more detailed work needs to be carried out on refection in small mammal species. For species like Clethrionomys with their bulky diet of foliage, berries, etc., it may be necessary for them to forage more often than Apodemus and refection may play a smaller part in their dietary requirements.

In the first series of experiments, from January to April, the uncovered run may have been a rather "hostile" environment for the voles and the four-hourly rhythm could have been a regular feeding activity disrupted by a strong stimulus as mentioned in the summated results section (Page 62). When the run was covered to approximate more closely to natural conditions and grain was scattered randomly in the run to produce the need for foraging as the vole would have had to do in the wild, then the rhythm broke down. Soon the animal began to store food and ceased to use the run merely as corridors between nest and food boxes, indeed, after a few days, subsidiary nests were built in the corridors near to

some of the food stores. Both sets of experiments would seem to indicate that short-term rhythmical activity may be unusual in the wild. The need to collect and store food, make nests and become involved in social interactions means that the animal will respond to many non-rhythmical stimuli during the diel cycle.

A failing of most activity recording apparatus is that it seldom records anything but feeding or occasionally movement (Ashby 1972). For example, what were the voles doing when they were "inactive" according to the automatic recording? There are many aspects of the life of small mammals which can only be studied by visual observation over a prolonged period or by very sophisticated equipment linked to a computer to analyse the data. The second series of experiments using direct observation showed that the vole studied was seldom "inactive", though it may not have been actively moving about the cage. This fact could not have been more than guessed at except by direct observation. The techniques used in the direct observation experiments were similar in principle to those used by Crowcroft (1966) to study social interactions in the house mouse. A percentage breakdown of activities has been given in the results section. About 60% of every diel cycle was spent immobile and asleep and resting and 35% of the total was spent in activities which could have either been seen above ground or deduced by trapping. The vole studied in these direct observation experiments was in a

restricted environment compared with that found in the "run" and in the wild. The cage was small, food was readily available and there was no need for prolonged explorations or foraging activity, hence resting (eyes open, respiration normal) may not be as important in the wild. A fair proportion of the 19% total for this activity should be perhaps transferred to feeding/exploration under natural conditions. It must be emphasised that, though the vole is in its burrow or nest, it is not necessarily inactive, and also that doze/sleep which is the only period of time of inactivity rarely occupies as much as fifteen minutes consecutively. It is rare for any other activity to last more than five minutes continuously. One minute is the modal period shown in the observed activity graphs.

The condition of the fur in small mammals is vital to their health, hence the 13% of the time spent in grooming. In species like Clethrionomys which spend lengthy periods underground in damp burrows and forage extensively in leaf-litter, etc., the fur could rapidly become dirty and matted with earth and vegetable refuse, which would impair its efficiency as an insulator. Grooming also can help to remove ecto-parasites such as fleas, lice and mites.

It is interesting to note that the relative total time spent in each activity shows virtually no difference between the light and dark periods. This may not be a true reflection of normal behaviour since the results are so uniform. However,

the red filter used during the dark periods was the same as that employed by Cleminson. This filter was the only one immediately available at the time, and it had proved satisfactory in Cleminson's experiments, which would seem to rule out the possibility that the vole was registering daylight. Southern (1964) has indicated that C. glareolus does not respond to light in the deeper red end of the spectrum. If the behaviour of the vole studied was typical then it would indicate in uniform conditions C. glareolus may have the same activity spectrum during day and night, though once again, the extremely restricted conditions in which the animal was observed make it difficult to be sure that these results apply in wild populations. In any case, the lability of diel activity patterns in small mammals may be much greater than earlier restricted laboratory studies with restricted cages have shown. For example, Grodzinsky (1963) has shown that Microtus agrestis and C. glareolus have ratios of activity between day and night which vary with season. He suggests that they are mainly nocturnal in summer and diurnal in winter and spring. He also considers that there may be more short-term activity periods per diel cycle in winter than summer possibly correlated with increased need to obtain food to maintain body heat during the cold weather. He noted that in Apodemus agrarius, when living on a bulky diet, total activity per diel cycle increased and three nocturnal activity peaks were present instead of one when the

animal was fed on a concentrated diet during a nine or ten hour night. Thus the composition of diet is another factor which can affect short term rhythm in small mammals.

Long term, i.e. dawn and dusk, rhythms can also be surprisingly variable. This variation has been admirably demonstrated by recent work on water voles, Arvicola terrestris. Southern (1964) and Stoddart (1969) found that the populations that they studied were mainly diurnal. But Ashby, Harling and Whiles (1969) using visual observations of a population in Old Durham Beck, near Durham, have shown an almost constant level of activity throughout the diel cycle during the late spring and early summer. Later studies at the same time of year by Creasy, Duckett and Ashby (unpublished) on other vole habitats on the river gave even more divergent results. Initially, the River Wear, a few hundred yards from the previous study area, was watched by Ashby on a succession of evenings. No activity was recorded. Using a tracking technique Creasy and Duckett then studied the area concerned over periods of 24 hours. They used the extent of footprints made by Arvicola as an index of activity. This technique involved recording the number of sites visited by Arvicola, the proportion of each site walked over and the intensity of footprinting. Four trials were carried out during a three week period in which the mud at 50 sites was examined and then smoothed over at four-hourly intervals. The activity recorded was concentrated in the period from 22.00 to 06.00

hrs. A parallel study on a small side stream some distance away again showed more nocturnal and crepuscular activity than diurnal and the most intense activity was recorded before midnight.

Duckett (unpublished) also accompanied this field study by a laboratory study carried out in spring and summer on six males and two females using a modification of the automatic recording unit described in this thesis. During the spring normal seasonal increase in daylength was used. In midsummer daylength was reduced from 16 hours to 12 hours and again to 8 hours. The timeswitch used provided a dawn and dusk effect and a few days acclimatisation were allowed after each change before activity records were made.

In March, the degree of activity by day and night was almost the same. With normal daylength, in summer activity was higher in darkness by about 75%, but with reduced daylength the distinction between nocturnal and diurnal activity was reduced but not removed. Synchronous peaks of activity were shown in a colony kept in separate runs, five peaks were present in 24 hours using 12 hours and 16 hours of daylight and four using 8 hours daylength. No differences between sexes were apparent in this study.

These results show clearly that the diel activity patterns of the water vole can vary considerably in the field and it can also vary in the laboratory depending on the conditions provided. Ashby (personal communication, 1972) considers that

disturbance may be a factor in the difference between activity on the River Wear and the other sites, but that it could not be completely responsible. He suggests that the amount of cover available along the water courses (thicker cover on the side streams) may account for the high degree of diurnal activity. Vincent (unpublished) in a more recent study near Durham concluded that the factors controlling activity patterns in Arvicola are complex and that the activity pattern is highly labile and variable. These conclusions may also apply to the activity patterns in Clethrionomys in view of the results described here using the automatic activity monitoring unit during the months from May to August, where cover was provided. In this series of experiments rhythmical activity was removed when more "natural" conditions (cover and food foraging) were provided instead of an open run. It is clear from Figs. 5 - 8 that diurnal activity and nocturnal activity were nearly the same and during the direct observation experiment the vole used also showed almost the same activity pattern during light and dark periods (Fig. 29).

Work by St. Girons (1960) found that in the six C. glareolus males subjected to normal lighting and daily temperature variation which she studied, a short-term rhythm of two to three hourly periodicity appeared. This was unaffected by seasonal variation of either factors mentioned above, daylength or temperature. This result is interesting in that throughout the author's series of experiments using

the run, the short-term rhythm was also unaffected by the photoperiod or time of dawn and dusk.

However, Grodzinski (1963) has pointed out that diurnal and nocturnal ratios of activity in small rodents can vary markedly with seasonal changes. He considers that Microtus agrestis and Clethrionomys glareolus have been shown to be mainly nocturnal in summer and diurnal during the rest of the year, that there are more short-term activity periods per 24 hours in winter (8 - 10) than in summer (5 - 7), that overall activity is greater in winter than in summer and that males are more active than females. The last conclusion may indicate that more females should have been used in the author's experiments. Grodzinski also noted that diet can affect activity patterns; when Apodemus agrarius was fed a bulky diet, the length of time spent active in each 24 hour cycle increased and three peaks of activity occurred during the night. On a concentrated diet only one peak of activity occurred during a 9 - 10 hour night.

Work by Stebbins (1968) supports Grodzinski's conclusions about the lability of rhythmical activity in small mammals and has added to the number of factors known to cause variability in activity of members of the Cricetidae. His experiments were carried out in the field, on the seasonal changes in the activity of C. gapperi, C. rutilus and Peromyscus maniculatus kept in wire mesh enclosures containing nest boxes. Two areas of study were used one at Edmonton,

and at Heart Lake (62°N) in the north of the forest belt of Canada. The most interesting results were those obtained by a comparative study of activity of C. gapperi from the two stations. During the summer overall activity increased when the animals were in breeding condition and though the amount of activity was much the same at both sites, its distribution differed markedly and consistently throughout the year. First, at the northern site, in summer and winter, a strong peak of activity occurred one and a half hours after sunset followed by a second peak three hours later. A small peak occurred one and a half hours after sunrise and then an irregular activity series for the remainder of the diel cycle. Secondly, in the southern site this picture was almost completely reversed. The main peak of activity, in summer and winter, occurred about an hour after sunrise, a smaller peak three to four hours afterwards, followed by an irregular rhythm for the rest of the diel cycle. The lowest activity was recorded in the early morning. Thus, in the north, C. gapperi was virtually nocturnal and in the south diurnal. Even more interesting is that individuals changed from north to south changed from nocturnal to diurnal activity, strongly indicating that their activity patterns were governed largely by environmental considerations. This is a conclusion which is supported by the author's results. As soon as the uniform laboratory environment was changed by the introduction of a disturbance or cover, regular rhythmical activity was

removed. But as Ashby (1972) has pointed out, Stebbins' animals could not have been affected by disturbances as they needed to burrow through snow in winter to reach their food. Daylength, however, was not the most important factor since it varied in the northern site more extensively than in the southern, being longer in winter than summer.

The effect of daylength was not intentionally studied in the author's experiments. In the visual observation experiments there was no provision made for a dusk and dawn effect. However, natural daylength was used throughout the automatic recording series. Thus daylength varied throughout the period of study from January to August. In January there was a peak of activity at dusk and dawn but these were of much the same size as those at other four-hourly rhythm peaks during the undisturbed phase. During the disturbed phase there were small peaks at dusk and dawn. In February, the female used showed an activity peak at dawn and not dusk in the undisturbed phase. During the disturbed phase a peak at dusk and dawn was evident. In the recovery phase peaks at dusk and dawn were shown. In March each phase showed dusk and dawn peaks though the mid-day peak shown by this vole was higher than either dusk or dawn. In April the disturbed and recovery phases showed a dawn peak while a dusk peak appeared only during the undisturbed week; the recovery and disturbed phases showed a definite drop in activity at this time.

In May, the first of the covered versus uncovered series,

the uncovered phase showed no peak at dawn but one at dusk, during the covered phase there was a slight increase in activity at dawn but none at dusk. During June, a peak was evident at dawn in both phases but only at dusk in the uncovered weeks. In July, activity peaked at dawn and dusk during the uncovered phase. During the covered weeks, however, no peaks appeared at either time. Dusk and dawn in Durham (lat. 54°N) at this time are very prolonged and on Midsummer day darkness never really falls, there is almost continuous twilight. In August, activity peaked only at dusk during the uncovered phase, no other peaks were evident. No positive correlation between dusk and dawn and seasonal variation of activity can be deduced from these results.

These results do not correspond to those noted by St. Girons (1960, 1961) in C. glareolus. She found that the duration and height of peaks of activity were influenced by seasonal fluctuation in daylength. Her male voles were most active during the winter and activity was at its highest in February and lowest in September. She considers that the influence of the solar rhythm is important. A peak of activity was recorded shortly after dusk and another distinctly before dawn. The important factor seems to be sunrise. The number of activity periods increased during the winter, on average of 10 during the diel cycle in December and 5-7 in July. Diurnal activity in spring and summer was more marked than in winter representing 31% of the total diel activity in June and only 6% in November. She

attributes this variation to changes in daylength.

It may be useful to mention here an aspect of the local environment which the author had not considered during this series of experiments. This is the effect on "daylength" of the street lighting in the area of the laboratory in which the experimental animals were housed. The laboratory windows were large allowing light to fall on the run, the intensity was approximately that of full-moonlight. The possibility that these lights might have affected the results was not considered until all the experiments had been concluded. There is evidence that strong moonlight can prevent nocturnal activity in Apodemus sylvaticus (Kikkawa, unpublished). Thus the activity cycles of the voles used in these experiments may have been affected but without repeating the experiments excluding the street lights this effect, if any, cannot be deduced.

Behaviour in small mammals is a complex study, diel activity being an overall reflection of the way an animal reacts to its environment. Social interactions must be considered in such a study and their importance depends upon the social hierarchy in a particular population. Brown (1966 and 1969) has shown that a system of dominance is present in Apodemus sylvaticus. This social hierarchy produces a stable society controlled by a dominant male, which regularly patrols its territory of four to six acres maintaining its position by aggression and territory marking. Brown states that

intraspecific control by adult males keeps the population relatively stable during the spring and early summer when rapid breeding is occurring, the young being forced to avoid the dominants or disperse. Since the dominant male may be called upon to defend his territory at any time, certainly during the night, the time of maximum activity, short-term rhythms such as those shown by Miller (1955) may not be possible in the wild. Although there is no direct evidence that C. glareolus populations have the same kind of social hierarchy as A. sylvaticus i.e. where a dominant male may control a large territory, there can be little doubt each male and probably each female has its own territory and burrow systems which it will defend against intruders. During preliminary trials with the run a "strange" male was introduced to the run while its previous occupant was still in residence. This resulted in several bouts of mutual aggression with the intruder being attacked continuously until it was able to retreat behind a closed treadle. Each fight involved considerable preliminary squeaking. This was noted several times in the wild when trapping, if a released vole ran down the wrong burrow, it was soon ejected. However, the author was never able to ascertain whether the intruder had entered an Apodemus or Clethrionomys burrow.

Aggression can, therefore, be an important factor in controlling small rodent behaviour. In fact, Barnett (1965) and Grant and Mackintosh (1963) have demonstrated that agonistic conflict in male Rattus norvegicus can cause stress syndromes, e.g. enlargement of the adrenal glands and even

death, with little sign of external injury, where retreat by the subordinate is prevented. Any study of activity patterns in small rodents must therefore contain an element of social interaction if the results are to reflect what happens in the wild. The visual observation experiments were a preliminary attempt to produce a very general picture of the overall activity patterns of C. glareolus in a simple environment. Social interactions were to be studied later.

Ashby (1972) reports observations of a colony of C. gapperi which were continually active for six hours after a resting period possibly due to social stimulation. In the author's breeding colonies of forty A. sylvaticus and nine Acomys (spiny mice) once activity has begun (usually at dusk), it continues throughout the night without pause. While some individuals are resting, others will be active, some feeding, some fighting, etc. The cage containing the Spiny mice has a wheel which acts as an important "activity sink", much in the same way as a piece of metal in electronics can act as a "heat sink". One, two or sometimes three individuals use it at once, at least every five minutes. Kavanau (1966) indicates running activity in a wheel to be a reliable measure of total activity. It would have been interesting to compare wheel activity in C. glareolus with data from the automatic activity monitoring unit. However, the vole used could not be persuaded to run in the wheel provided. This may have been a quirk on the part of this individual since Ashby

(personal communication) had no difficulty in getting Clethrionomys to use wheels in his experiments.

The direct observation experiments show that Clethrionomys may be active for a far longer time during the diel cycle than Grodzinski et al have suggested. For example, Grodzinski and Gorecki (1967), Gorecki (1968) and Drozd (1968) have suggested that Clethrionomys is active i.e. moving about outside the nest, for about 15% of the 24 hours. In the experiments made by the author, the vole studied was active for 35% of the time during which it was observed, in both light and dark. This result shows that not only was this individual more active than Polish workers have considered Clethrionomys in general to be, but it showed virtually the same activity pattern during light and dark periods, which indicates that, in the wild, nocturnal and diurnal activity in Clethrionomys may be much more uniform than has hitherto been considered.

Sadleir (personal communication) has suggested that Peromyscus maniculatus spends a much greater portion of the 24 hours active than the authors mentioned above believe to be the case with Clethrionomys. Vincent (unpublished) has observed individuals and groups of Arvicola in large outdoor enclosures. He records that 25% of each 24 hours is spent active in winter and almost 40% in mid-summer.

The major conclusions which can be drawn from both the automatic recording and the direct observations are as follows.

The activity pattern of C. glareolus can vary considerably depending on the conditions in the laboratory. If a short-term rhythm appears it can be removed by a strong stimulus indicating that in the wild this kind of periodicity may rarely occur, though there is possibly an innate rhythm associated with the need to feed at regular intervals. In the laboratory a constant temperature was maintained. It may be that if temperature was lowered the four-hourly rhythm could become shorter as the need to eat more often to maintain body heat becomes apparent.

Activity peaks at dusk and dawn under natural lighting conditions in Durham are shown, but in many cases these are not greater than peaks at other times. No definite correlation between dusk and dawn stimuli and activity are shown. This may be associated with the fact that C. glareolus in the burrow and under cover may be continuously active throughout the diel cycle when conditions are favourable, e.g. lack of predators, absence of extreme heat or cold, good food supply, etc. Visual observations of activity demonstrate that the vole lives in short bursts of activity with "inactive" periods seldom lasting for more than fifteen minutes.

The summated results show that with an open run in uniform conditions a four-hourly rhythm is very marked. Activity is fairly constant with a covered run and the need to forage and store food.

It is suggested that more work is necessary on diel

rhythms in C. glareolus. Laboratory experiments in which the variety of stimuli found in nature are present should be designed and visual observations, both in the laboratory and in the field, may produce a more complex and complete picture of the life of this small mammal.

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APPENDIX

Statistical treatment of Direct Observation Results

Small numbers of random events tend to follow a Poisson Distribution and successive terms of the expansion $e^{-m} (1 + m + \frac{m^2}{2!} + \frac{m^3}{3!} + \frac{m^4}{4!} \dots)$ give the probability of the occurrence 0, 1, 2, 3, 4 events etc. where e is 2.7183 (a universal constant) and m is the average number of events. These probabilities can be obtained from tables of the Poisson Distribution Function $e^{-m} \frac{m^x}{x!}$ for the indicated values of x and m . Frequencies can then be calculated by multiplying the probability by the total number of observed events. Charts showing these data are given below and these are expressed graphically in Fig.41.

A "Chi-square" test can be applied to these data to show how well the observed data fit the figures which would be expected in a Poisson Distribution. Chi-square is the sum of the square of the difference between observed and expected frequencies divided by the expected frequency.

$$\text{i.e. } \chi^2 = \sum \frac{(O - E)^2}{E}$$

where χ^2 = Chi-square

\sum = "the sum of"

O = observed frequency

E = expected frequency

Having obtained a value for χ^2 we can use tables of χ^2 distribution, which show the probability of the differences between observed and expected frequencies arising by chance, for given degrees of freedom. The number of

degrees of freedom measures the extent to which the sample frequencies are known in advance to agree with the hypothesised frequencies. In all the following cases 2 degrees of freedom are lost because the mean has been estimated from data as well as making the totals agree. In all cases the values obtained for χ^2 show that the figures do not fit a Poisson Distribution and the differences between observed and expected frequencies are not due to chance.

SLEEP

Time spent sleeping (Add 0.5 min. results to 1.0 min. results because divisions must be of equal size for analysis)

<u>Number of observed sleeping periods</u>	<u>Time spent sleeping</u>
40	1 min.
20	2 mins.
12	3 mins.
7	4 mins.
8	5 mins.
9	6 mins.
4	7 mins.
6	8 mins.
1	9 mins.
2	10 mins.
0	11 mins.
0	12 mins.
1	13 mins.
0	14 mins.
1	15 mins.
1	16 mins.
Total	112

Mean length of sleep period is about 3.4 mins.

Length of Period	0	1	2	3	4	5	6	7	8
Probability of occurrence	.0334	.1135	.1929	.2186	.1858	.1264	.0116	.0348	.0148
Expected Frequency	3.7	12.7	21.6	24.5	20.8	14.2	8.0	3.9	1.7
Observed Frequency	-	40	20	12	7	8	9	4	6

Length of Period	9	10	11	12	13	14	15	16	Totals
Probability of occurrence	.0056	.0019	.0006	.0002	.0000	.0000	.0000	.0000	
Expected Frequency	0.6	0.2	.07	.02	0	0	0	0	111.99
Observed Frequency	1	2	0	0	1	0	1	1	112

SAMPLE SUM OF SQUARES = 1038.12

SAMPLE VARIANCE = 9.3

STANDARD DEVIATION = 3.05

MEAN = 3.4

Using probability table above and grouping 0 + 1, and 7, 8, 9, 10, 11 + 12, because the formula $\chi^2 = \sum \frac{(O - E)^2}{E}$ does not work for expected frequencies smaller than 5, we get a value for χ^2 of 58.95.

Number of degrees of freedom is (No. of groups tested) - 2,
= 7 - 2 = 5.

2 degrees of freedom are lost because the mean has been

estimated from data as well as making the totals agree. Since χ^2 58.95 is well above the value for 0.1 on the χ^2 distribution with 5 degrees of freedom we must assume that the observed figures do not fit a Poisson distribution at all, and that the differences between observed and expected frequencies must be due to something other than chance.

GROOMING

<u>Time spent grooming</u>	<u>Number of observed grooming periods</u>
1 min.	61
2 mins.	14
3 mins.	6
4 mins.	5
5 mins.	3
6 mins.	2
7 mins.	0
8 mins.	0
9 mins.	0
10 mins.	0
	Total 91

Mean length of grooming periods is 1.7 minutes.

Length of Period	0	1	2	3	4	5	6	7	8	9	10
Probability of occurrence	.1827	.3106	.2640	.1496	.0636	.0216	.0061	.0015	.0003	.0001	.0000
Expected Frequency	16.6	28.24	24.0	13.6	5.8	1.9	0.6	0.1	0.3	.009	0
Observed Frequency	-	61	14	6	5	3	2	0	0	0	0

SAMPLE SUM OF SQUARES = 21.44

SAMPLE VARIANCE = 0.21

STANDARD DEVIATION = 0.46

MEAN = 1.2

Working χ^2 out as before we get a value of 105.3 with 2 degrees of freedom, once again showing that the figures do not fit a Poisson Distribution.

DOZE

<u>Time spent dozing</u>	<u>Number of observed doze periods</u>
1 min.	51
2 mins.	21
3 mins.	8
4 mins.	6
5 mins.	3
6 mins.	0
7 mins.	2
8 mins.	1
9 mins.	0
10 mins.	0
	Total 92

Mean length of doze periods is 1.9

Length of Period	0	1	2	3	4	5	6	7	8	9	10
Probability of occurrence	.1496	.2842	.2700	.1710	.0812	.0309	.0098	.0027	.0006	.0001	0
Expected Frequency	13.8	26.1	24.8	15.7	7.5	2.8	0.9	0.2	0.06	.009	0
Observed Frequency	-	51	21	8	6	3	0	2	1	0	0

SAMPLE SUM OF SQUARES = 195.72

SAMPLE VARIANCE = 2.1

STANDARD DEVIATION = 1.4

MEAN = 1.9

Working χ^2 out as before we get a value of 41.9 with 3 degrees of freedom, once again showing that the figures do not fit a Poisson Distribution.

RESTING

<u>Time spent resting</u>	<u>Number of observed rest periods</u>
1 min.	38
2 mins.	18
3 mins.	7
4 mins.	9
5 mins.	4
6 mins.	2
7 mins.	0
8 mins.	1
9 mins.	0
10 mins.	0
	Total 79

Mean length of resting periods is 2.2 mins.

Length of Period	0	1	2	3	4	5	6	7	8	9	10
Probability of occurrence	.1108	.2438	.2681	.1966	.1082	.0476	.0174	.0055	.0015	.0004	.0001
Expected Frequency	8.8	19.3	21.2	15.5	8.5	3.8	1.4	0.4	0.1	.03	.008
Observed Frequency	-	38	18	7	9	4	2	0	1	0	0

SAMPLE SUM OF SQUARES = 23.66

SAMPLE VARIANCE = 0.25

STANDARD DEVIATION = 0.5

MEAN = 1.3

Working χ^2 out as before we get a value of 71.76 with 2 degrees of freedom, once again showing that the figures do not fit a Poisson Distribution.

The figures for sleep, doze and rest and those for explore, alert and groom were added in an attempt to compare passive and active behaviour. Poisson distributions for each group were calculated and all four distributions are expressed graphically in Fig. 42 . Since all six activities separately have already been tested for goodness of fit to Poisson Distributions and have been shown not to follow this pattern, it was decided not to use the Chi-square test for these results. The difference between the observed activity and the expected activity using a Poisson Distribution is shown fairly well in the graph.

It can also be seen from the graph that the modal value for passive and active behaviour is the same, although the mean for passive behaviour is 2.4 mins. while that for active behaviour is 1.4 mins.

PASSIVESLEEP, DOZE, REST

<u>Time spent in Passive Behaviour</u>	<u>Number of observed periods</u>
1 min.	152
2 mins.	59
3 mins.	27
4 mins.	22
5 mins.	15
6 mins.	11
7 mins.	6
8 mins.	8
9 mins.	1
10 mins.	2
11 mins.	0
12 mins.	0
13 mins.	1
14 mins.	0
15 mins.	1
16 mins.	1
Total	306

Mean is 2.4 mins.

Length of Period	0	1	2	3	4	5	6	7	8
Probability of occurrence	.0907	.2177	.2613	.2090	.1254	.0602	.0241	.0083	.0025
Expected Frequency	27.7	66.6	79.9	63.9	38.4	18.4	7.4	2.5	0.8
Observed Frequency	-	152	59	27	22	15	11	6	8
Length of Period	9	10	11	12	13	14	15	16	
Probability of occurrence	.0007	.0002	0	0	0	0	0	0	
Expected Frequency	0.2	0.06	0	0	0	0	0	0	
Observed Frequency	1	2	0	0	1	0	1	1	

ACTIVEEXPLORE, ALERT, GROOM

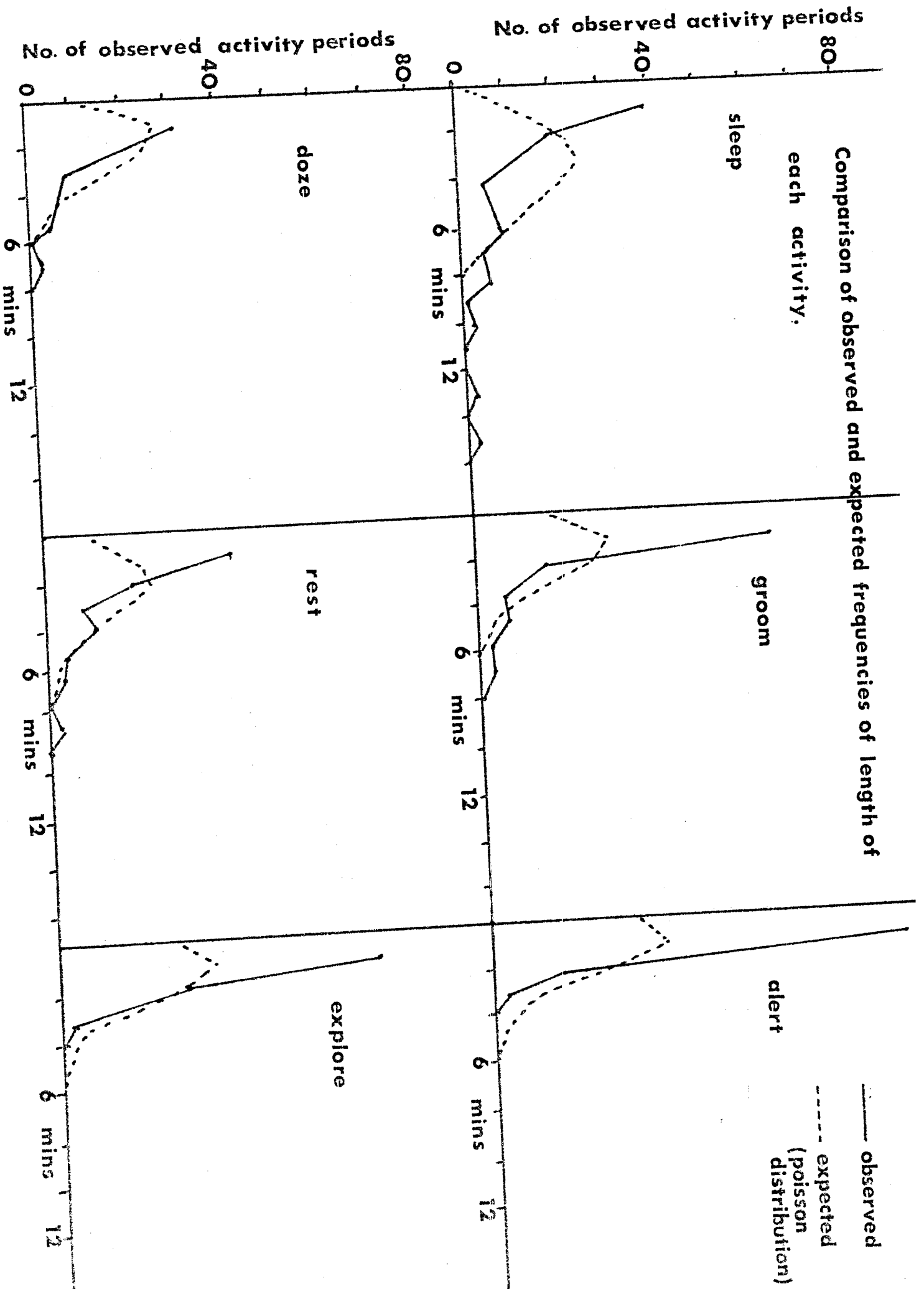
<u>Time spent in Active Behaviour</u>	<u>Number of Observed Periods</u>
1 min.	214
2 mins.	51
3 mins.	11
4 mins.	5
5 mins.	3
6 mins.	2
7 mins.	0
8 mins.	0
9 mins.	0
10 mins.	0
	Total 286

Mean is 1.4 mins.

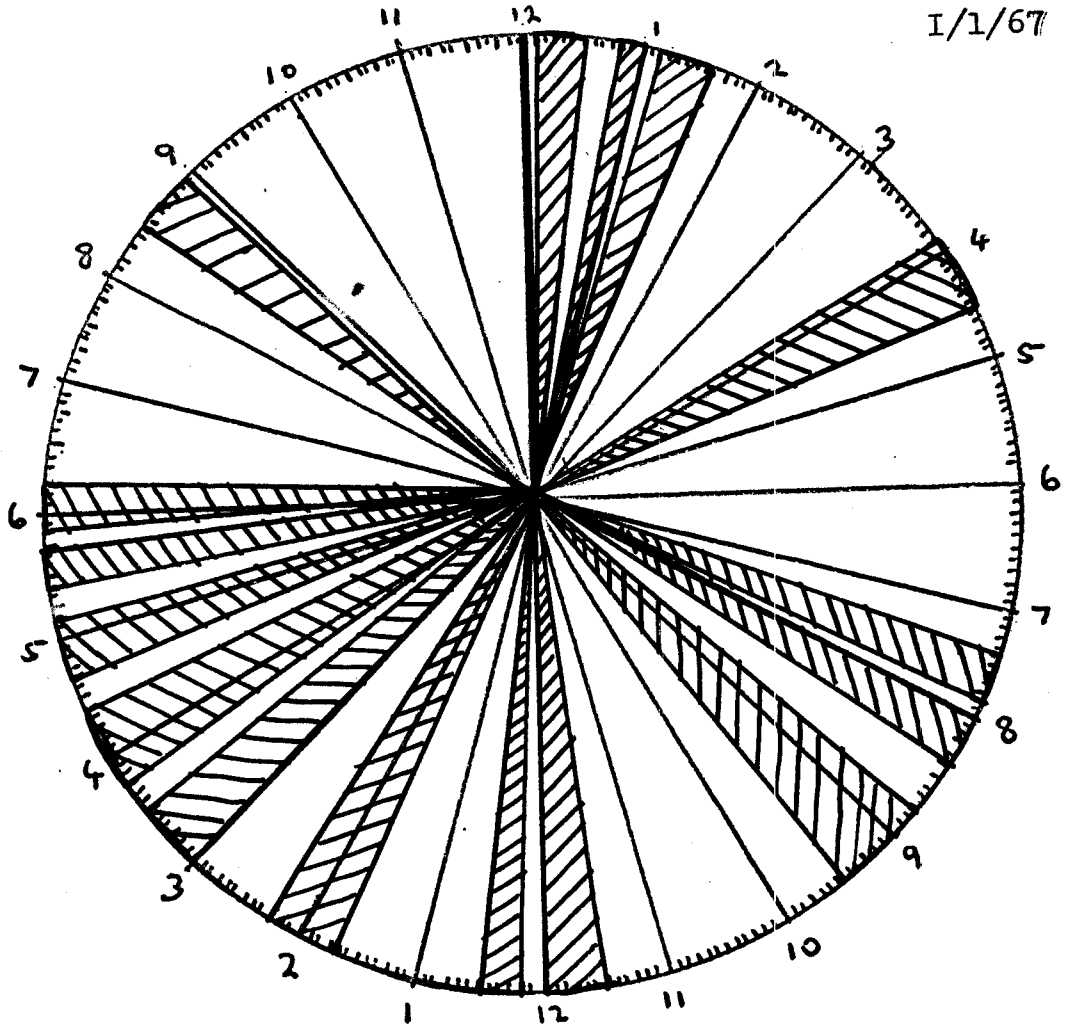
Length of Period	0	1	2	3	4	5	6	7	8	9	10
Probability of occurrence	.2466	.3452	.2417	.1128	.0395	.0111	.0026	.0005	.0001	0	0
Expected Frequency	70.5	98.7	69.1	32.3	11.3	3.4	0.8	0.2	.03	0	0
Observed Frequency	-	214	51	11	5	3	2	0	0	0	0

A Chi-square test was applied to see how well the data in Fig. 29 for total time spent in each activity in the dark fitted the data in the same figure for the total time spent in each activity in the light. The value of χ^2 obtained was 0.72 with 12 degrees of freedom showing that there is no statistically significant difference between these two sets of figures.

Fig. 41

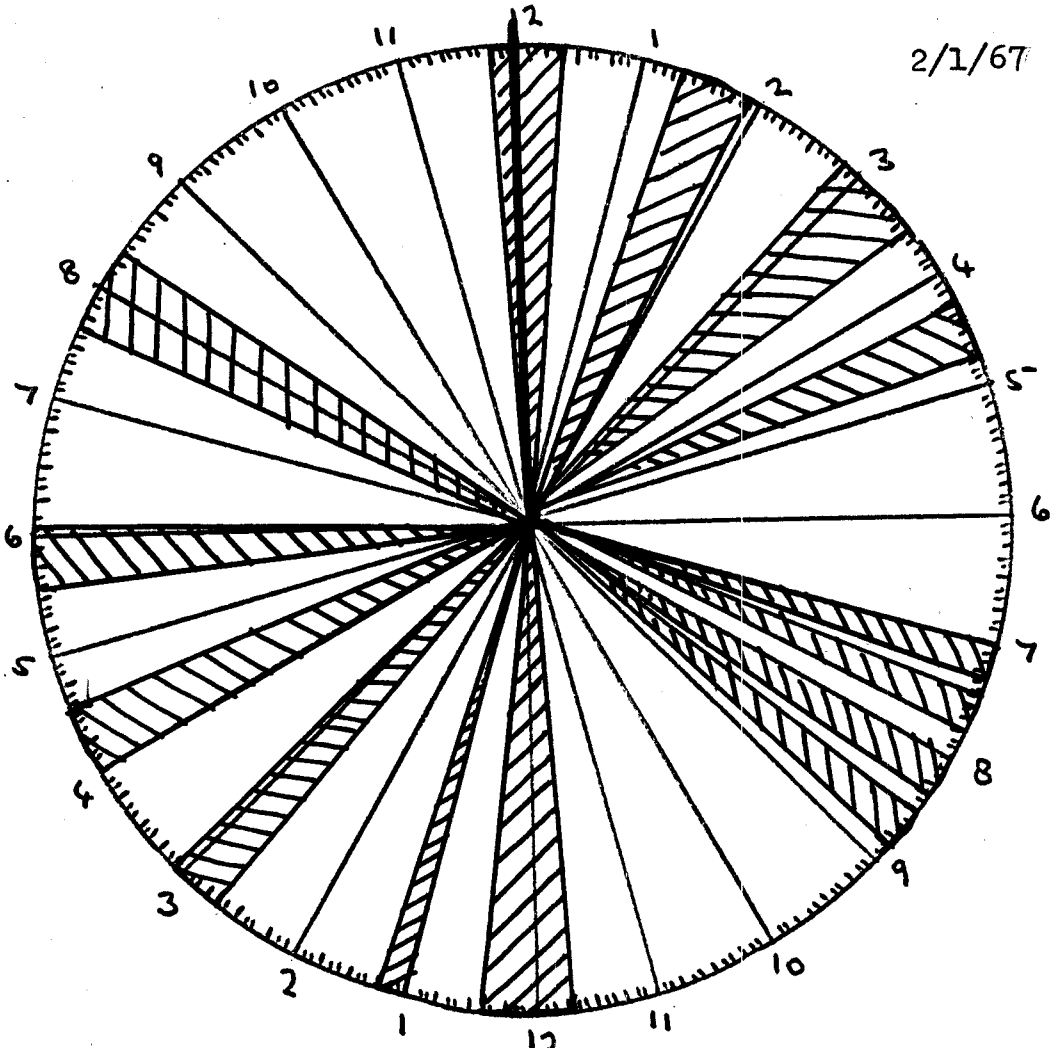


I/1/67

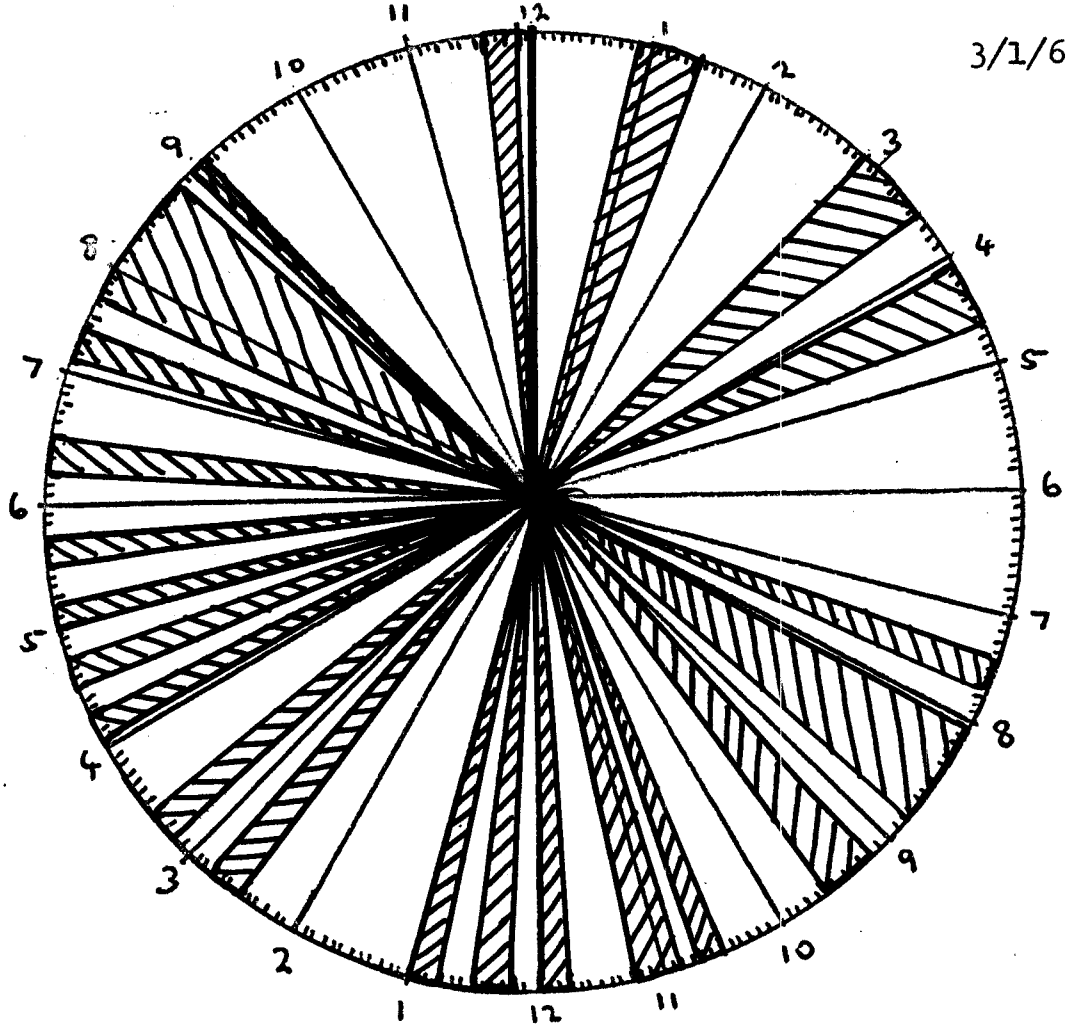


MIDNIGHT.

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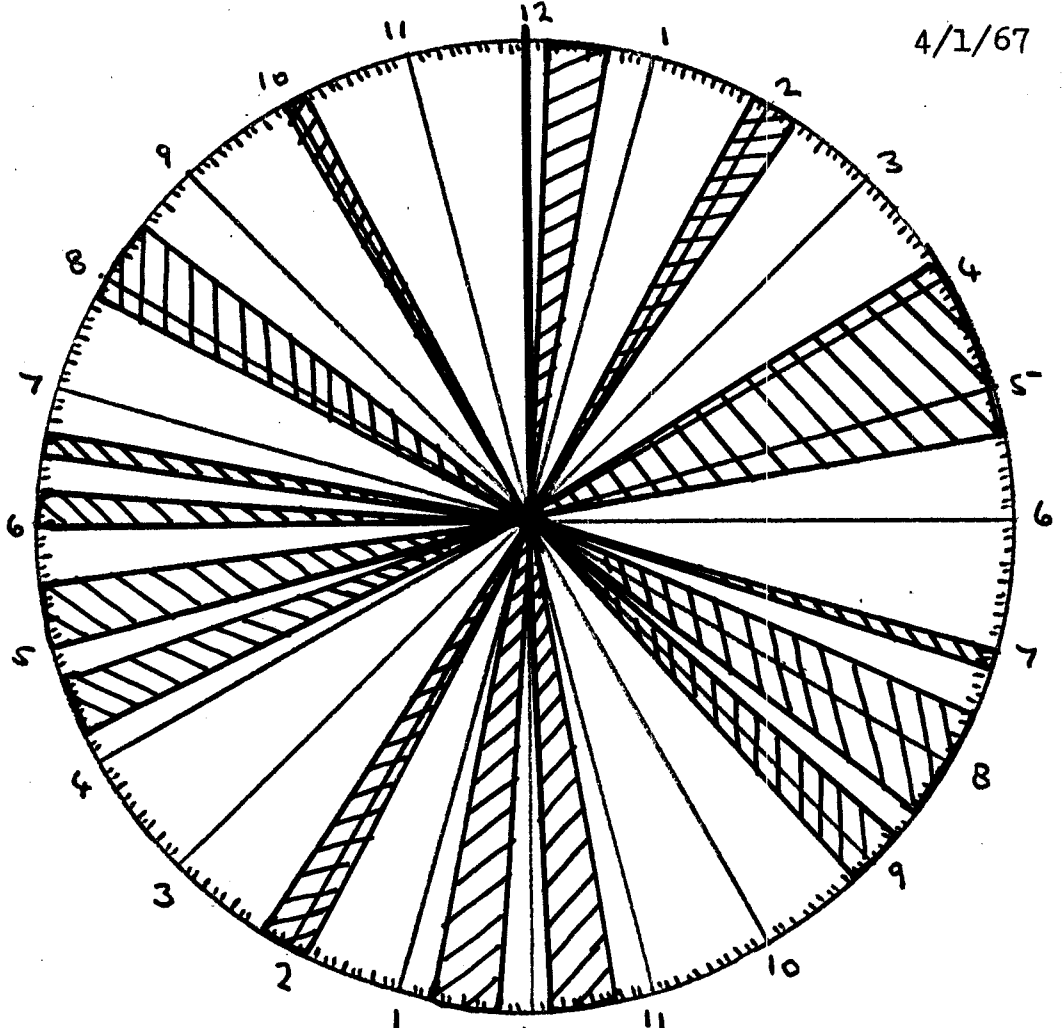


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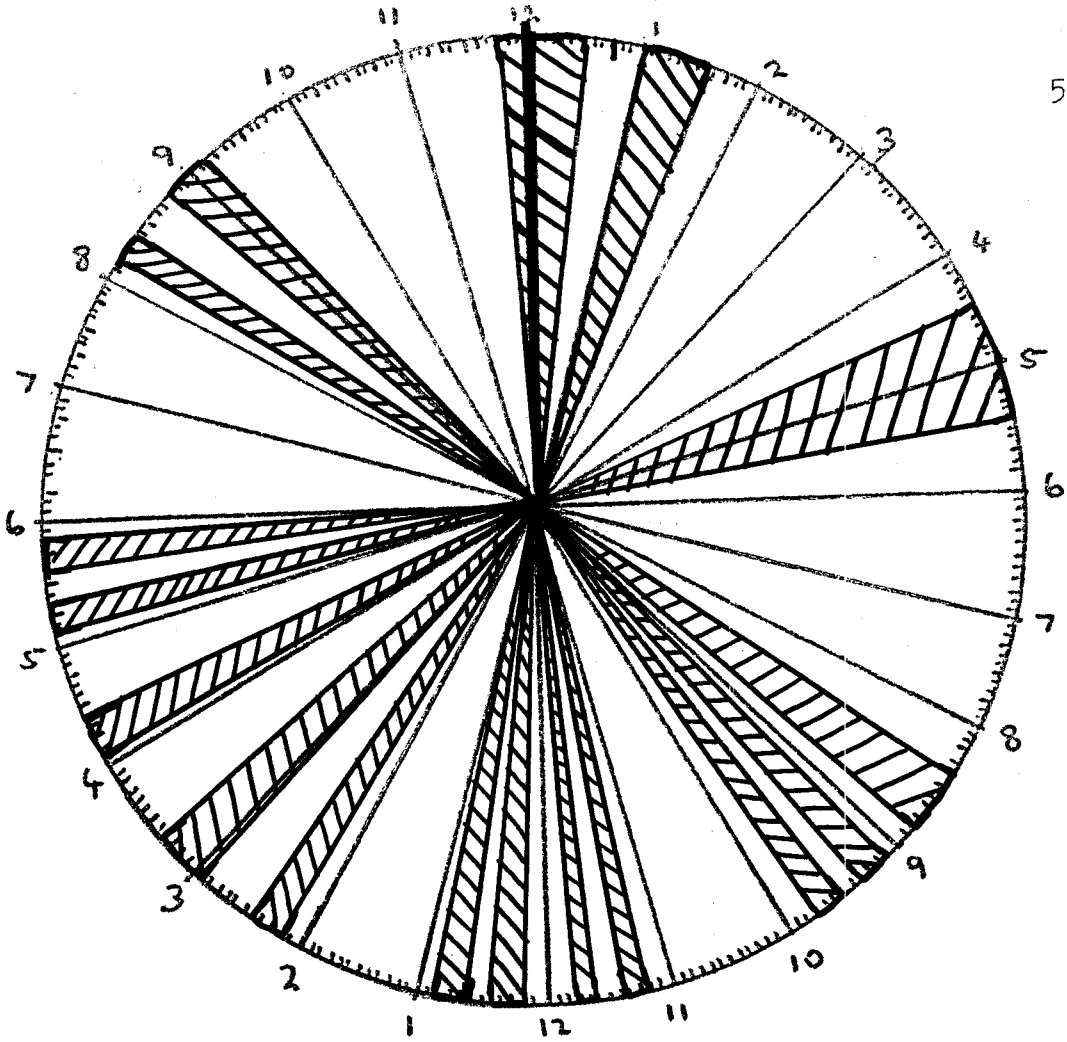


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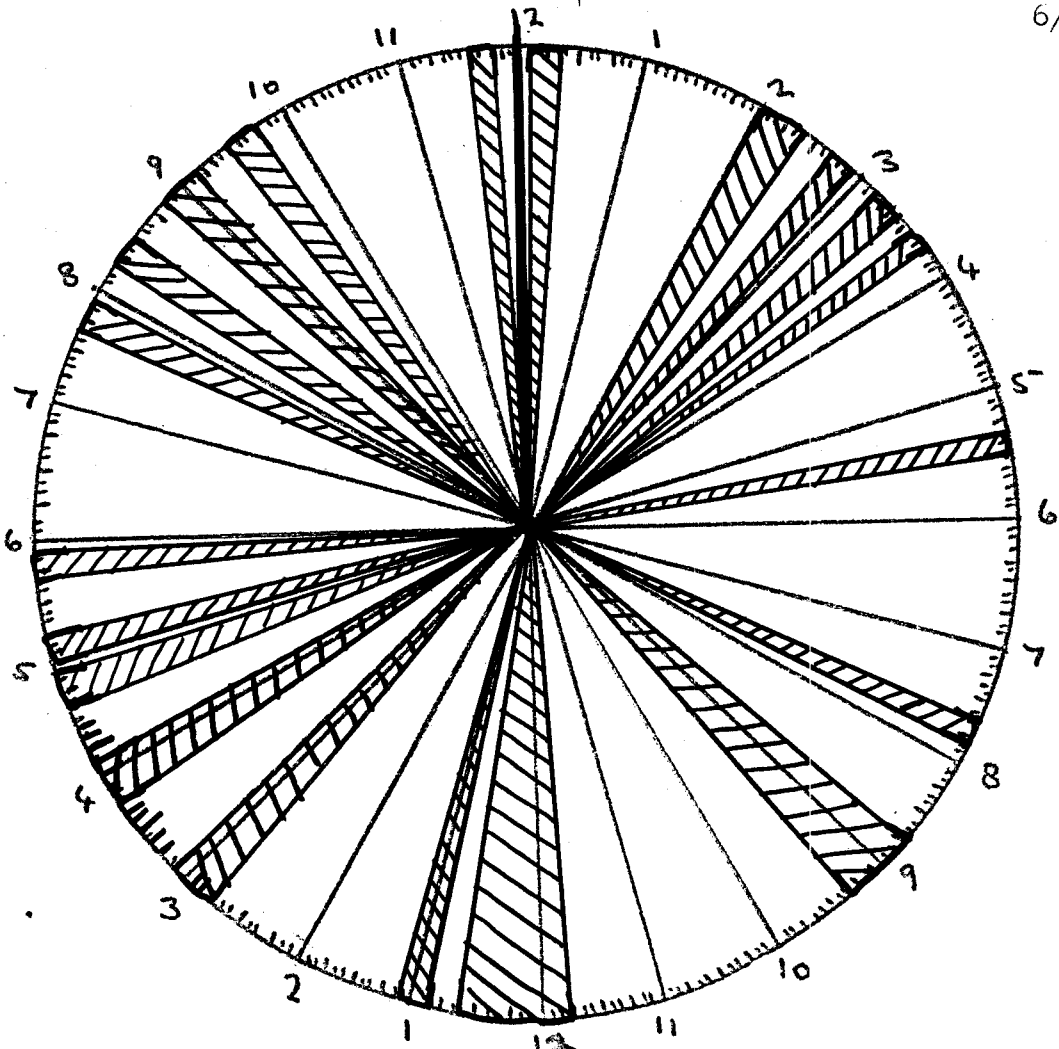


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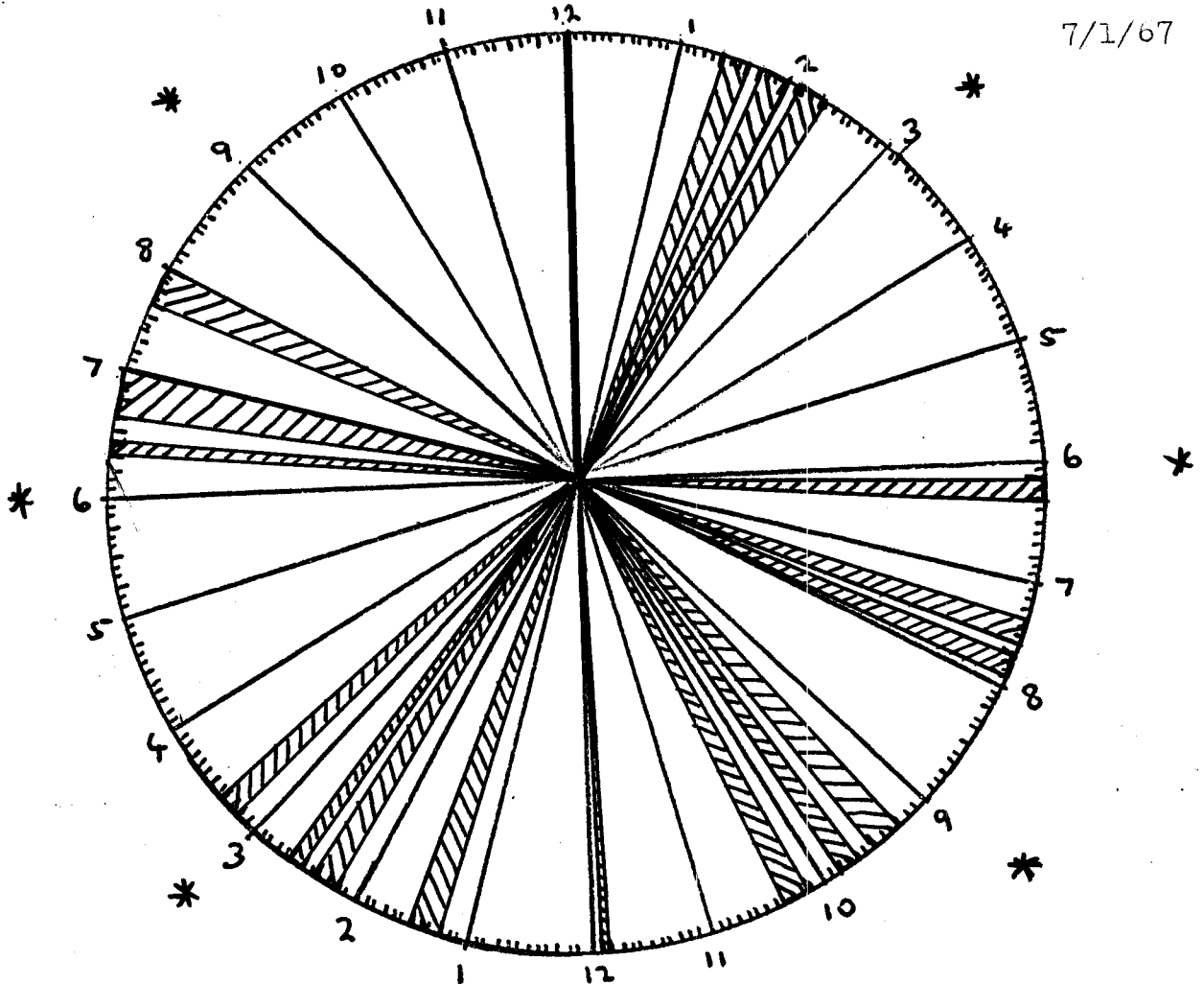
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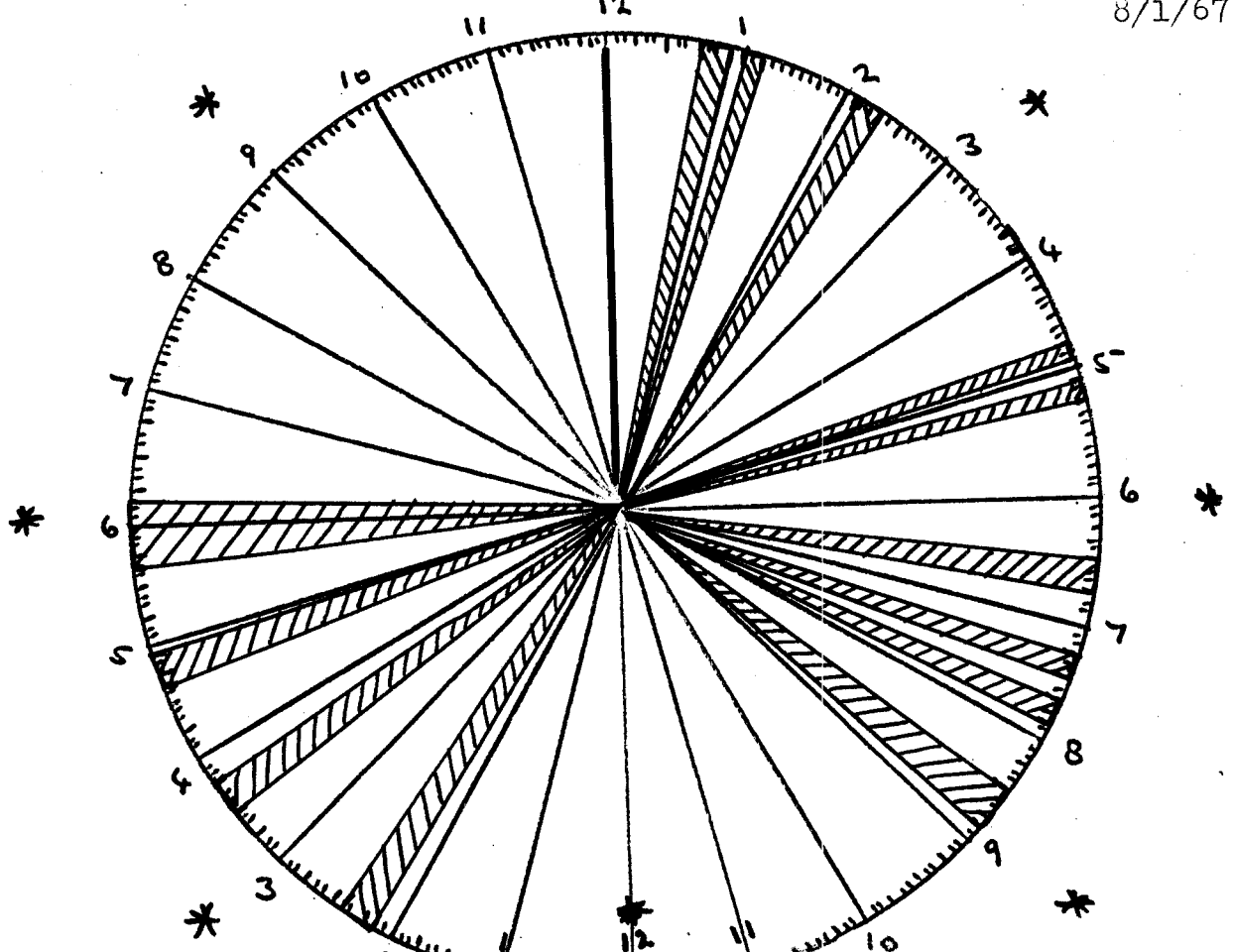
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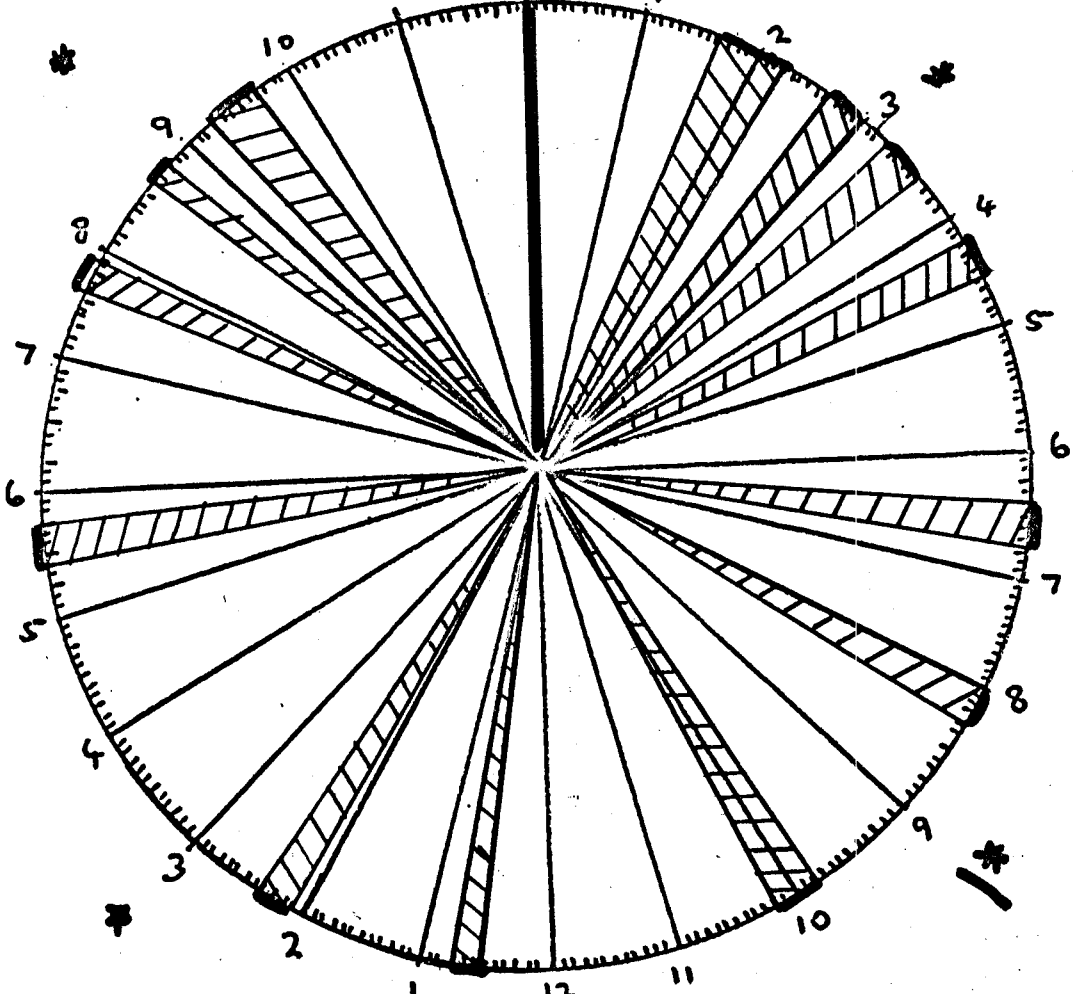
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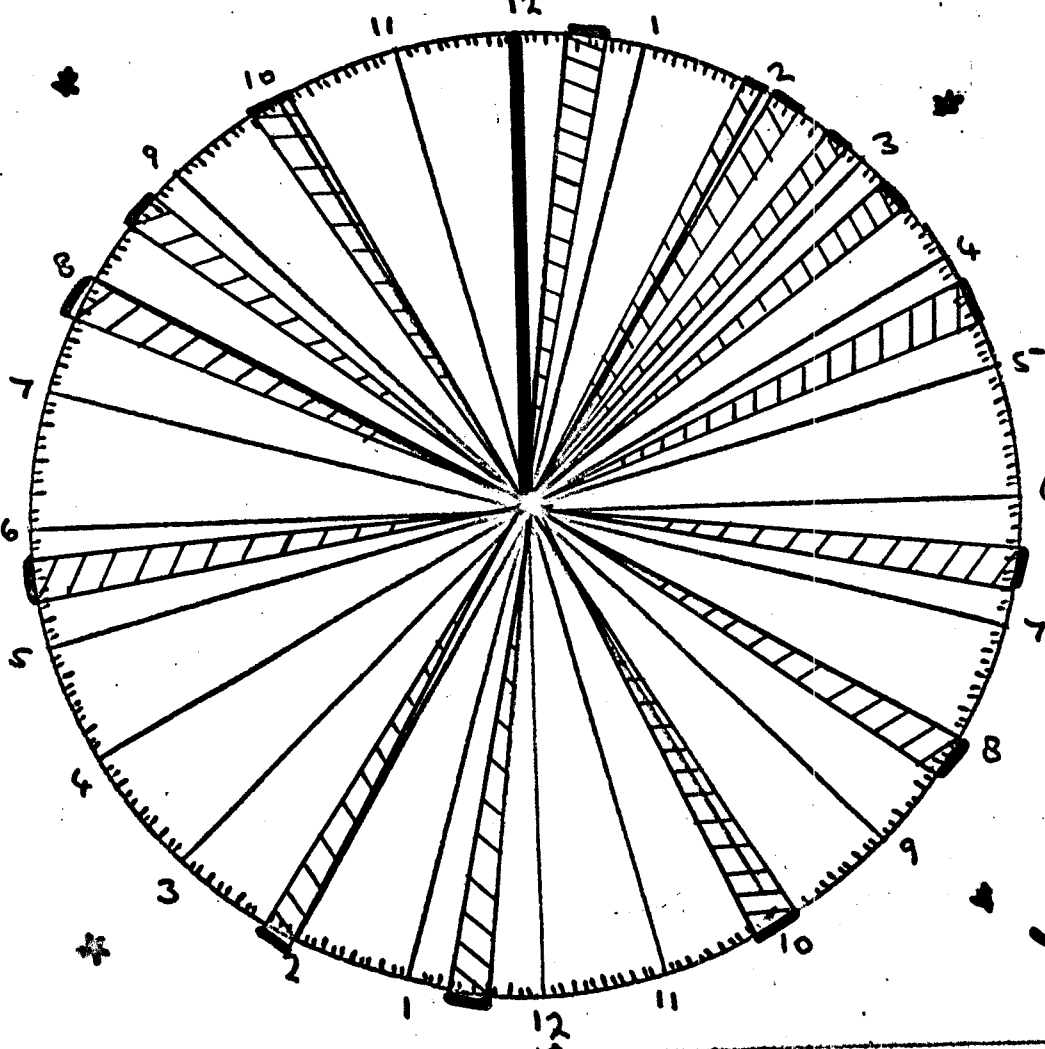
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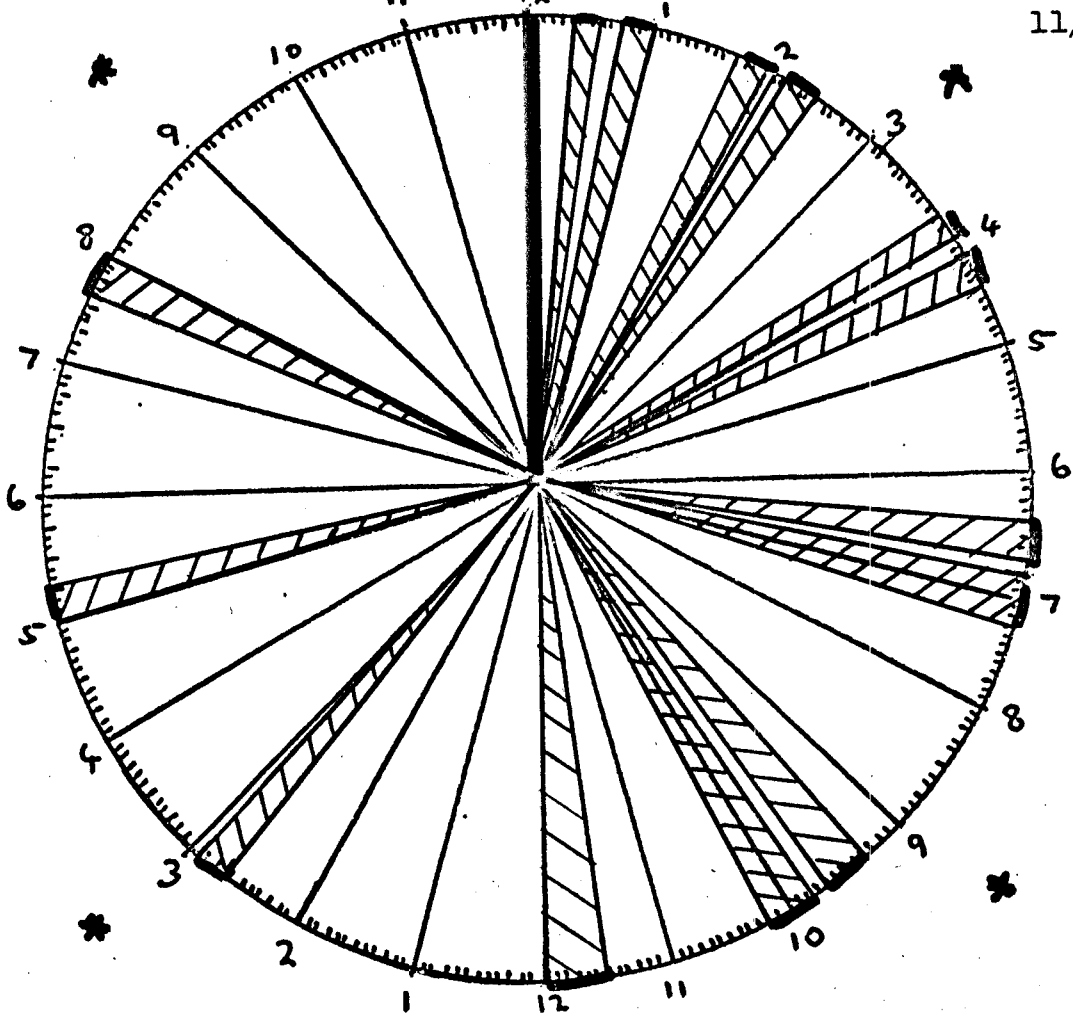


MIDNIGHT.
Faint text below

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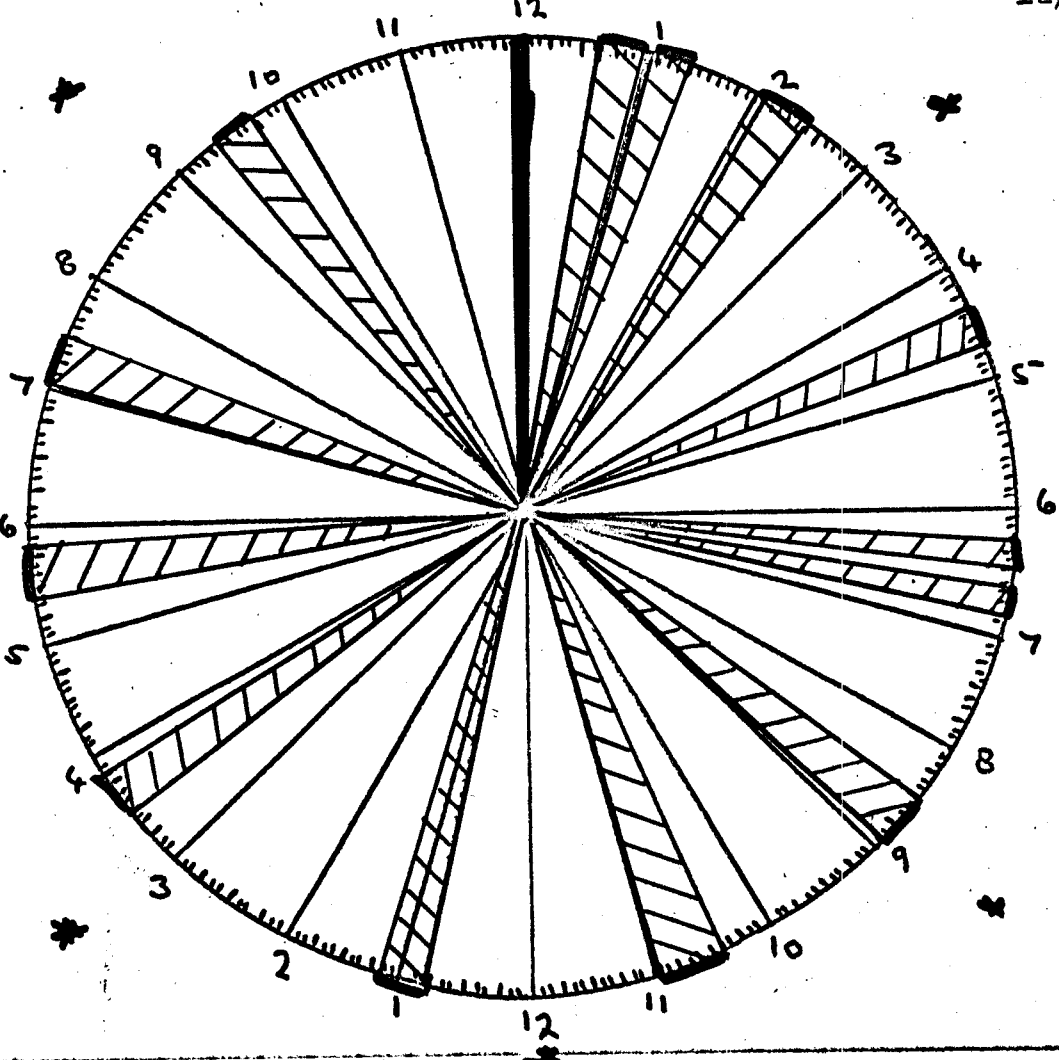


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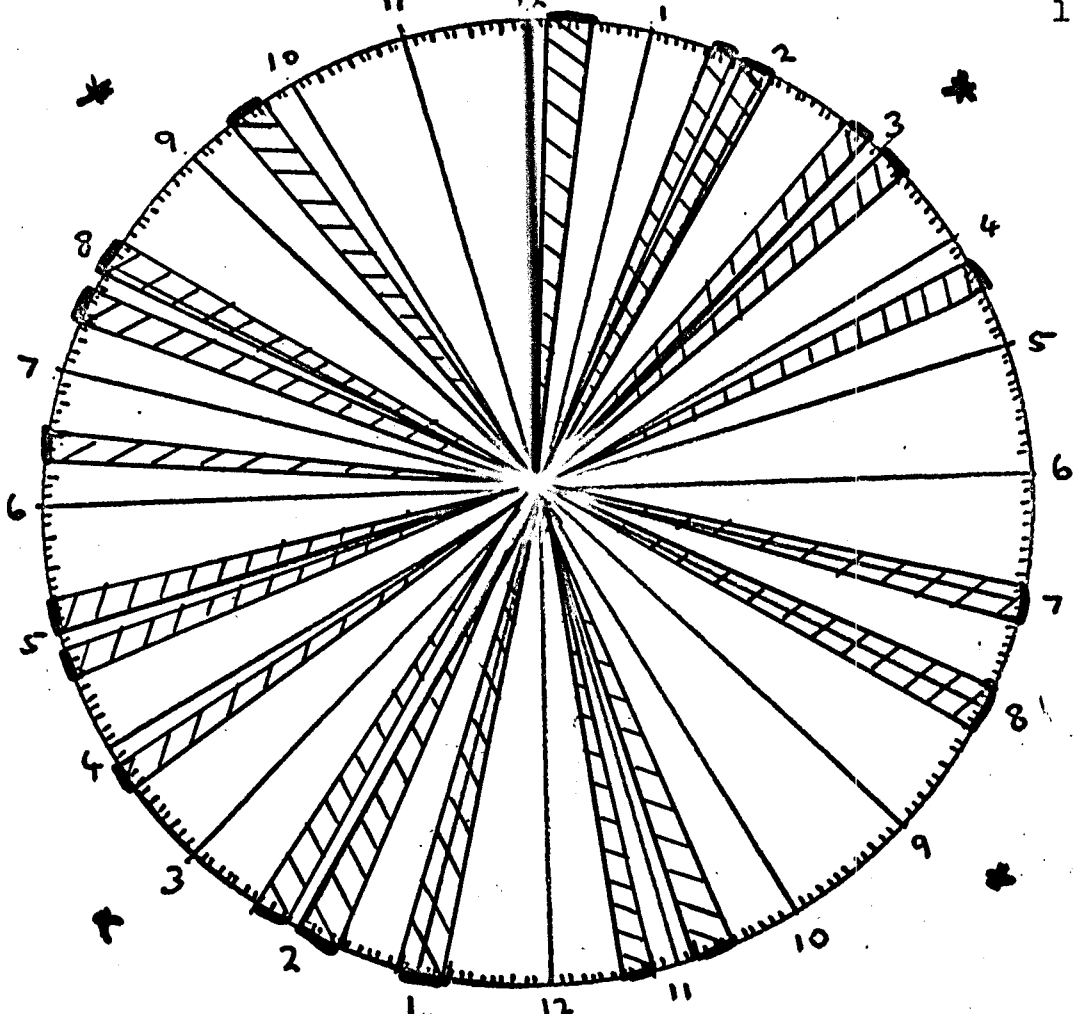


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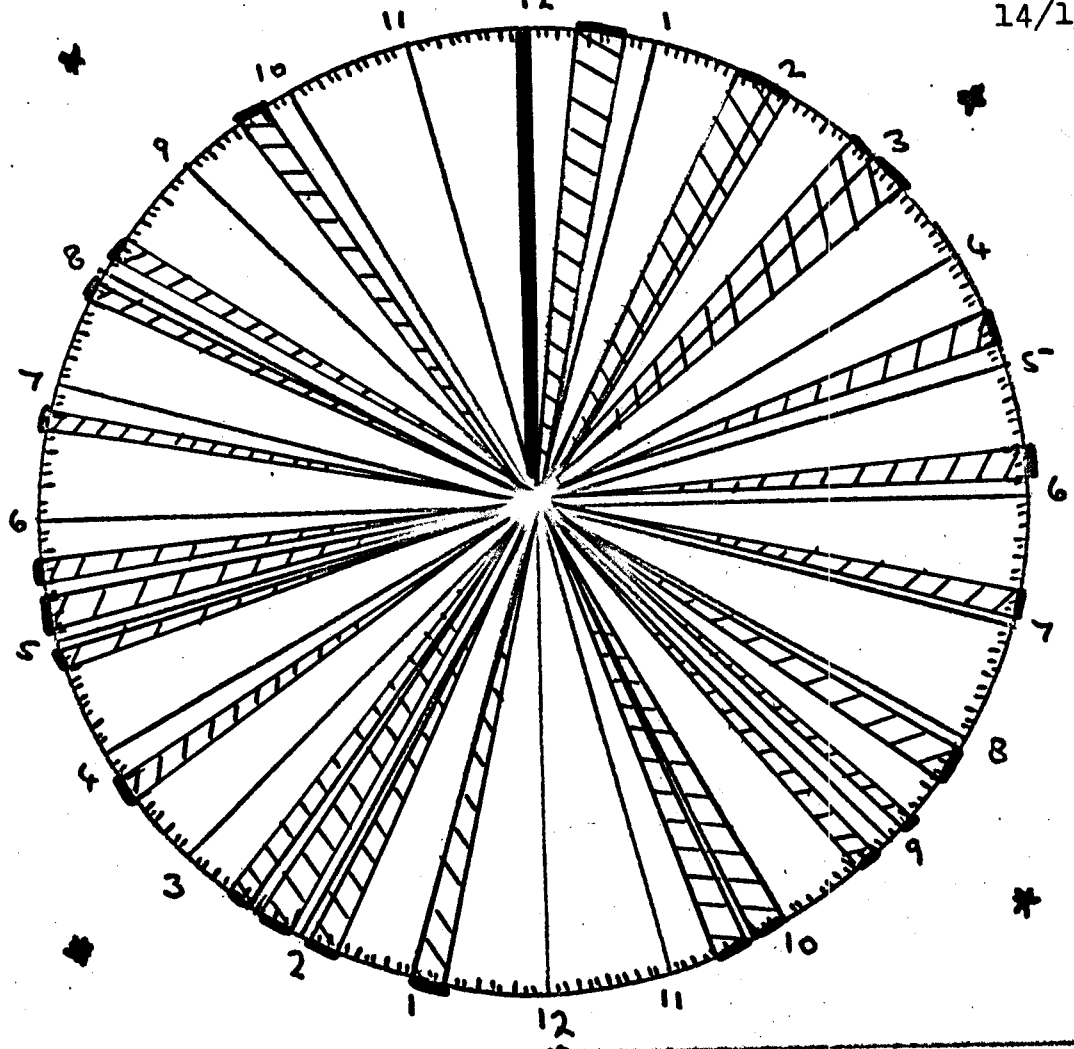


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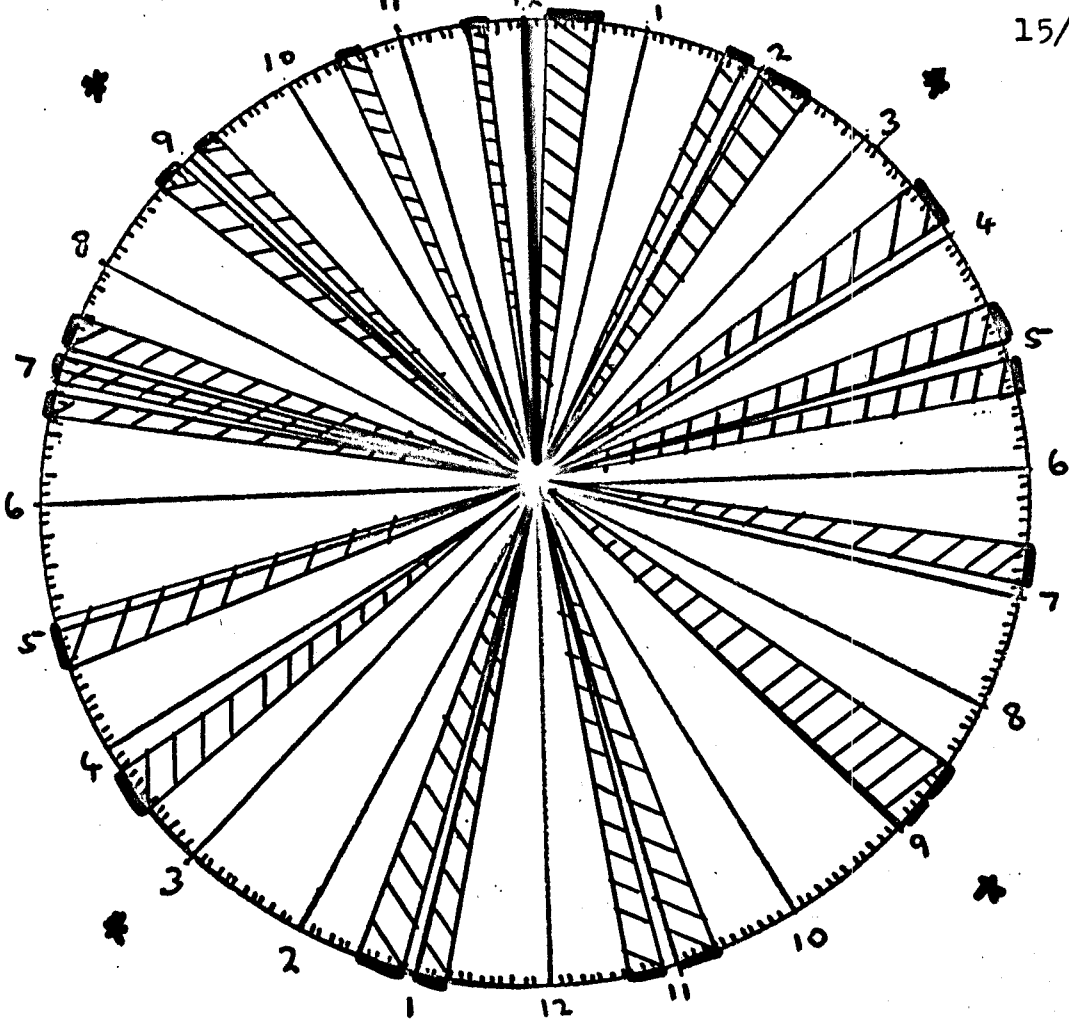


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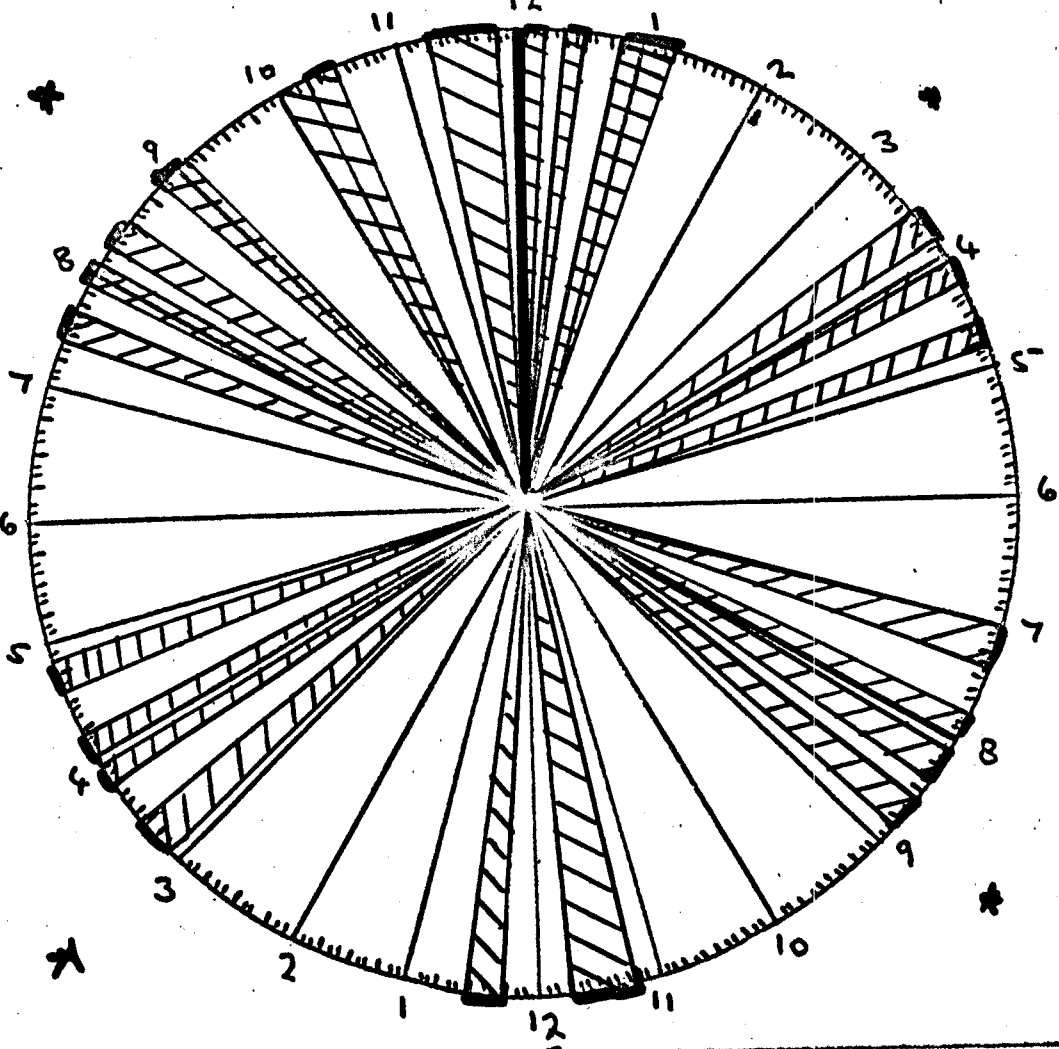


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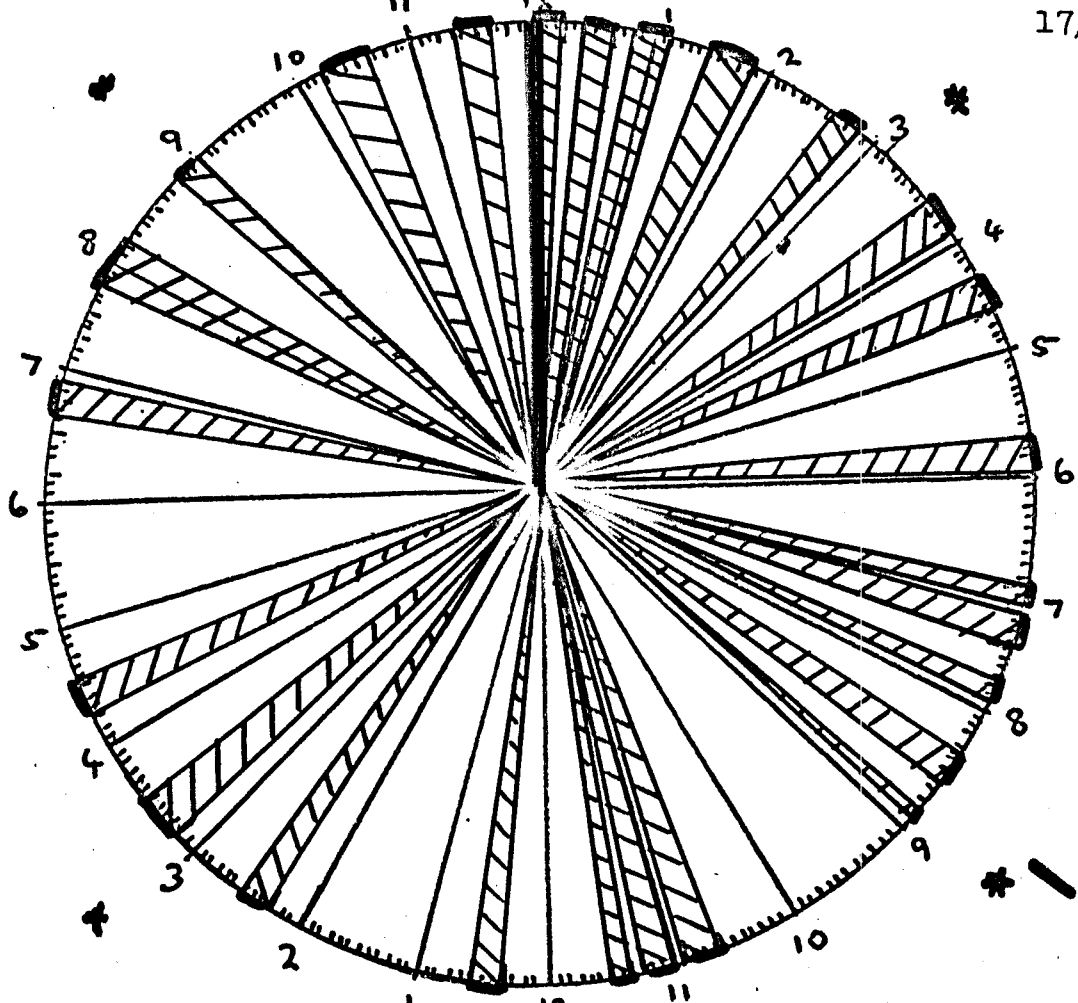


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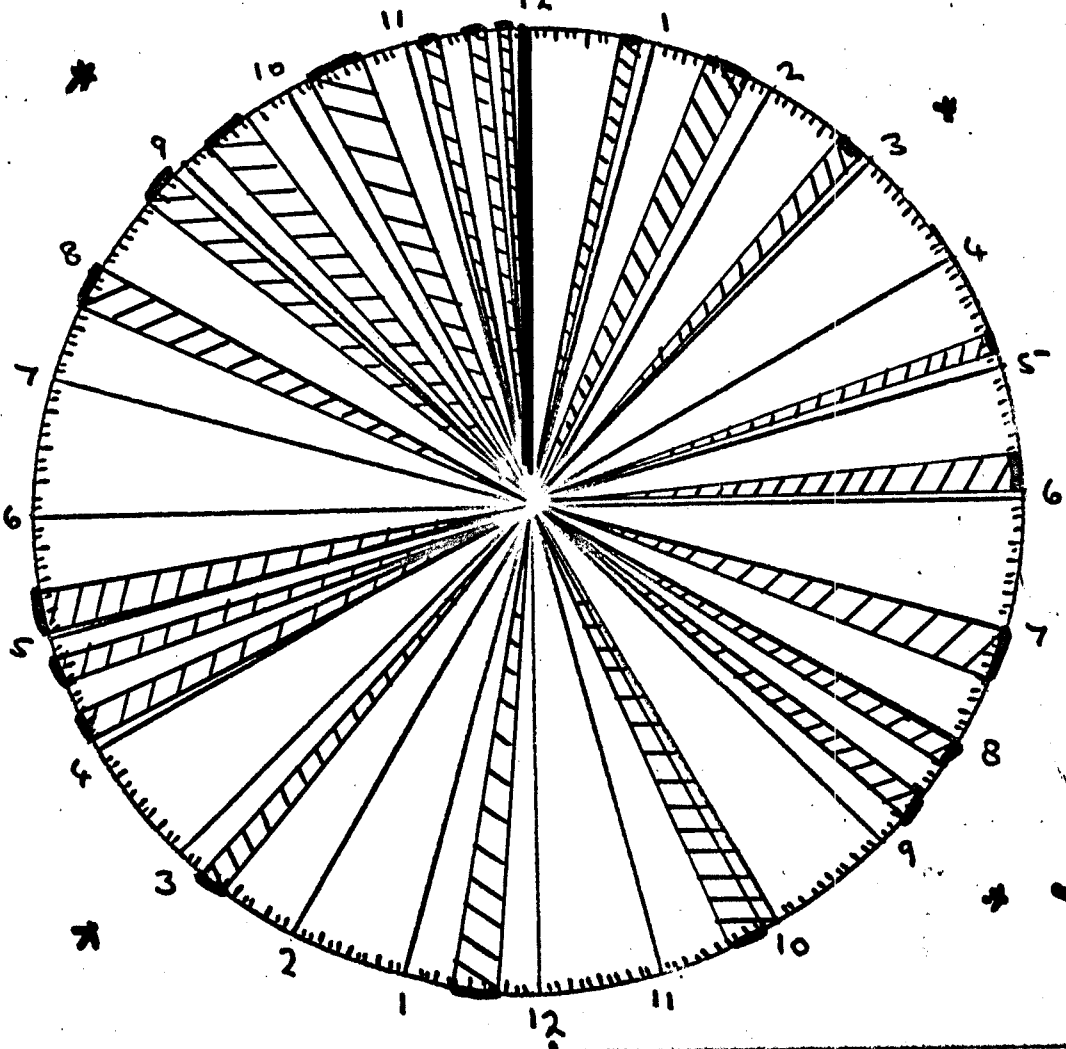


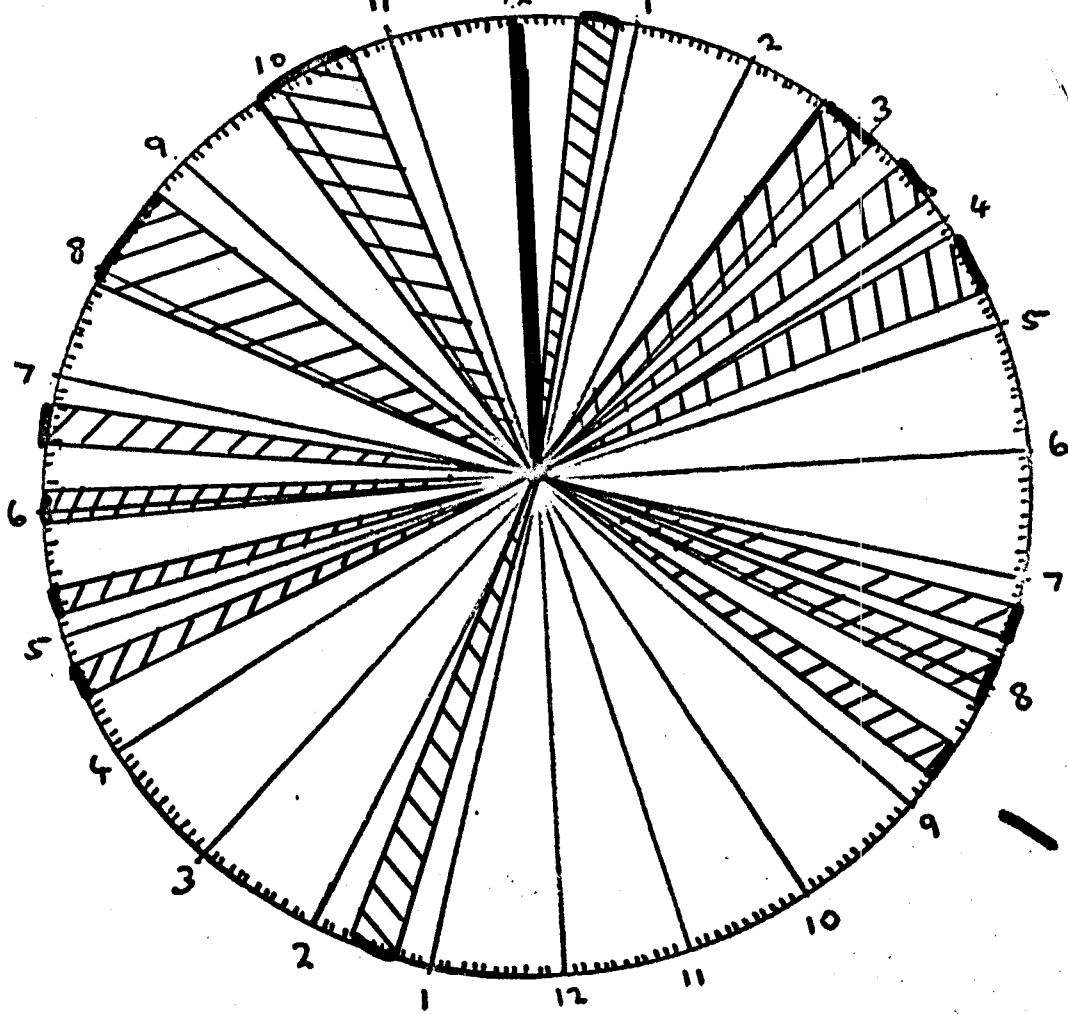
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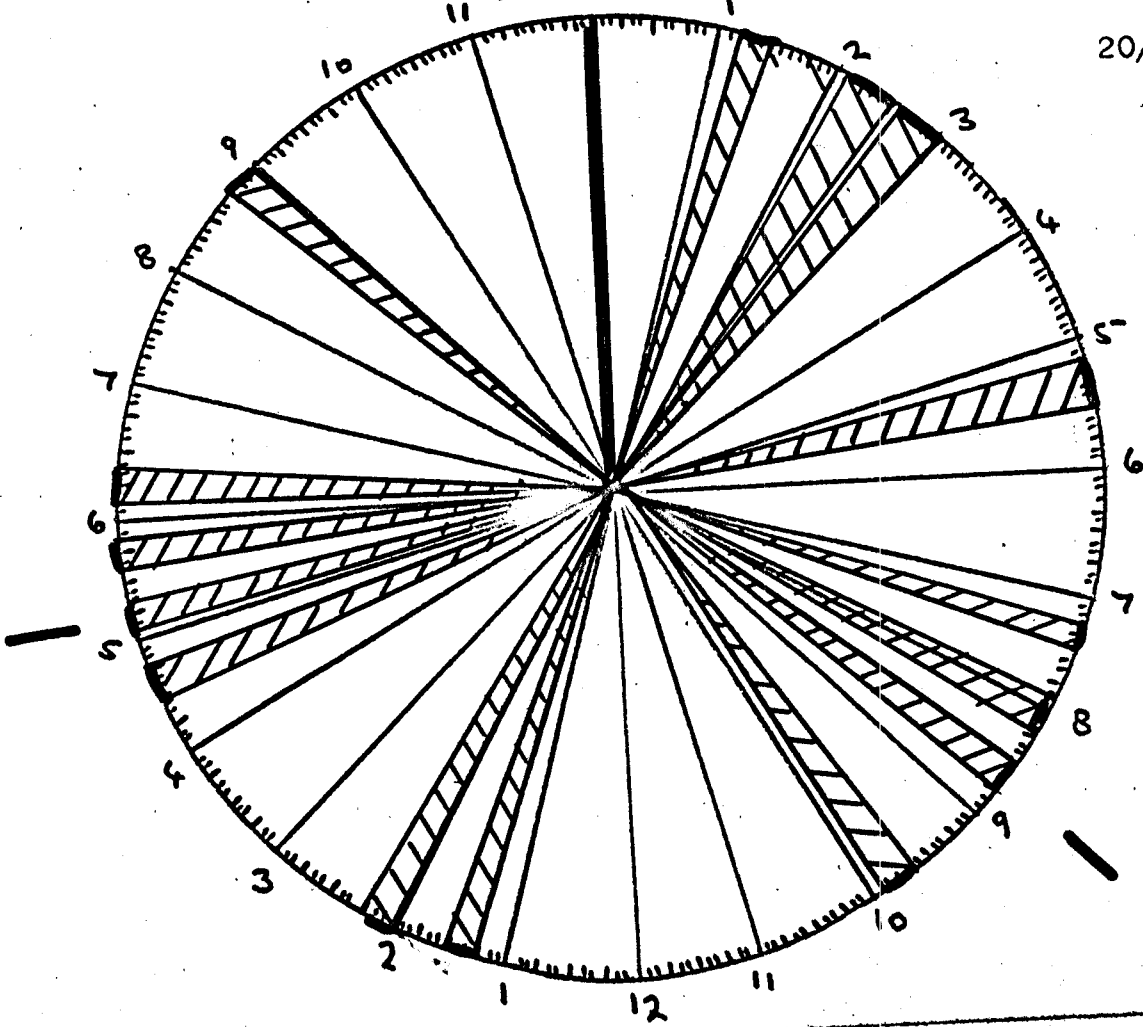




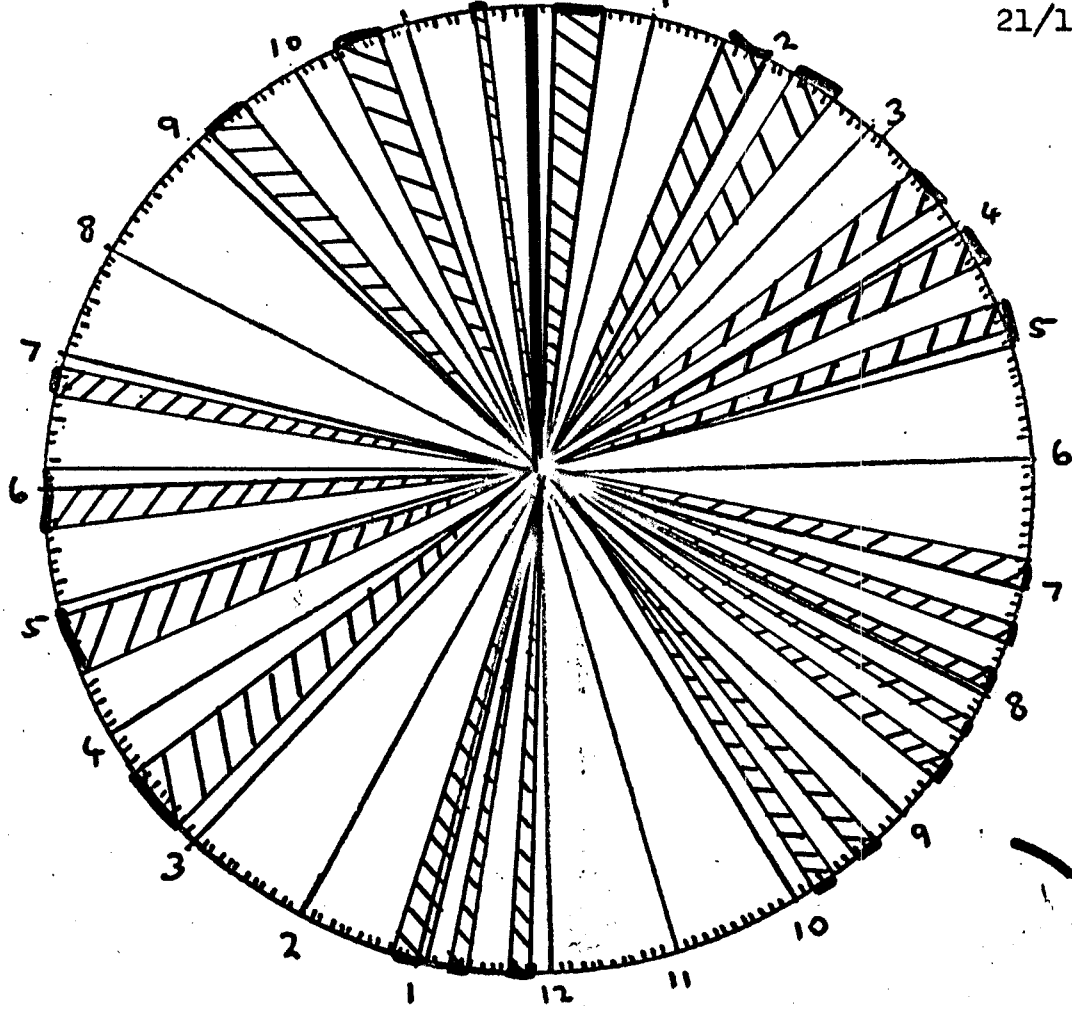
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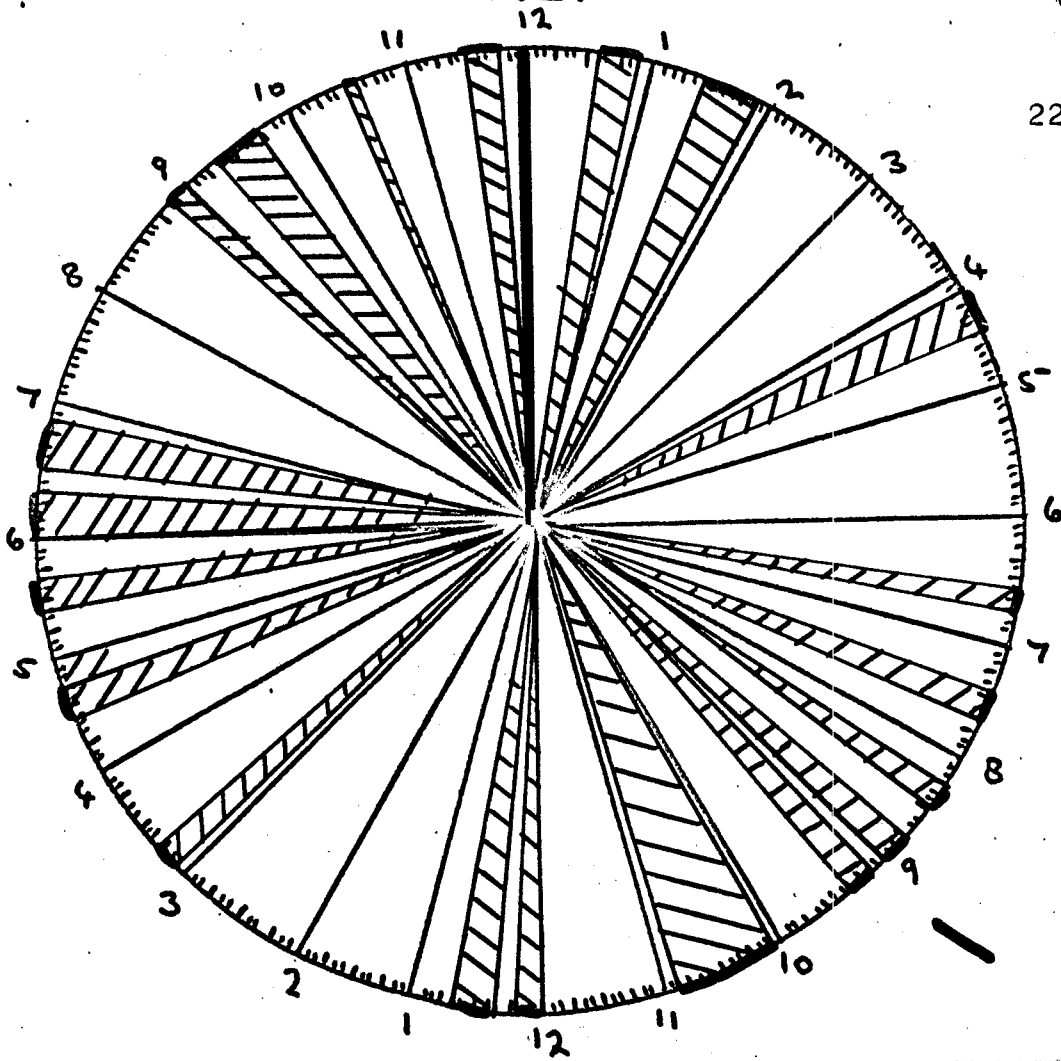


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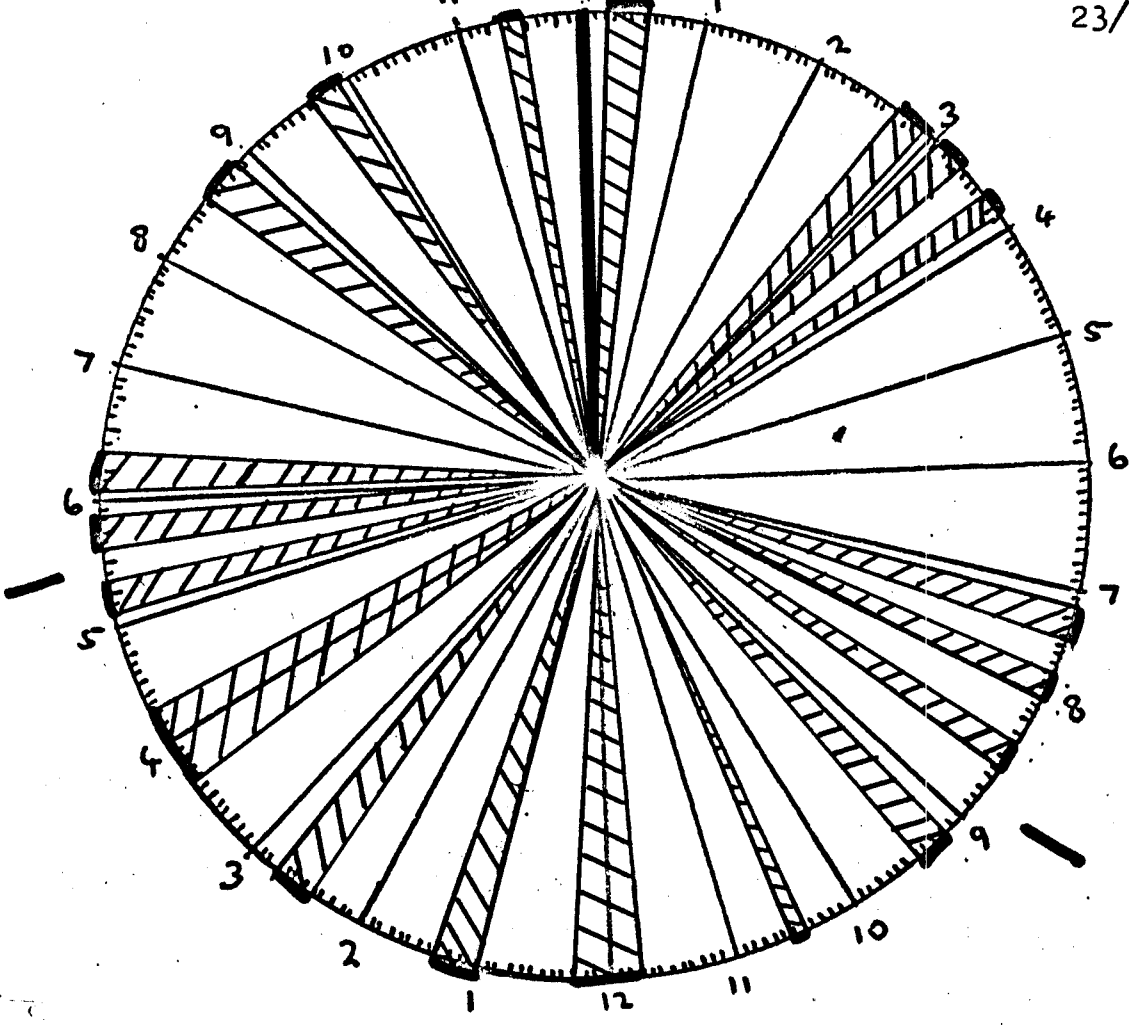


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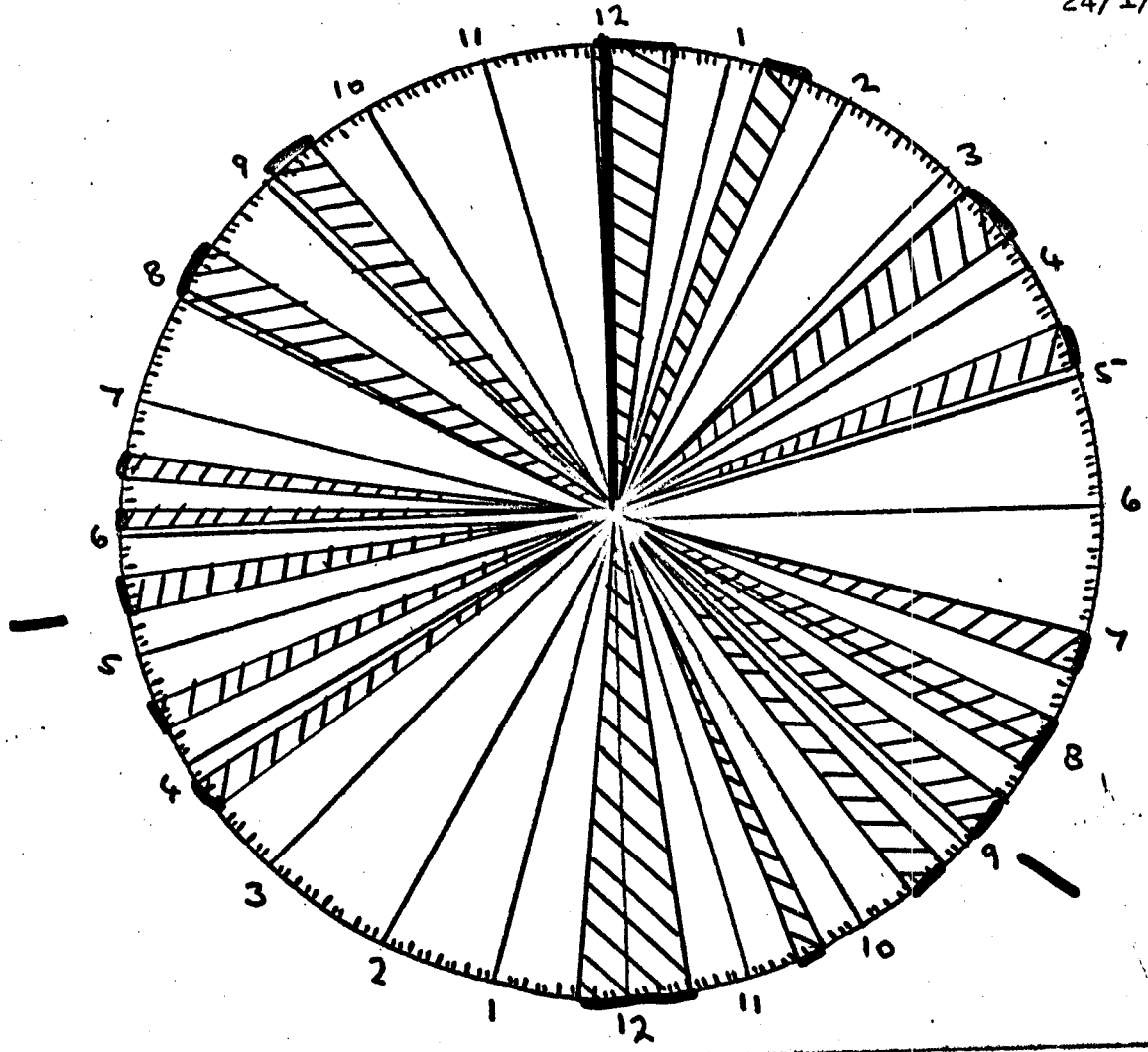


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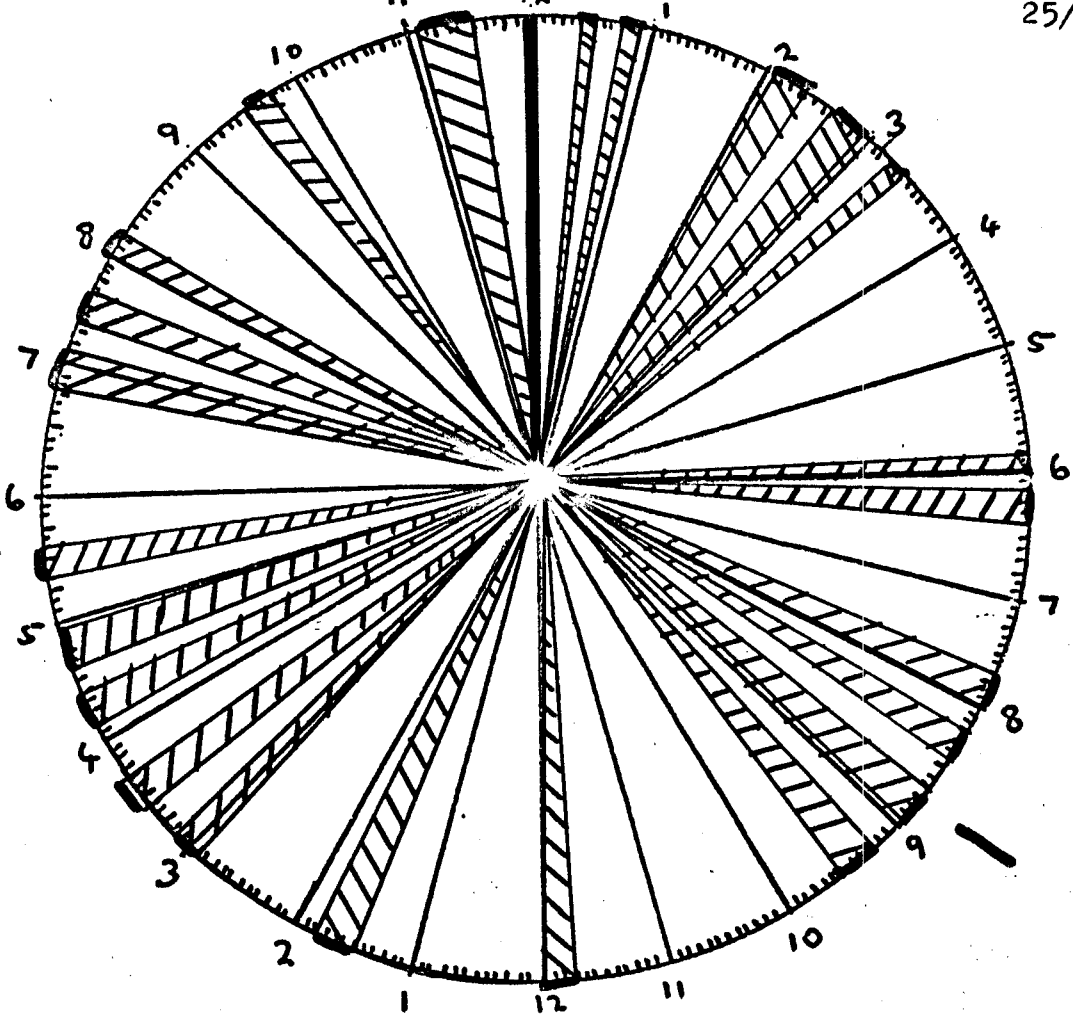


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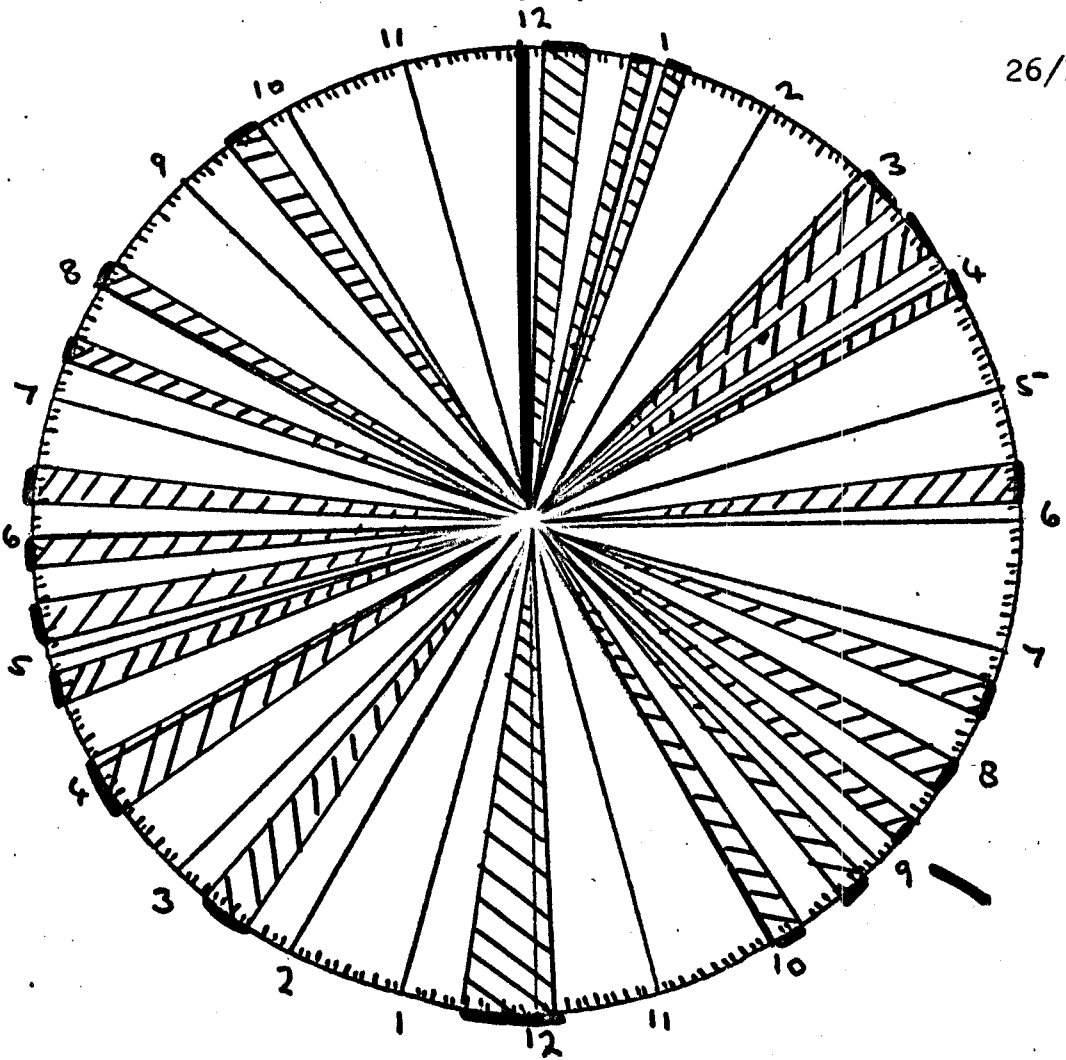


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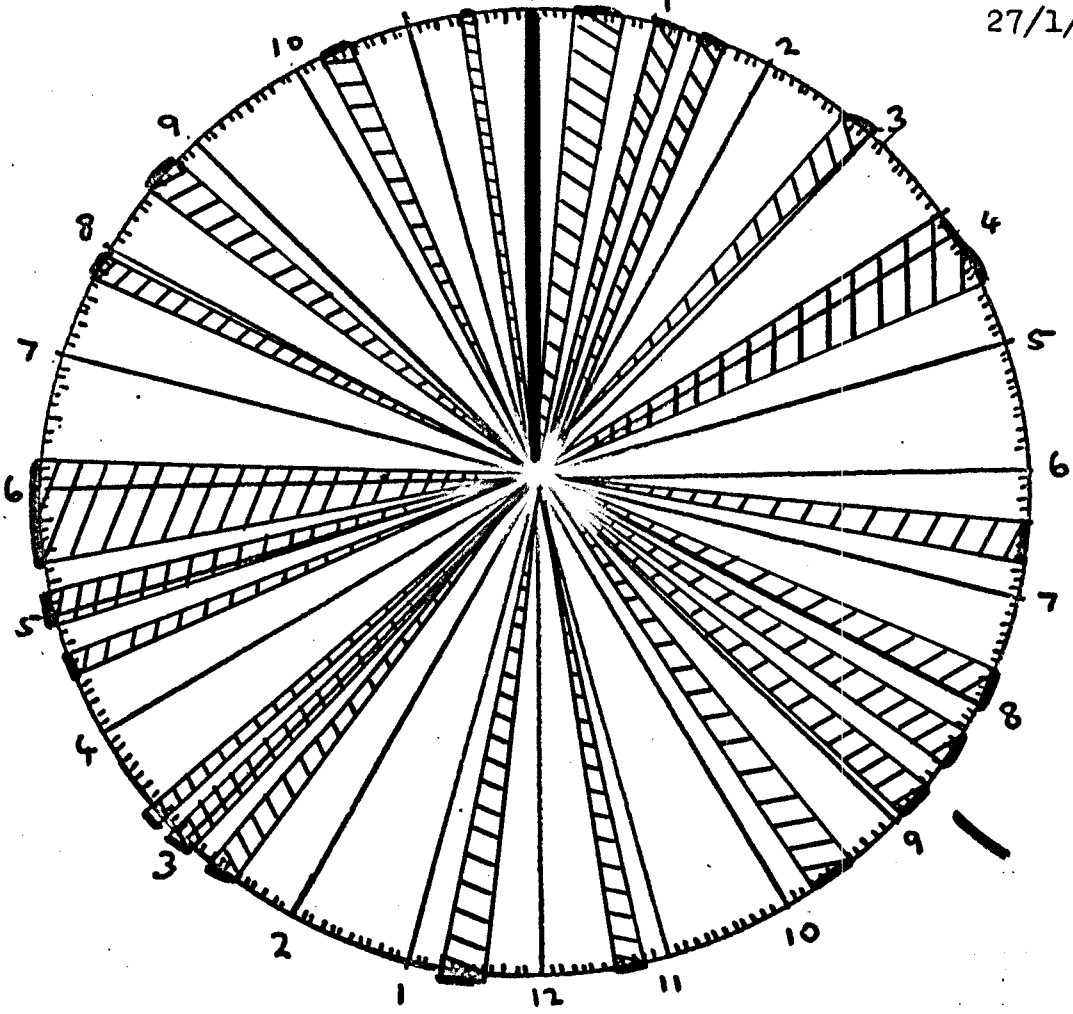


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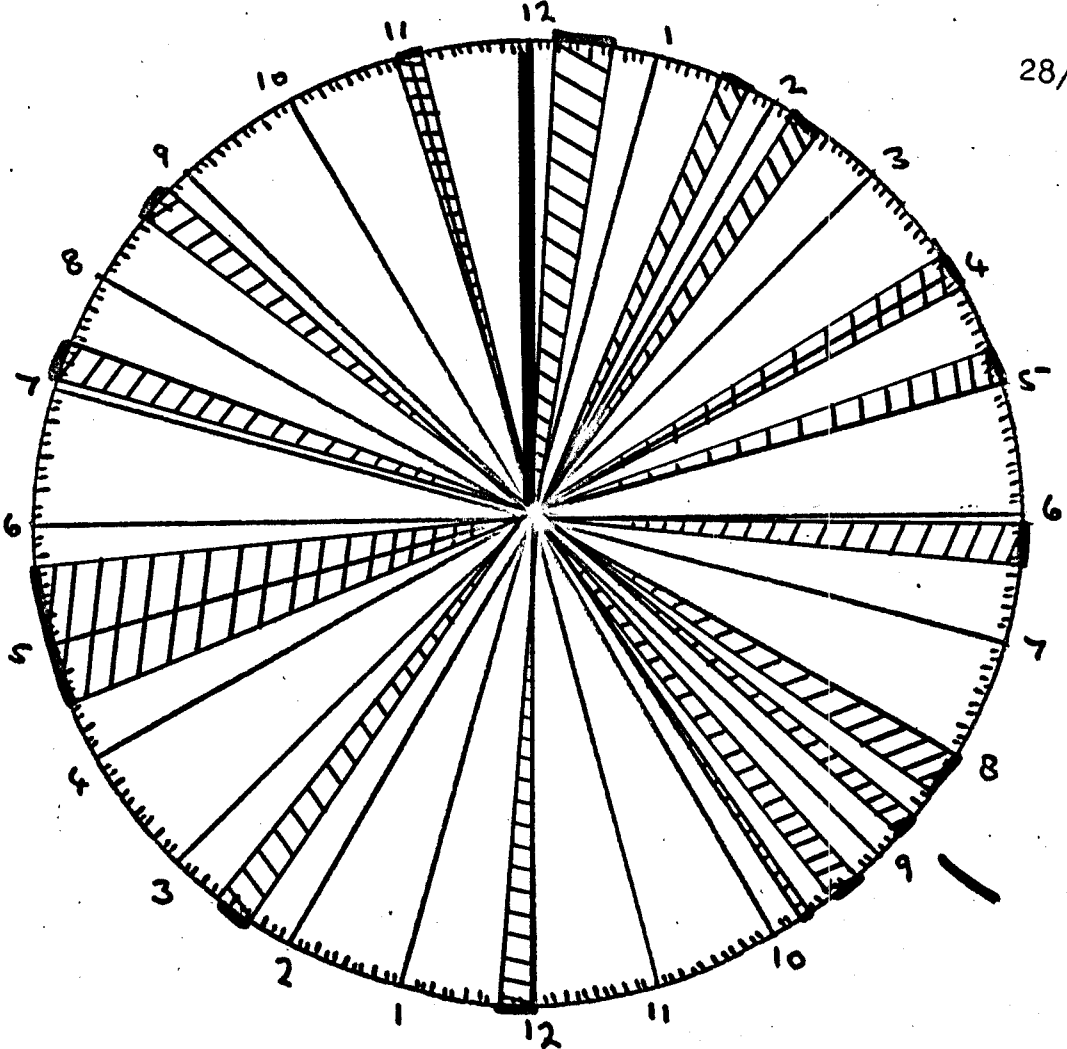


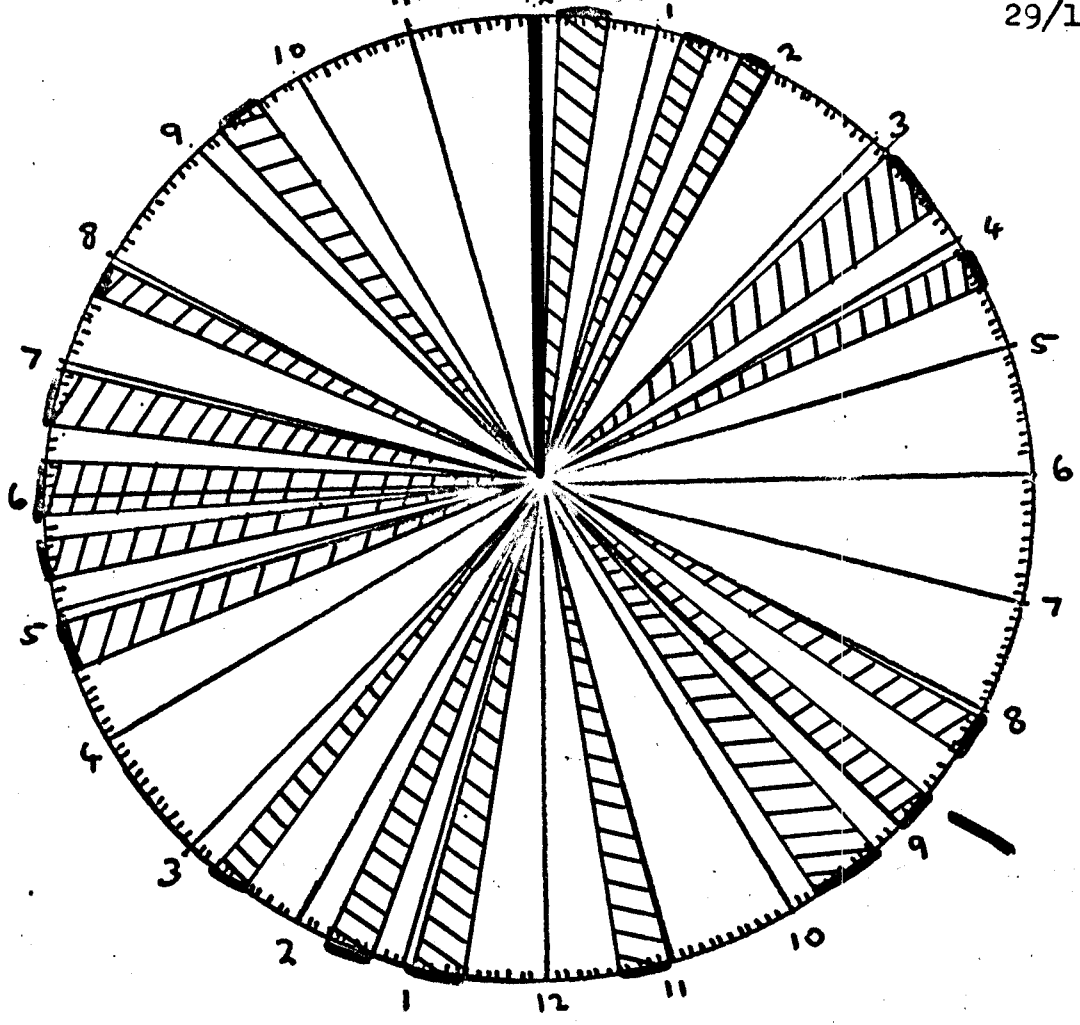
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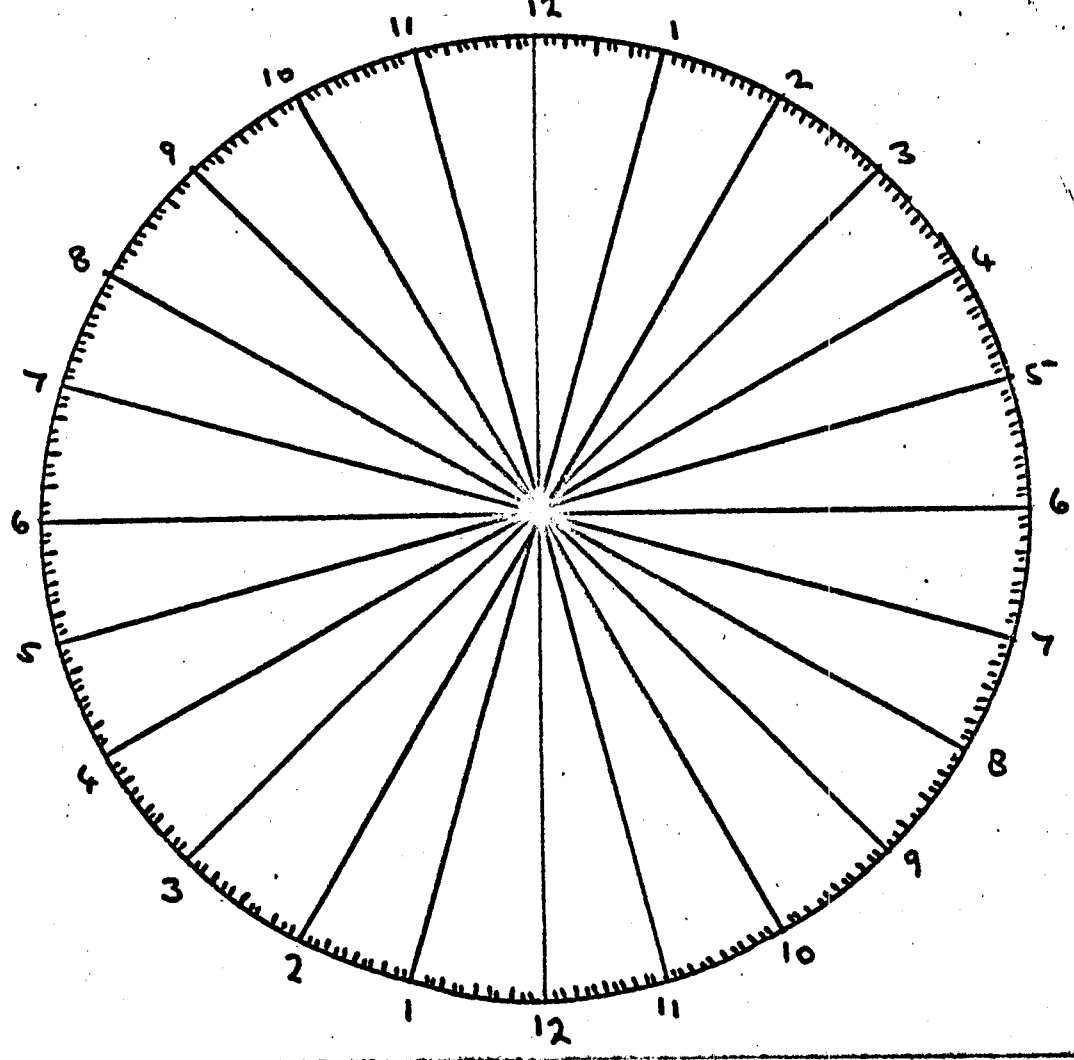
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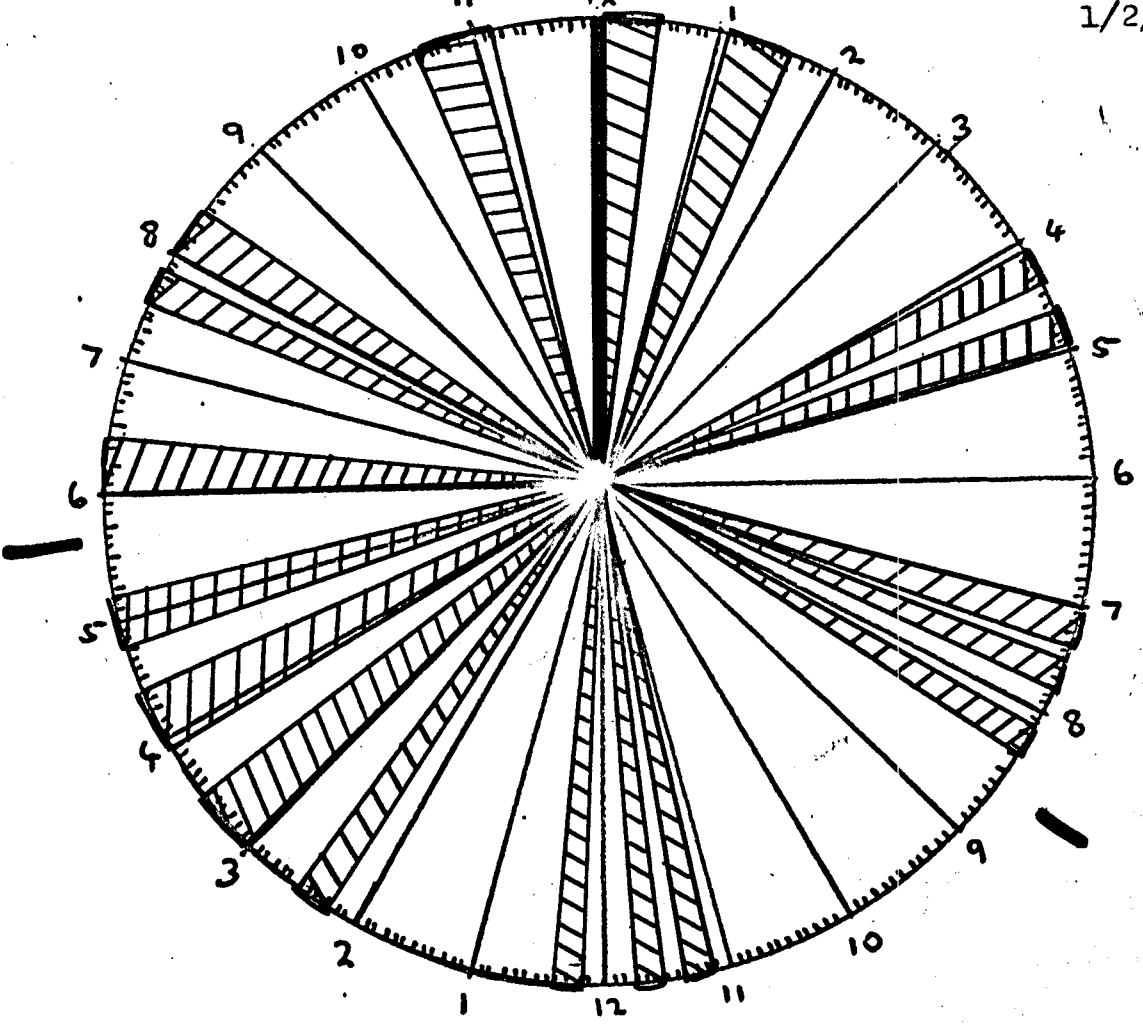




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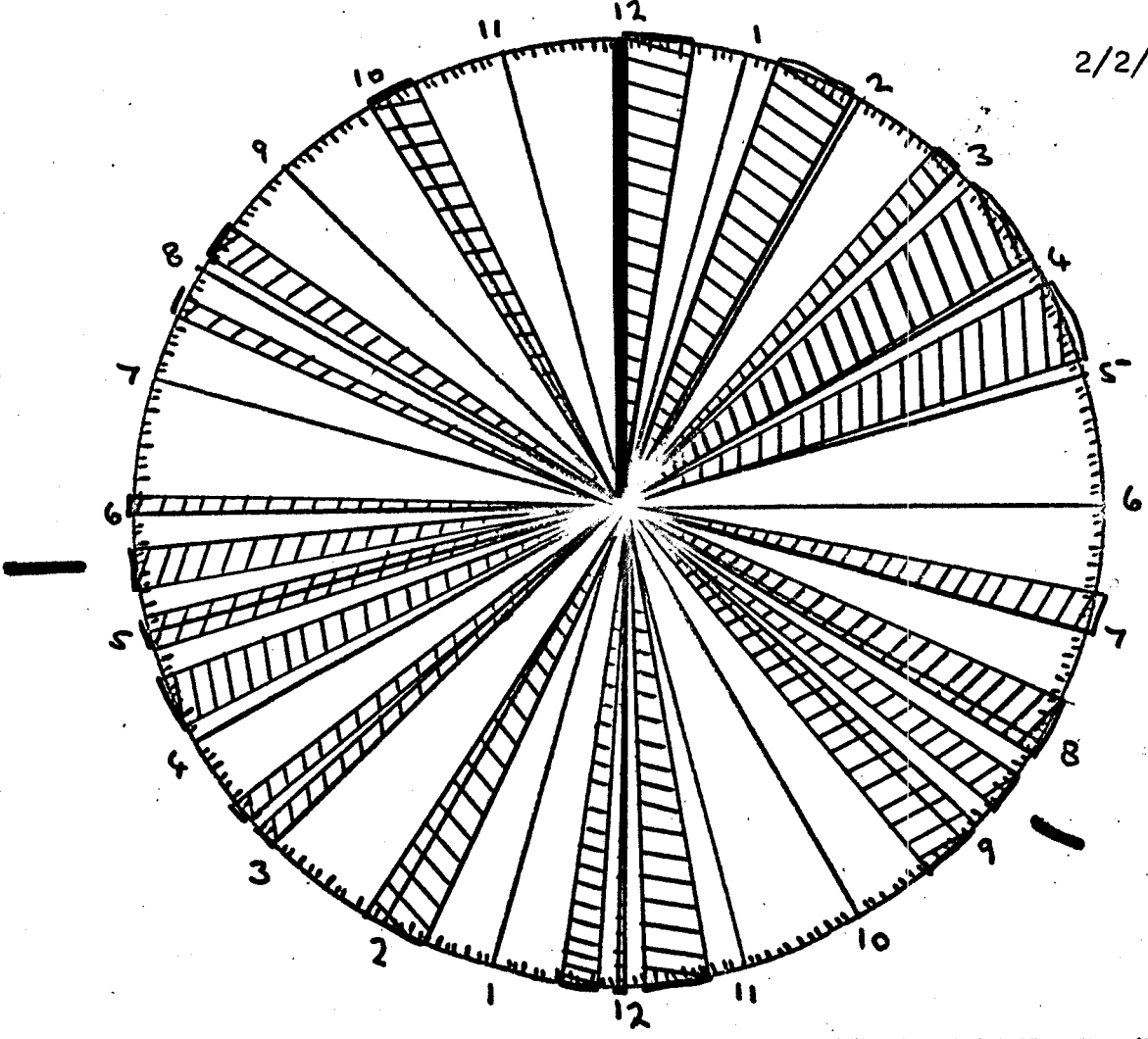


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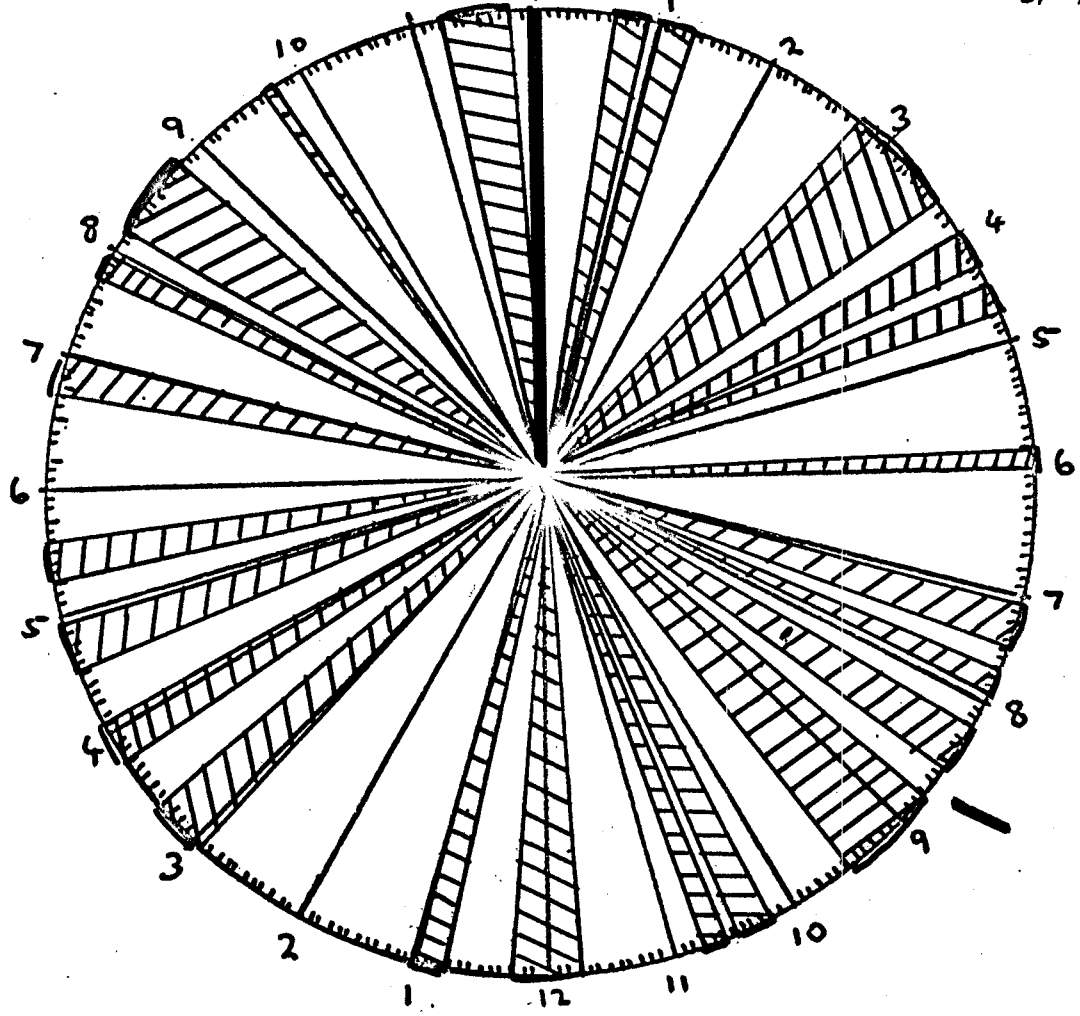


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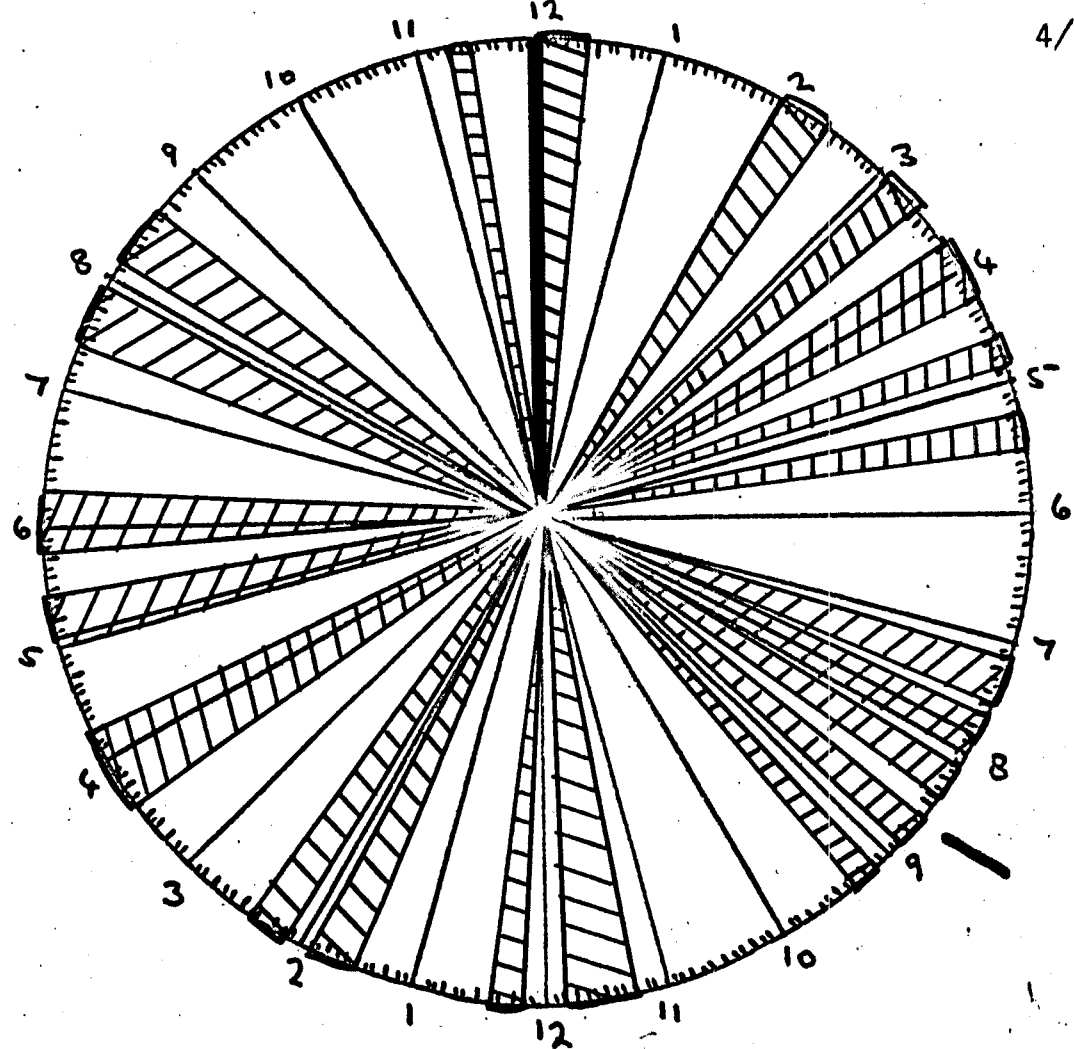


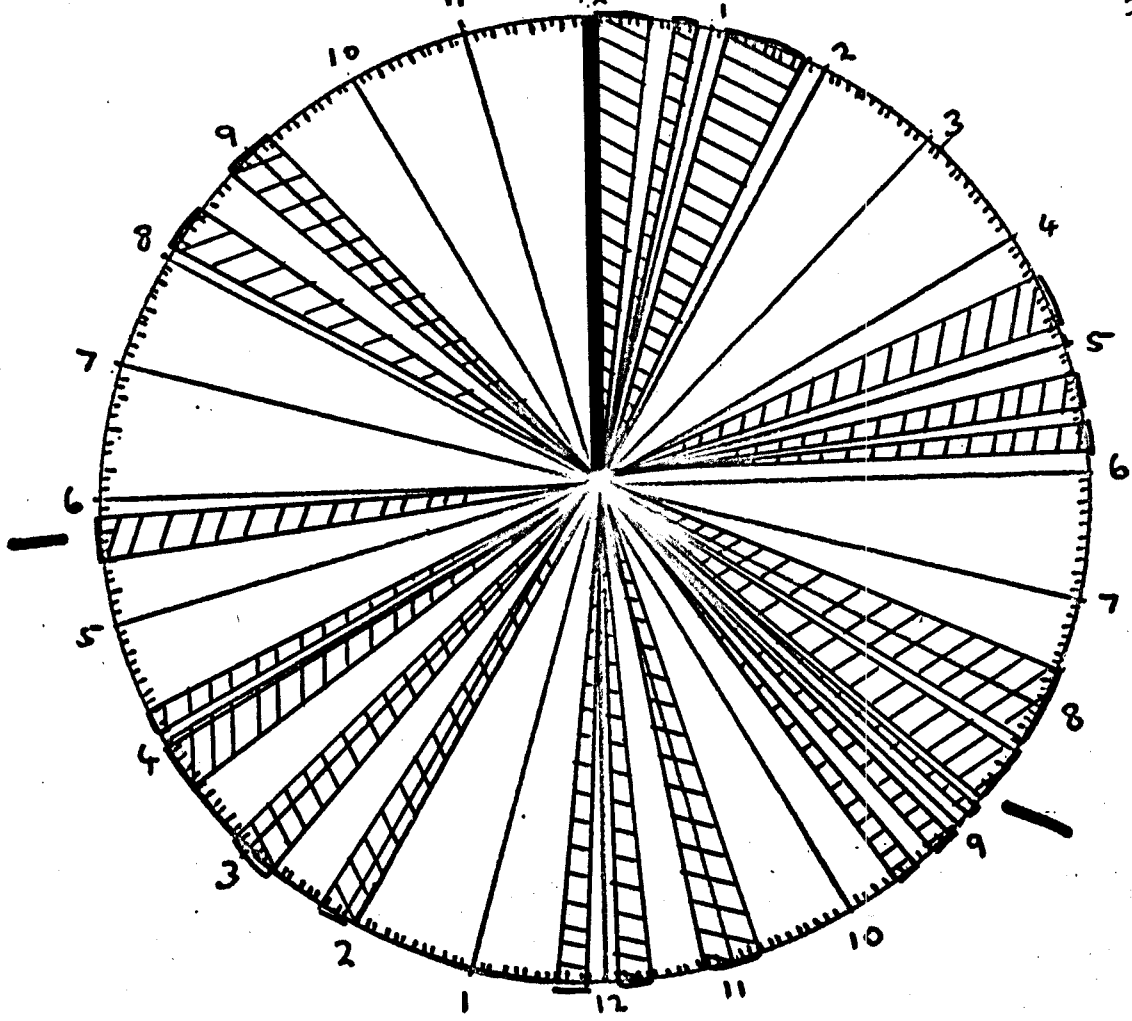
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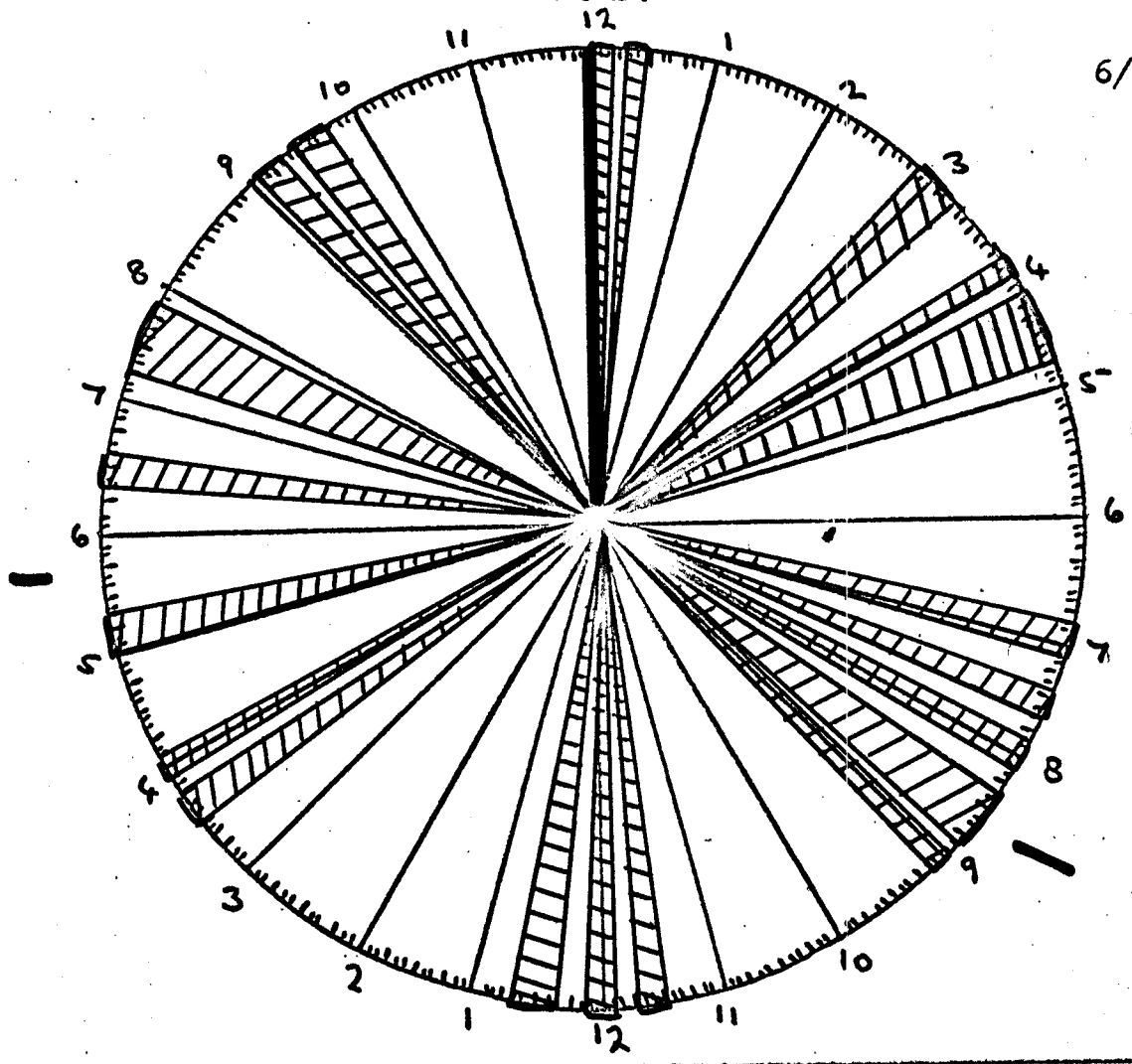
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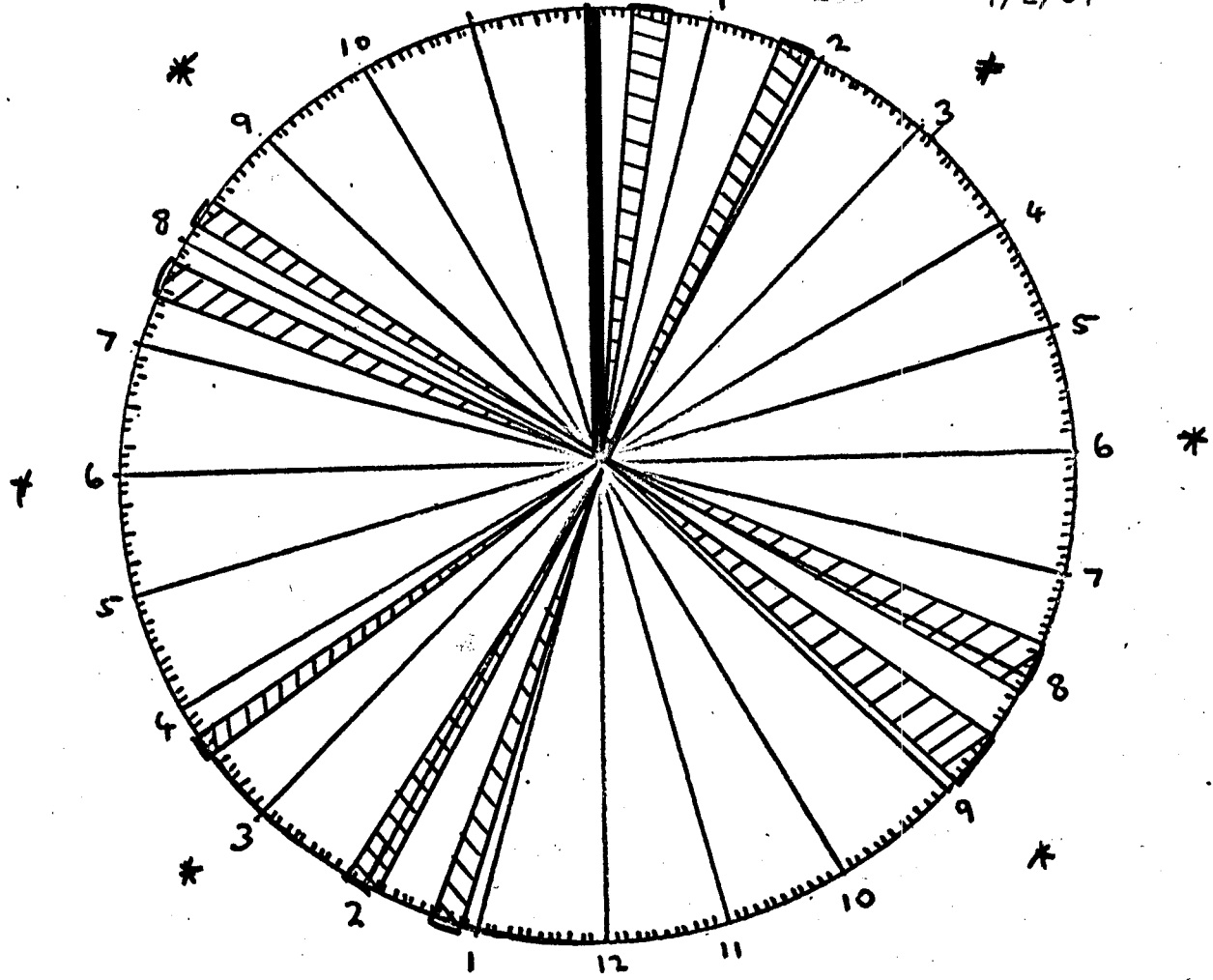




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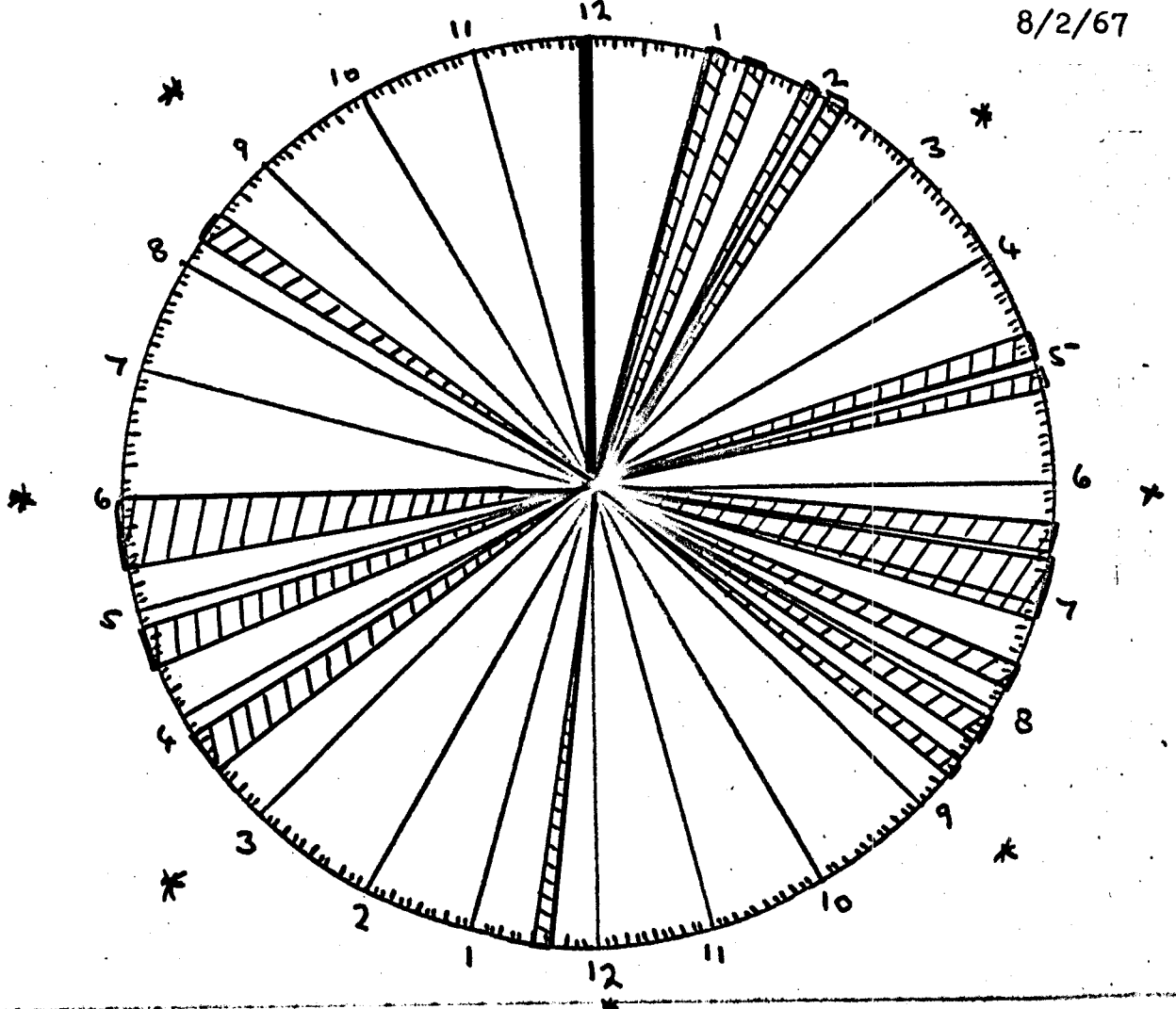
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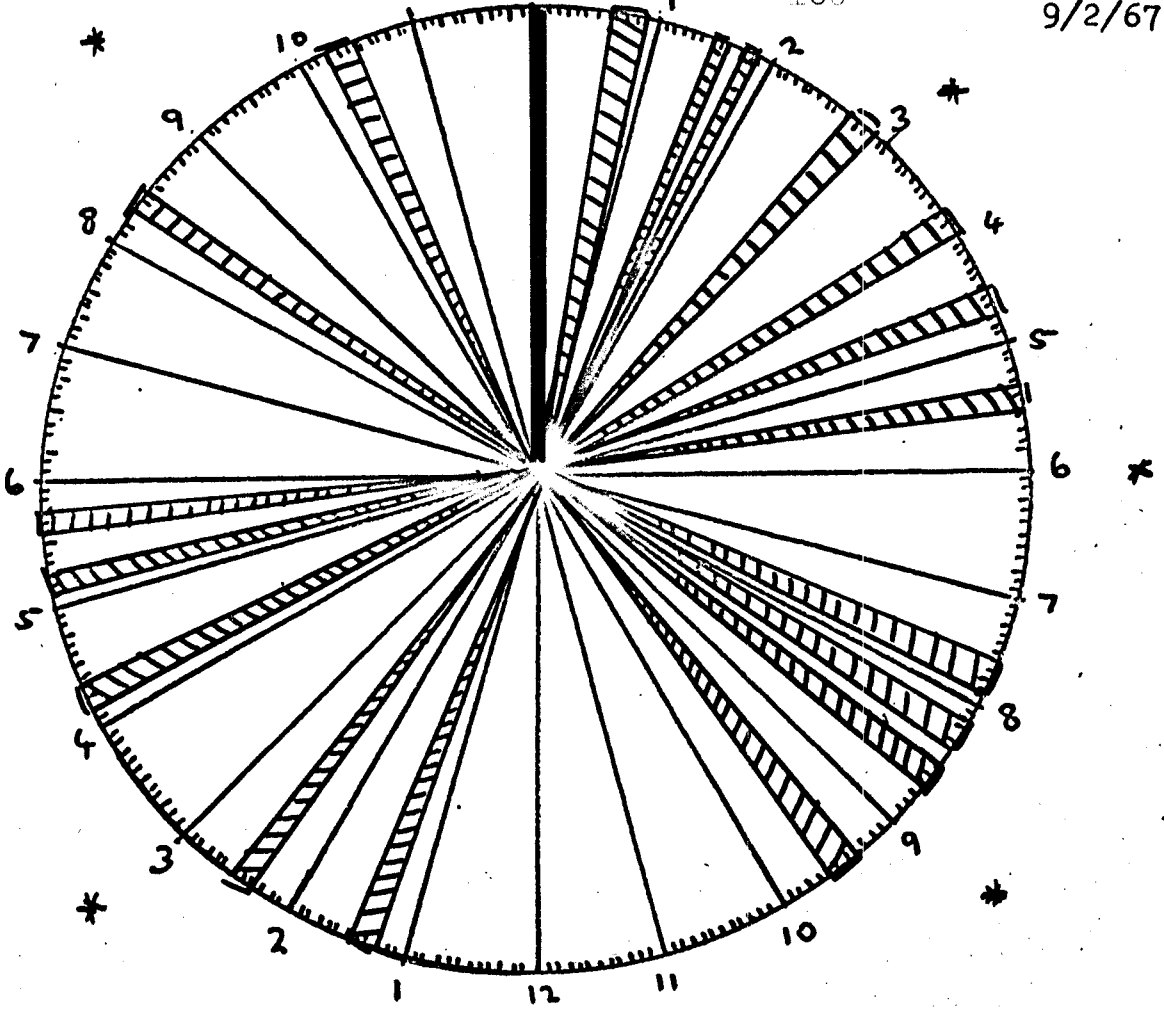


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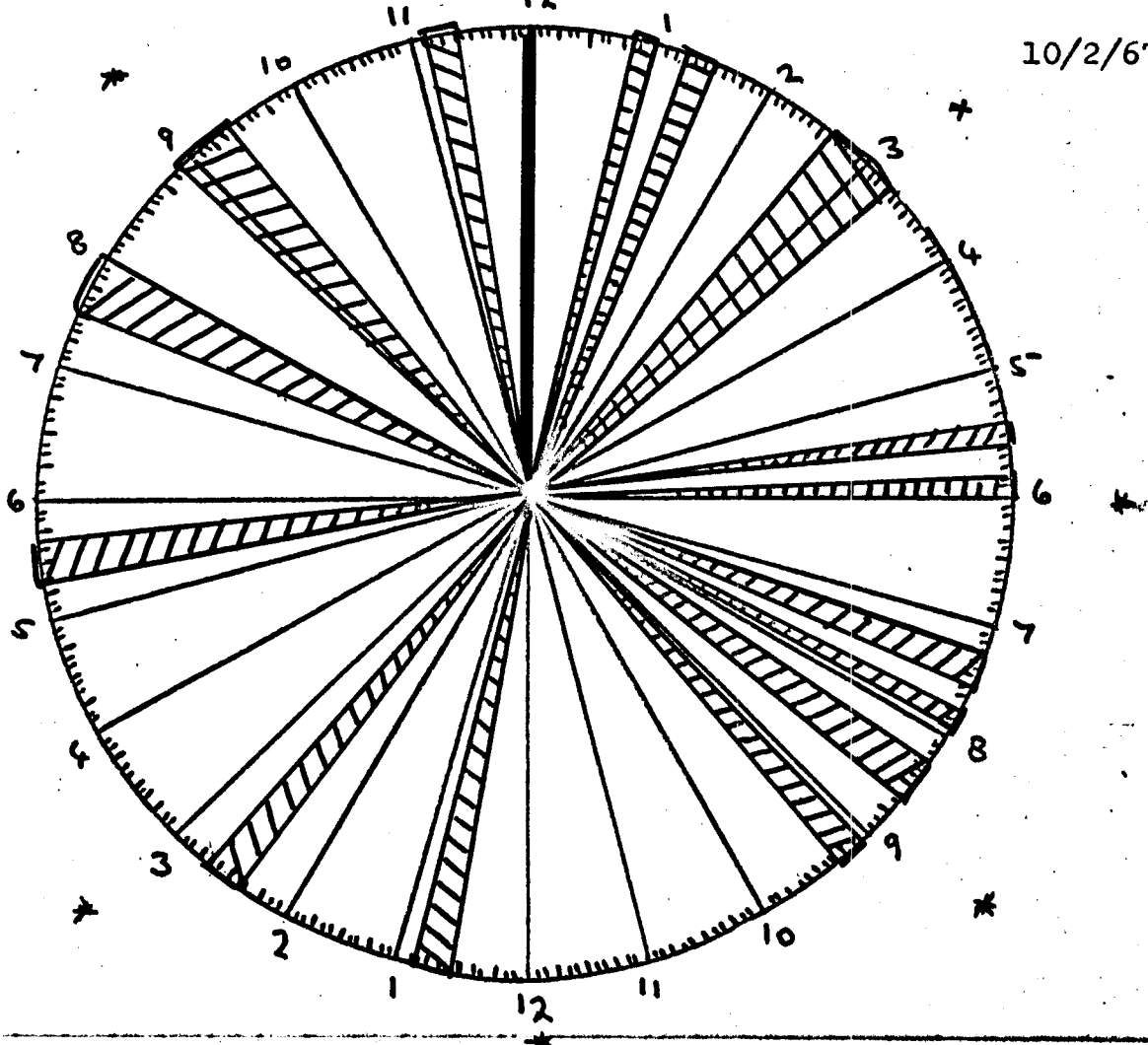


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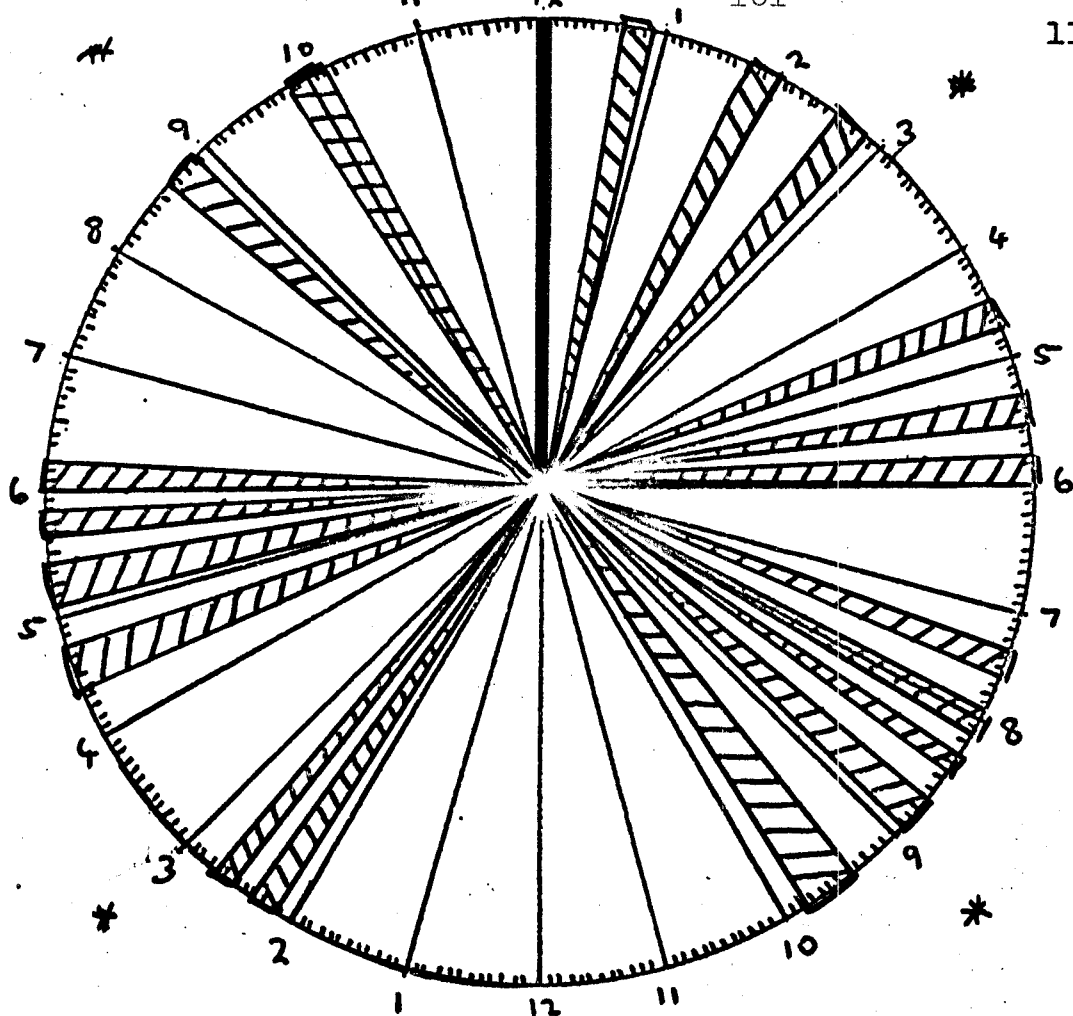


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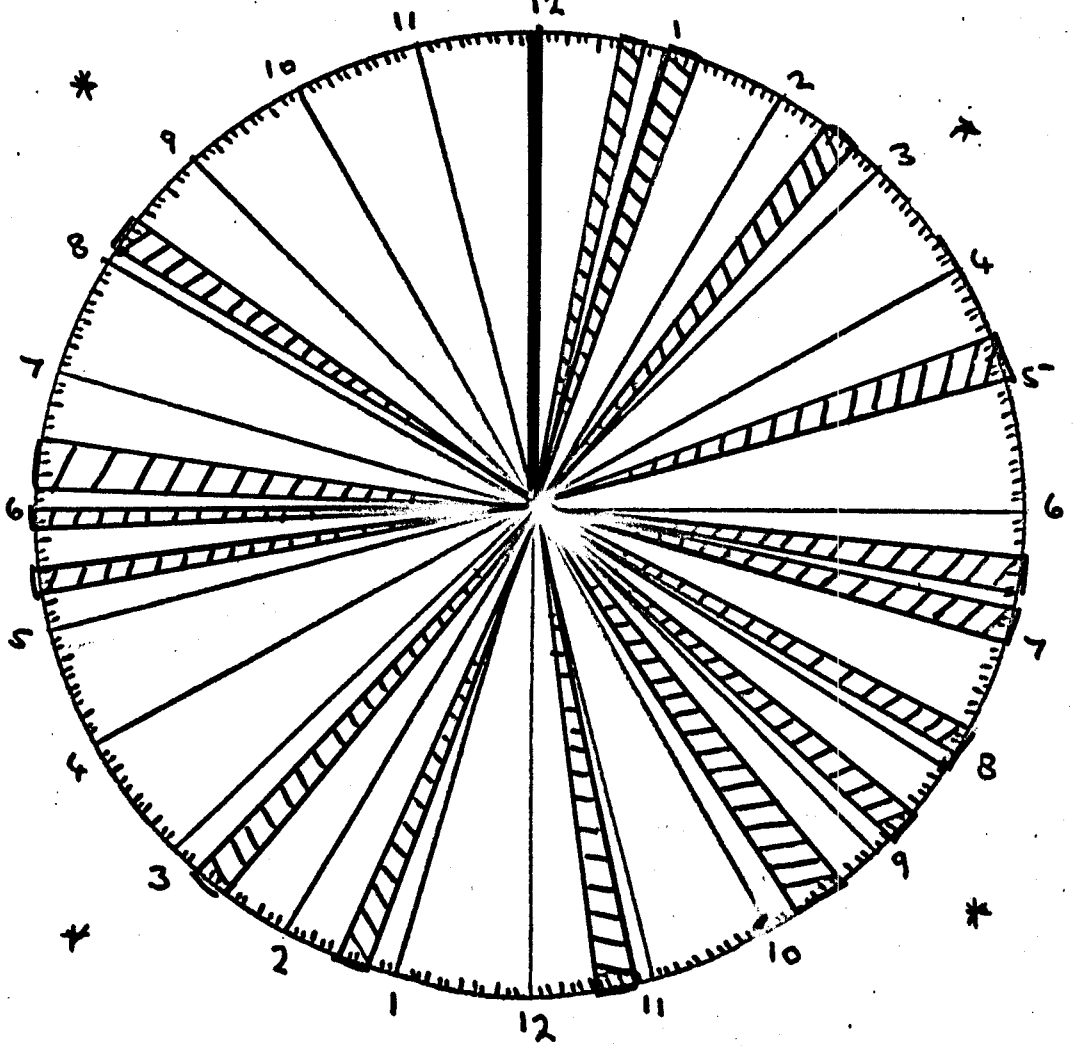


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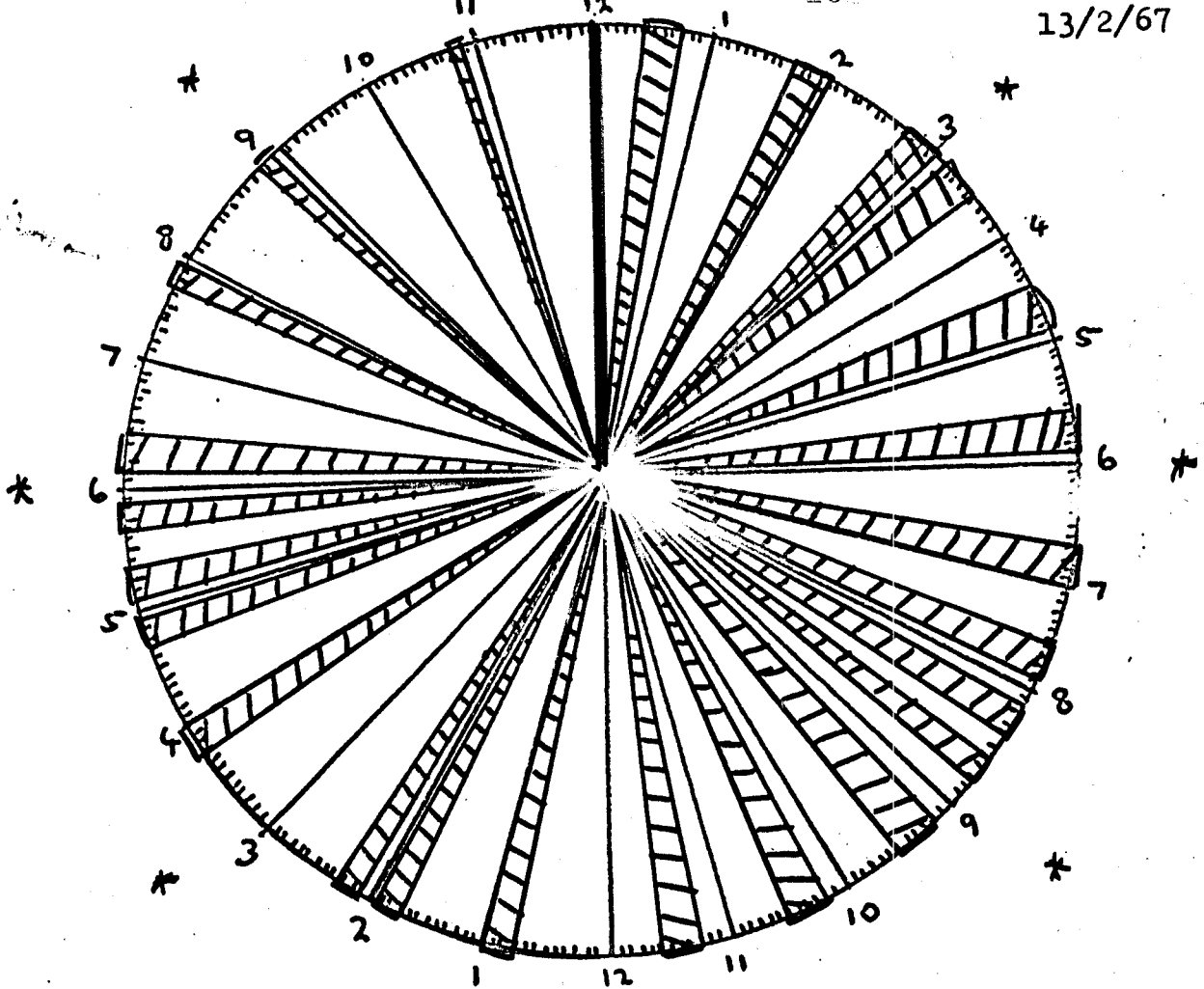


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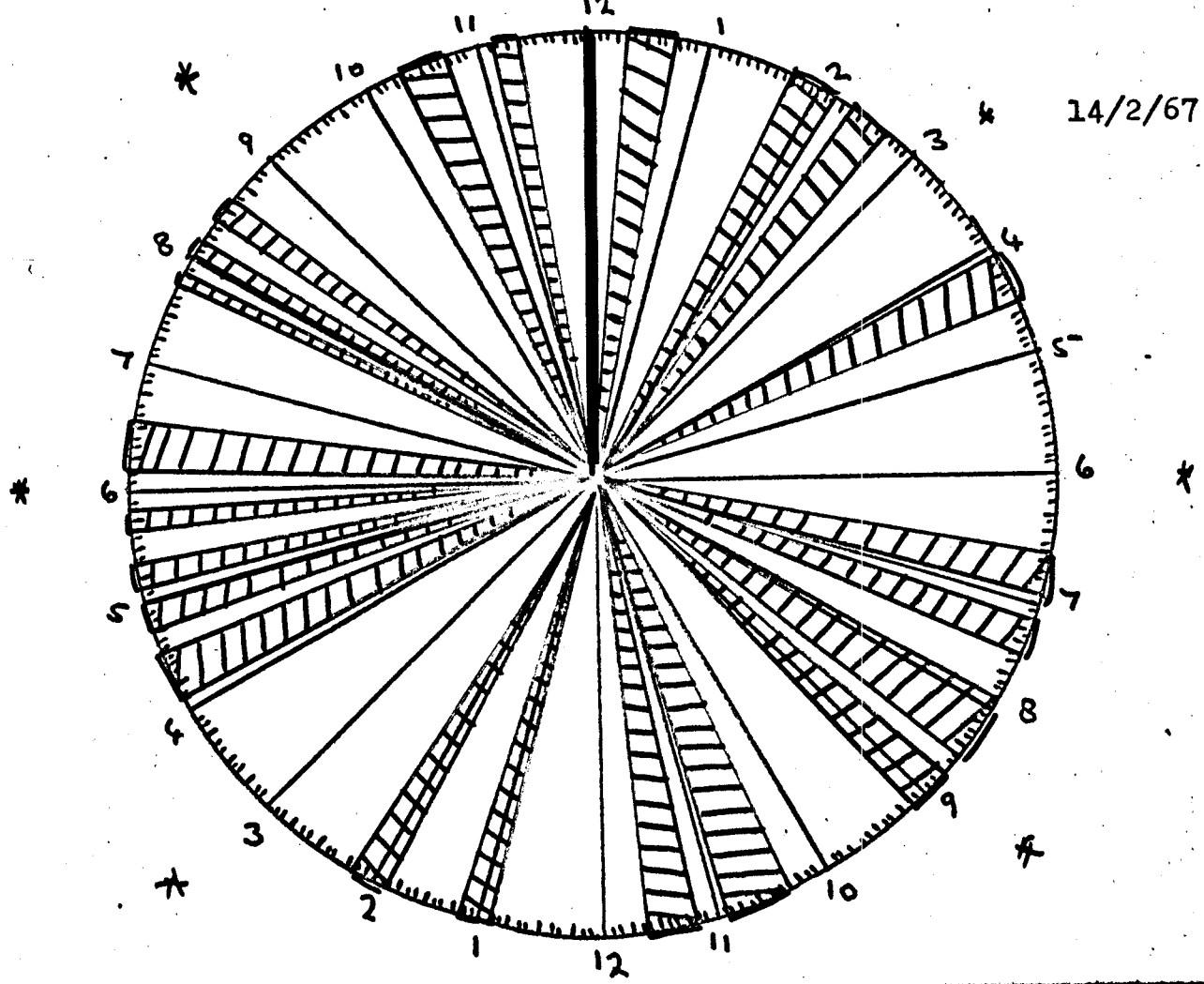


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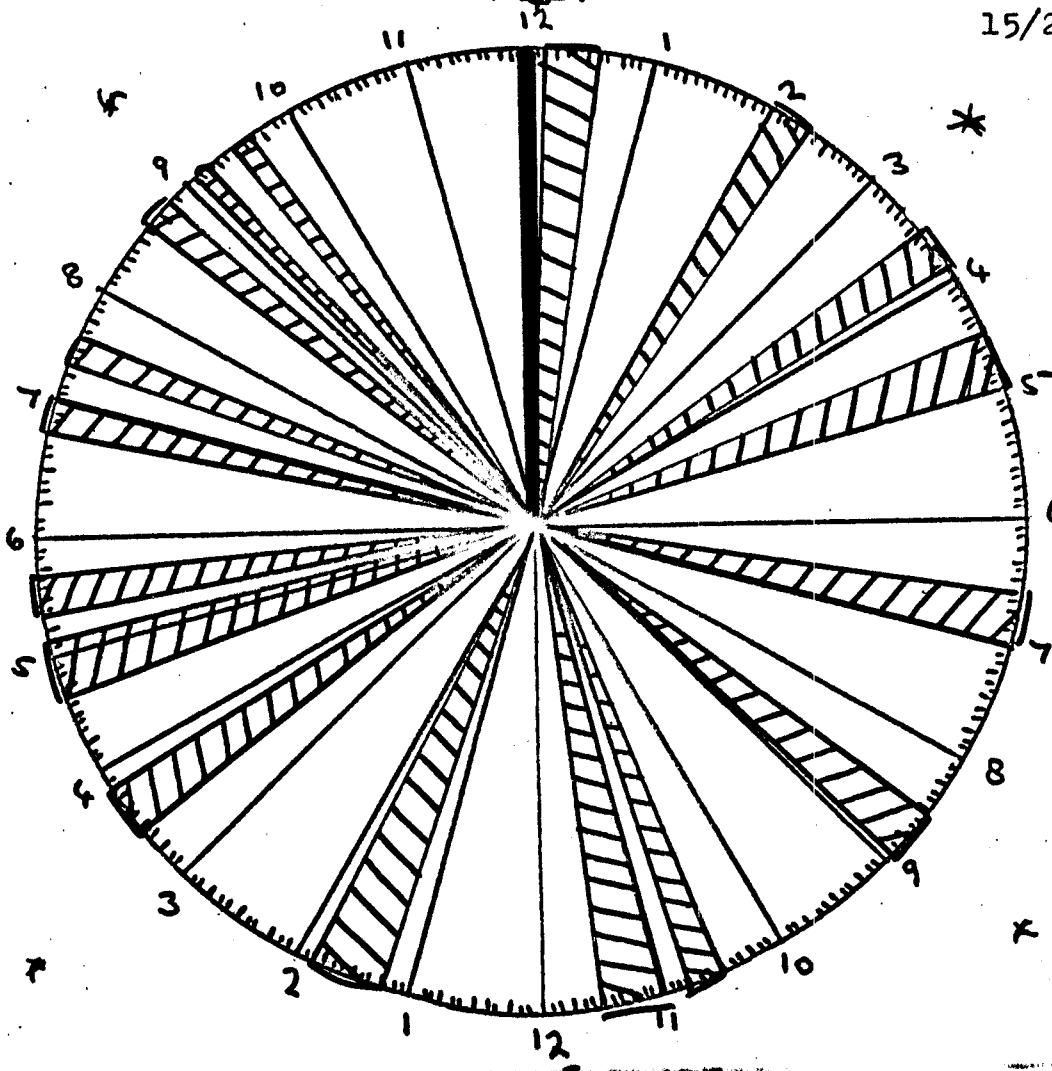


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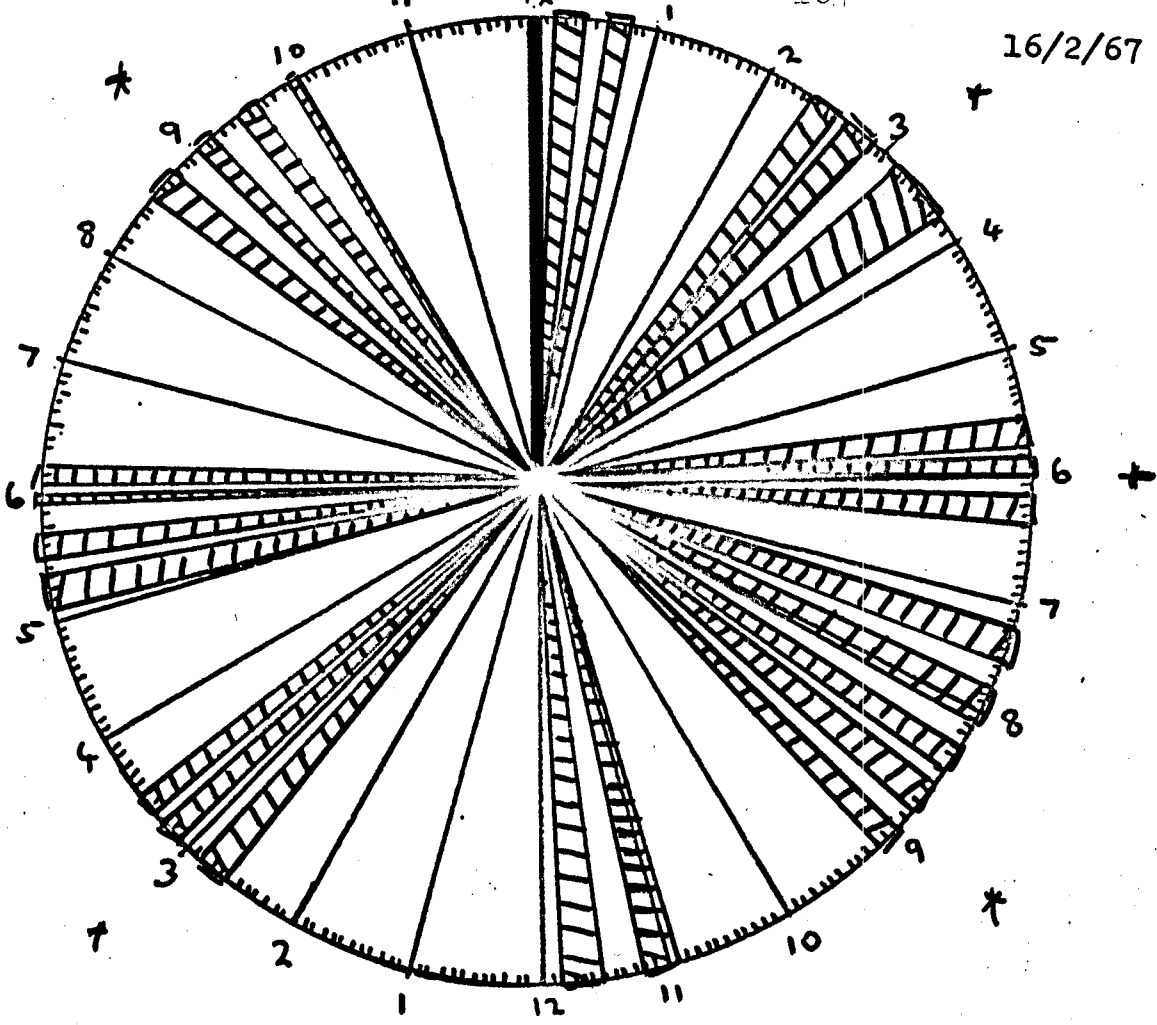
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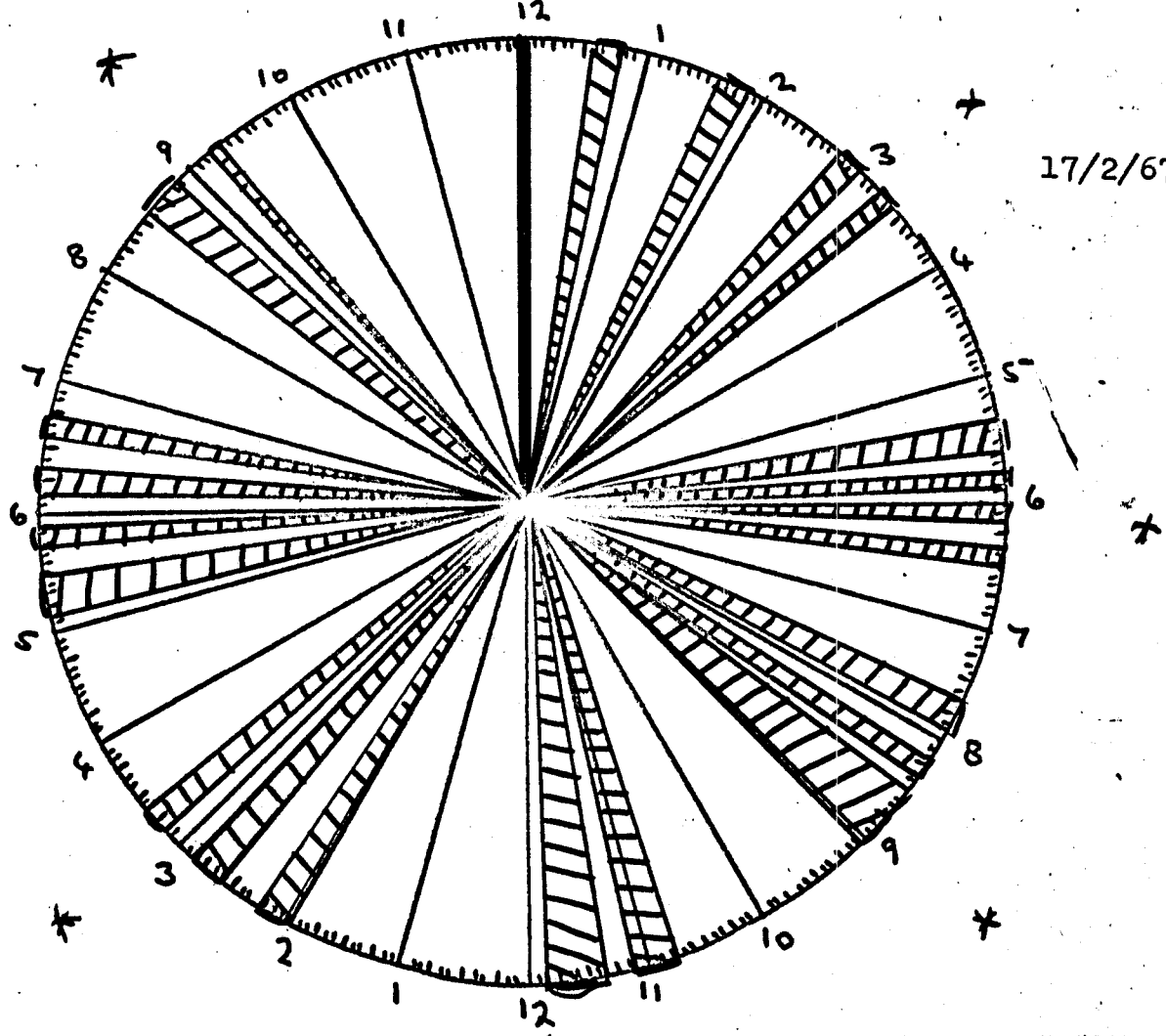


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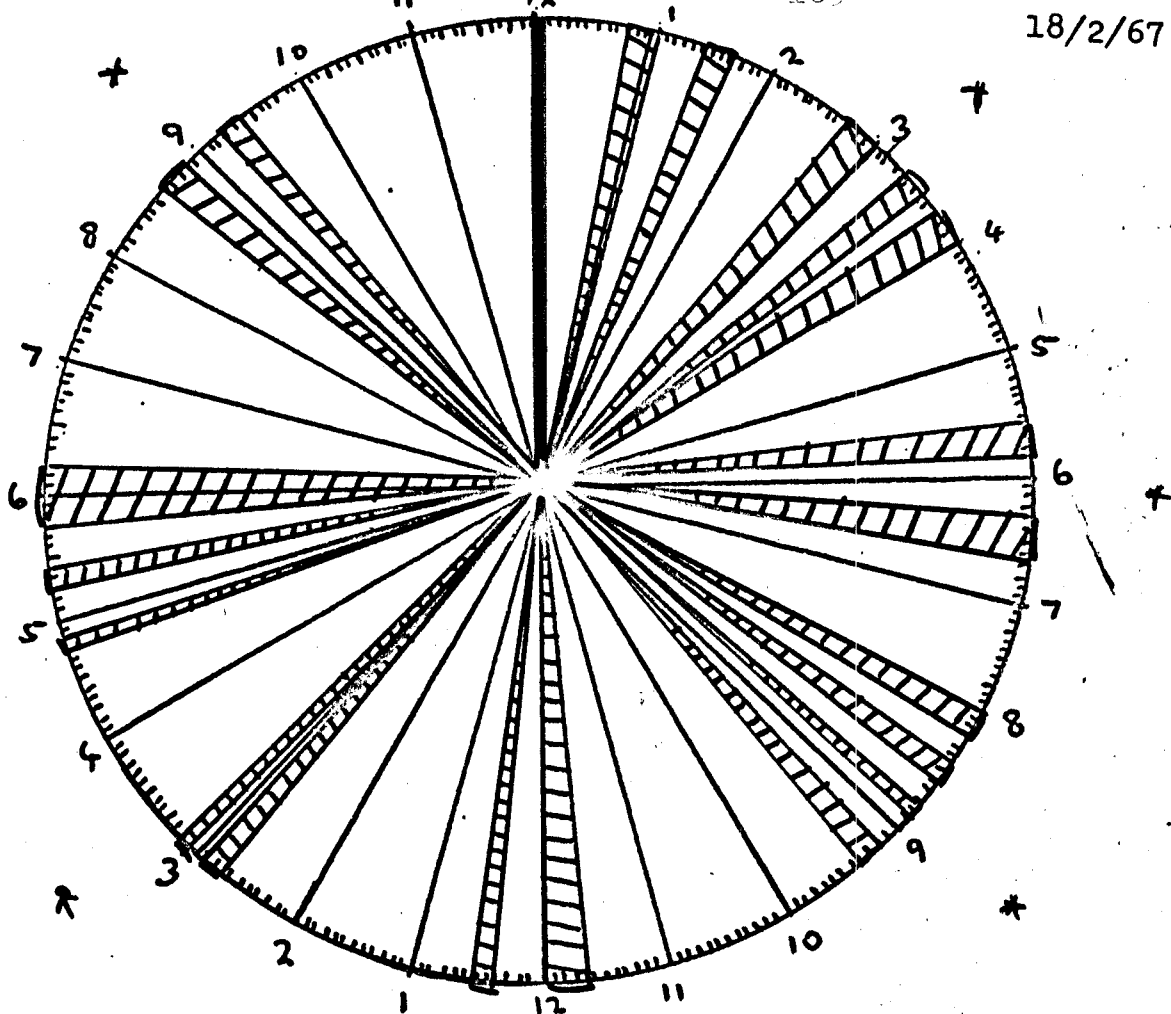


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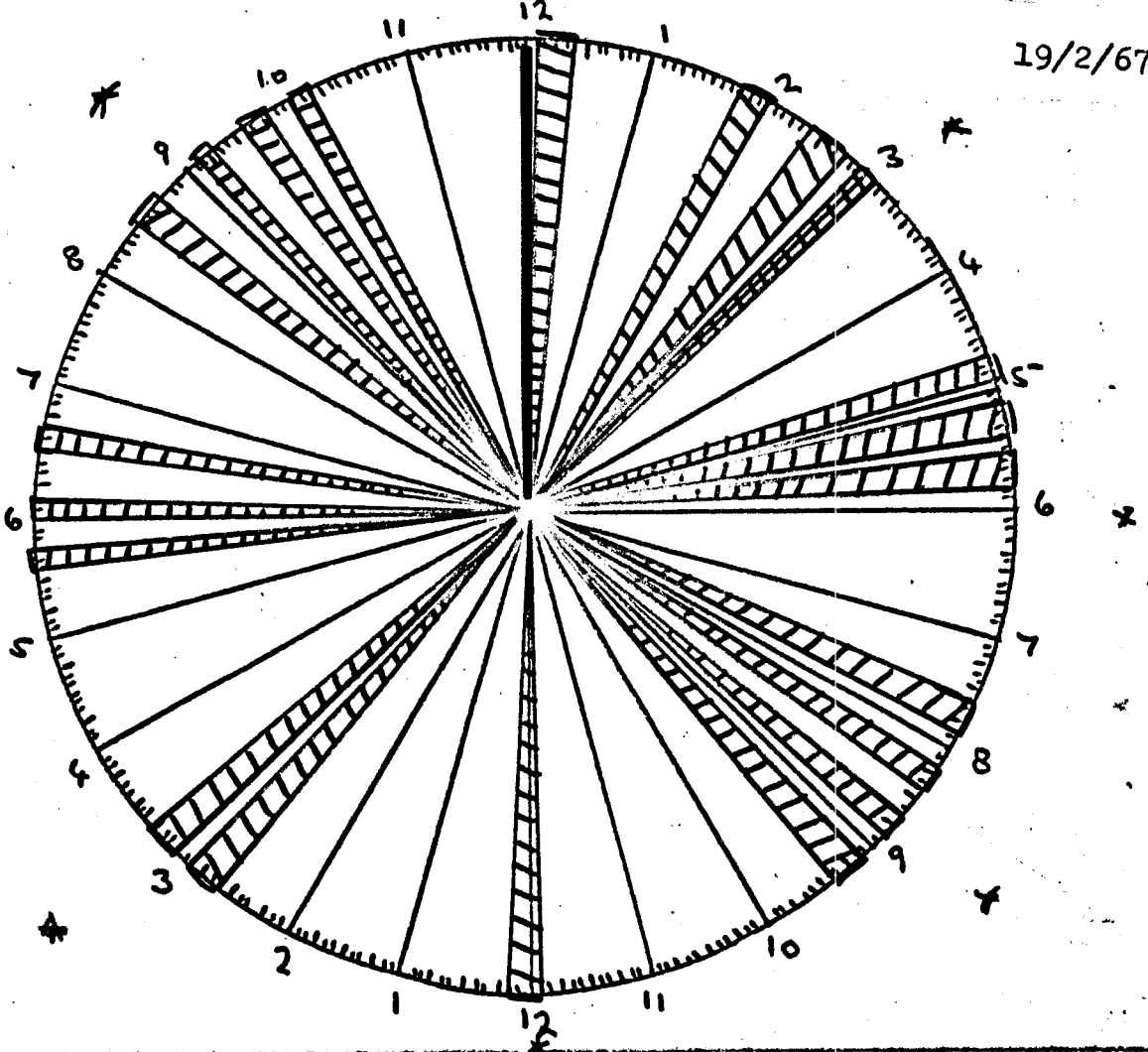


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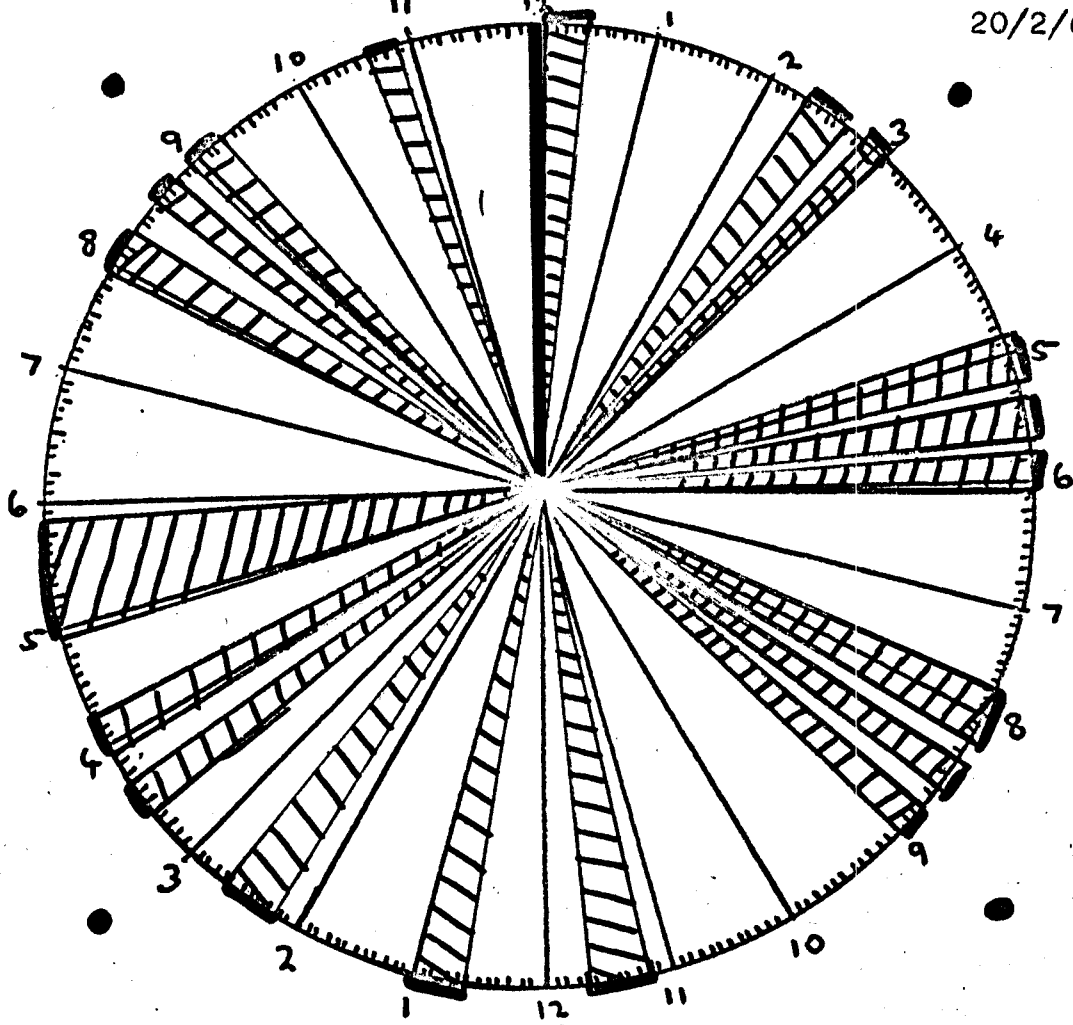


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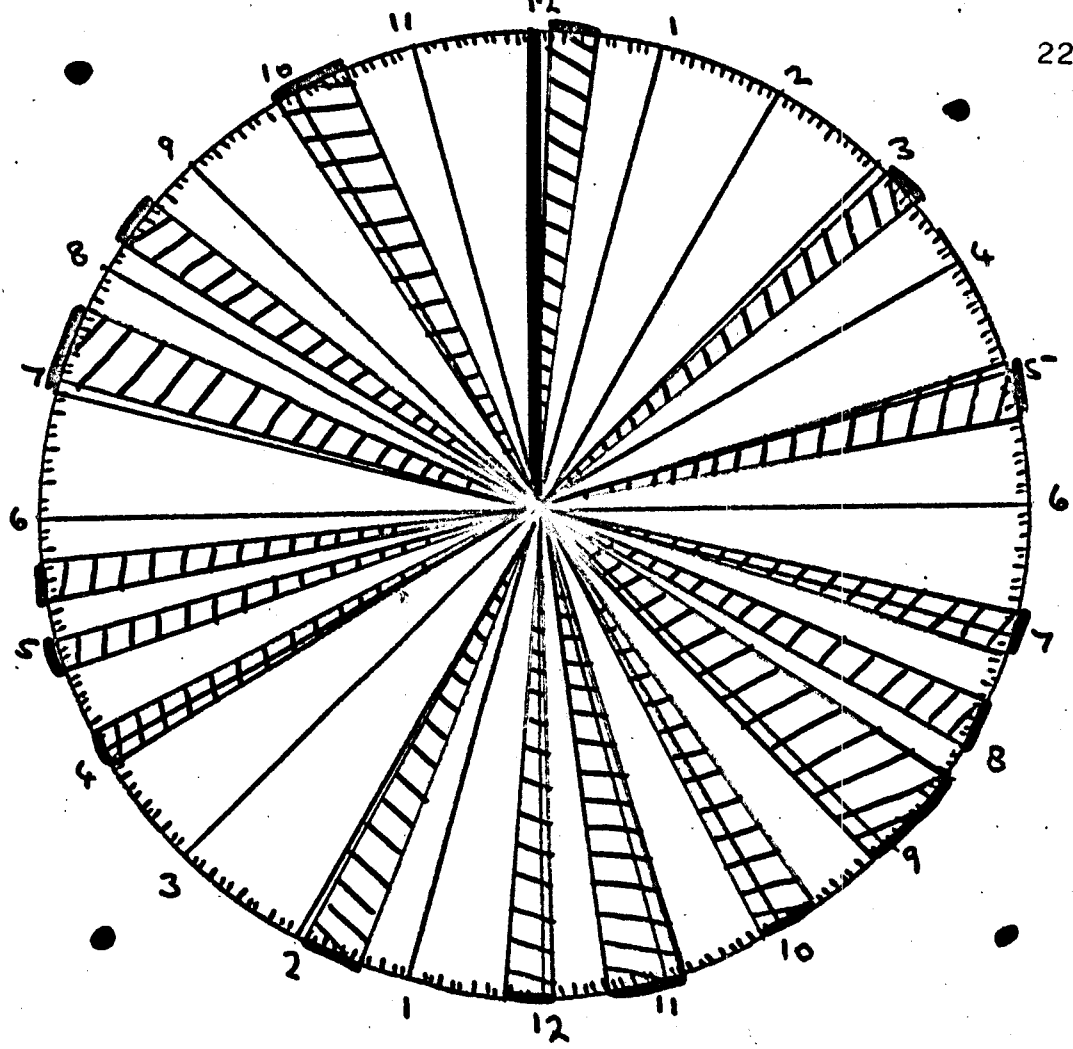


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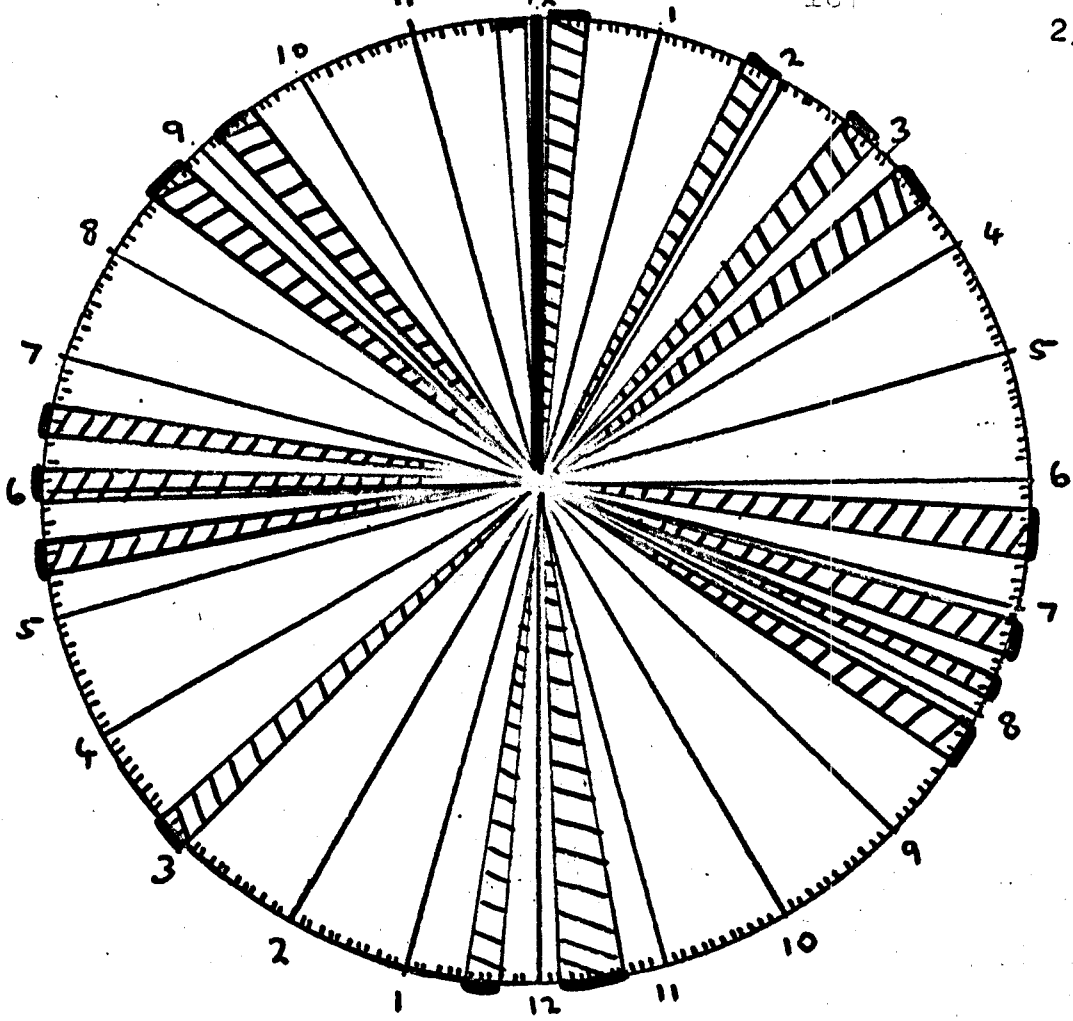


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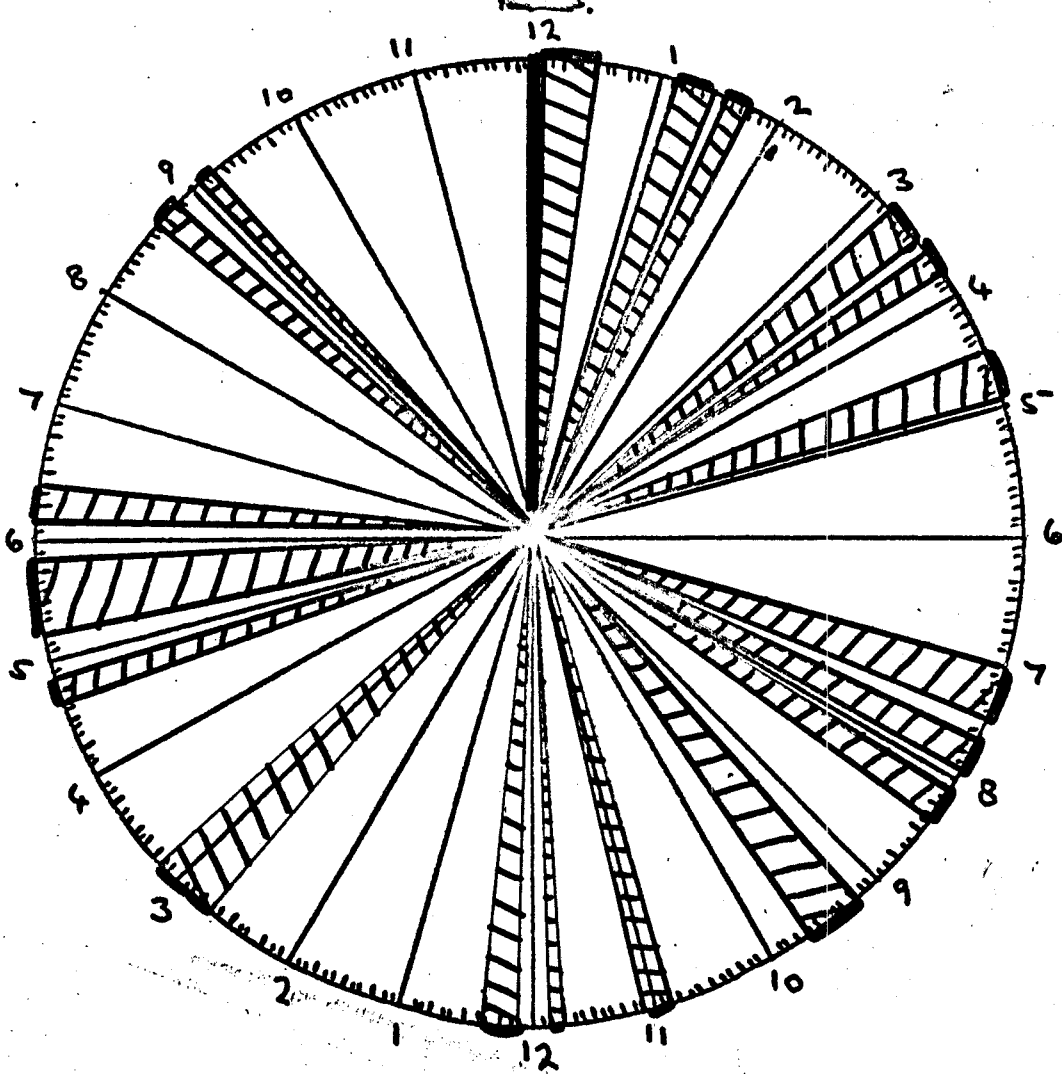


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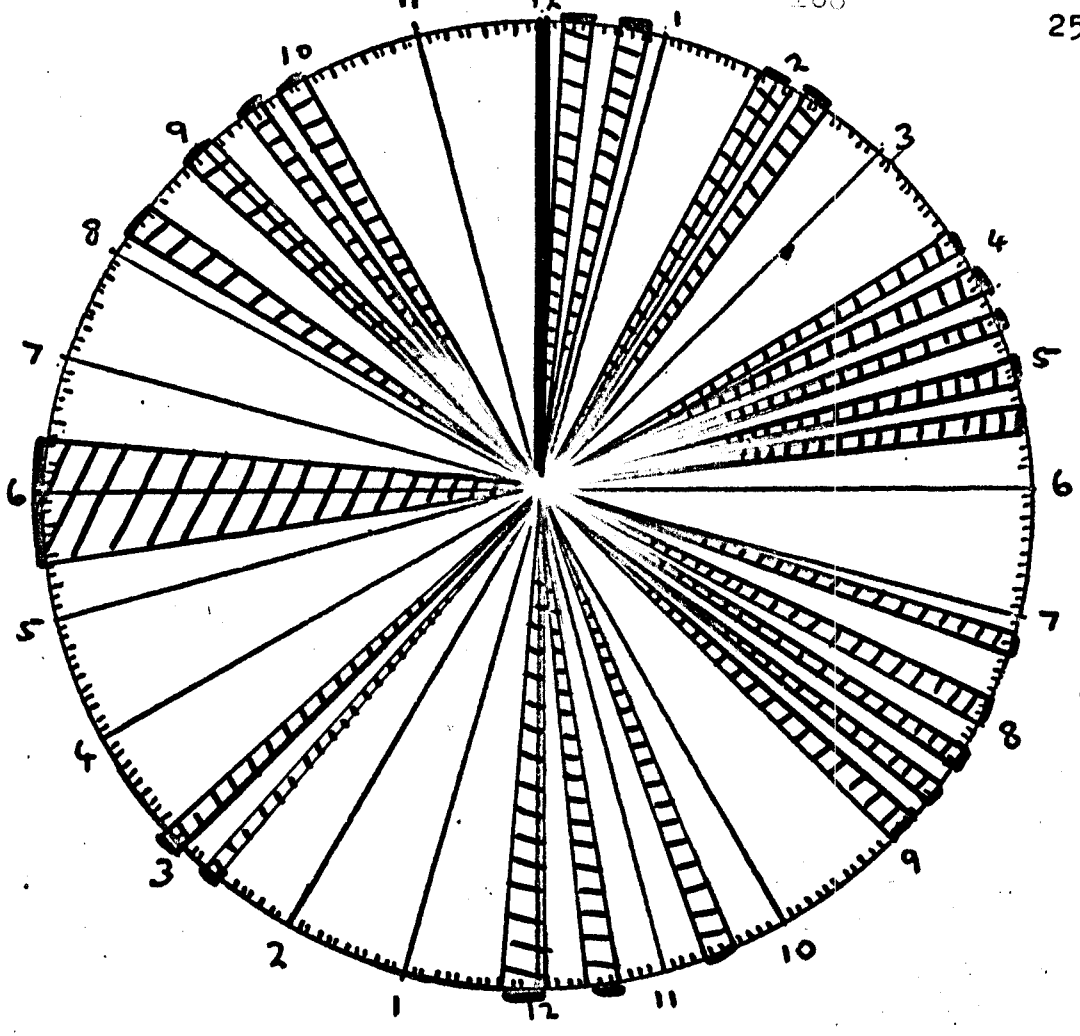


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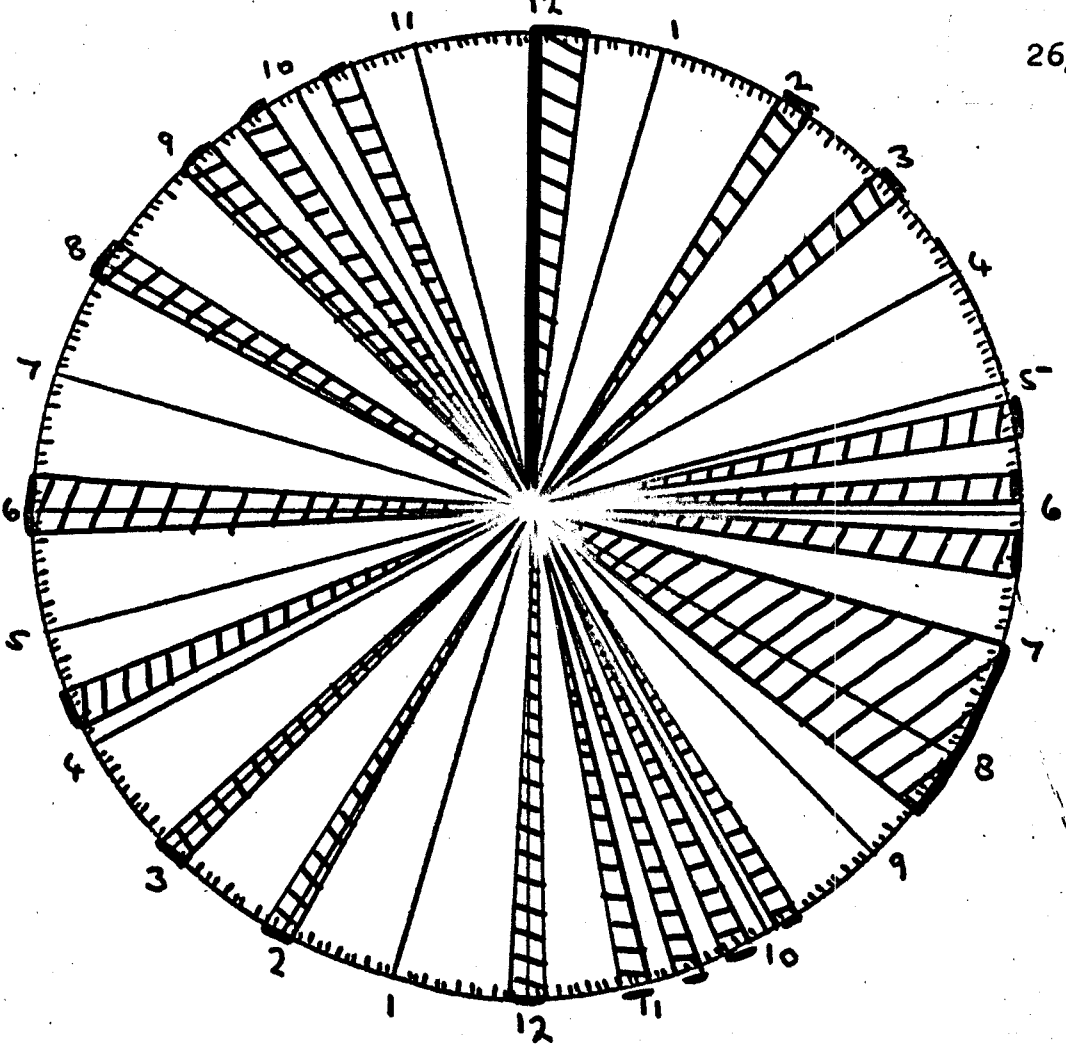


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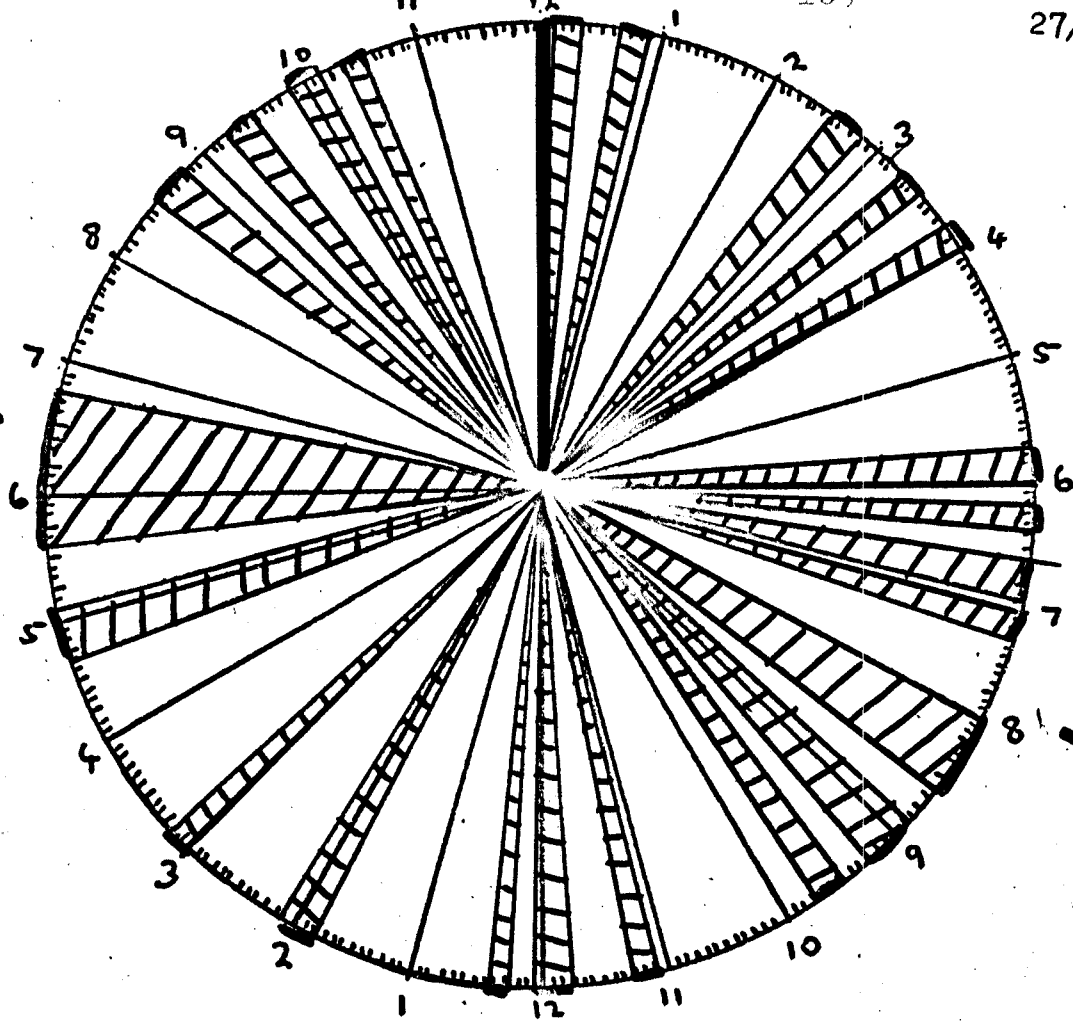


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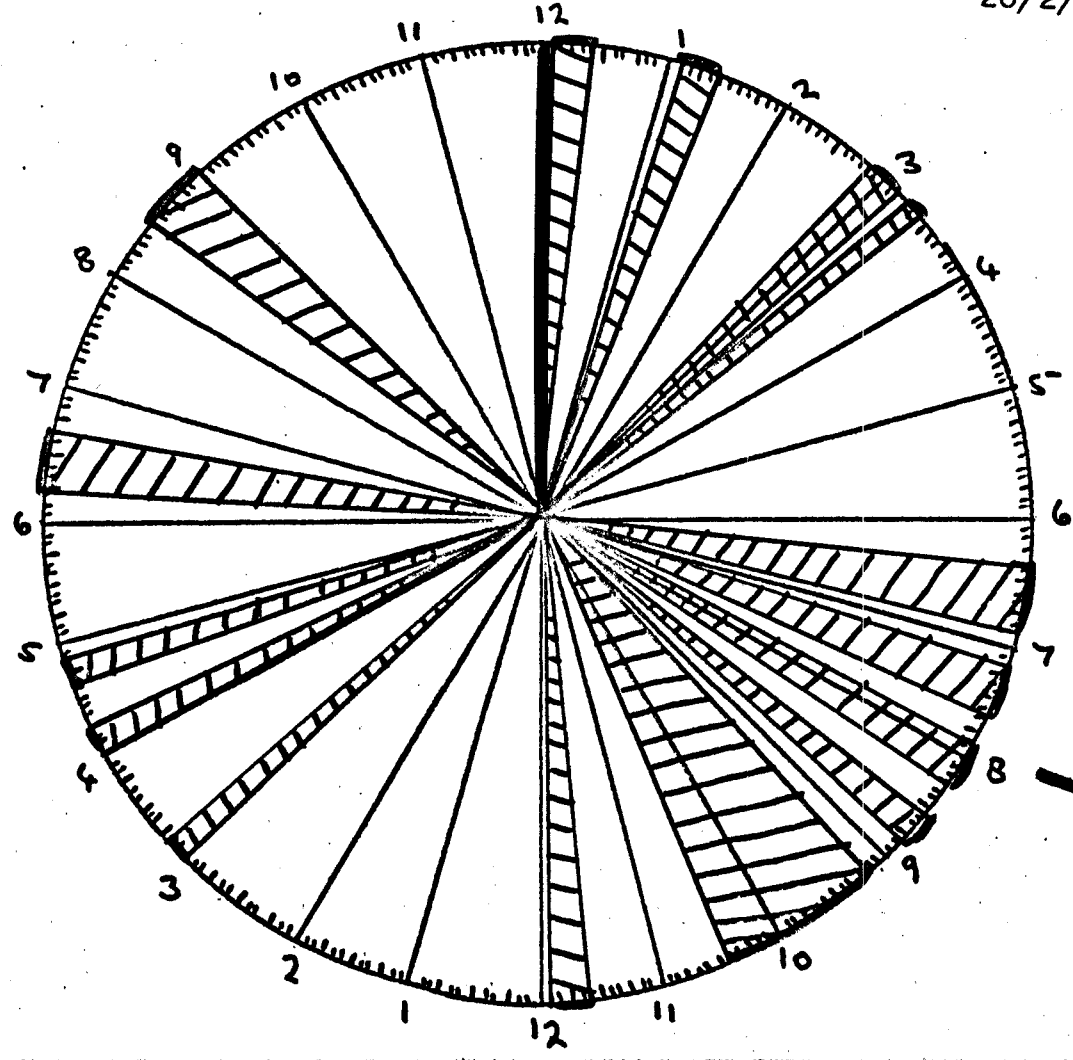


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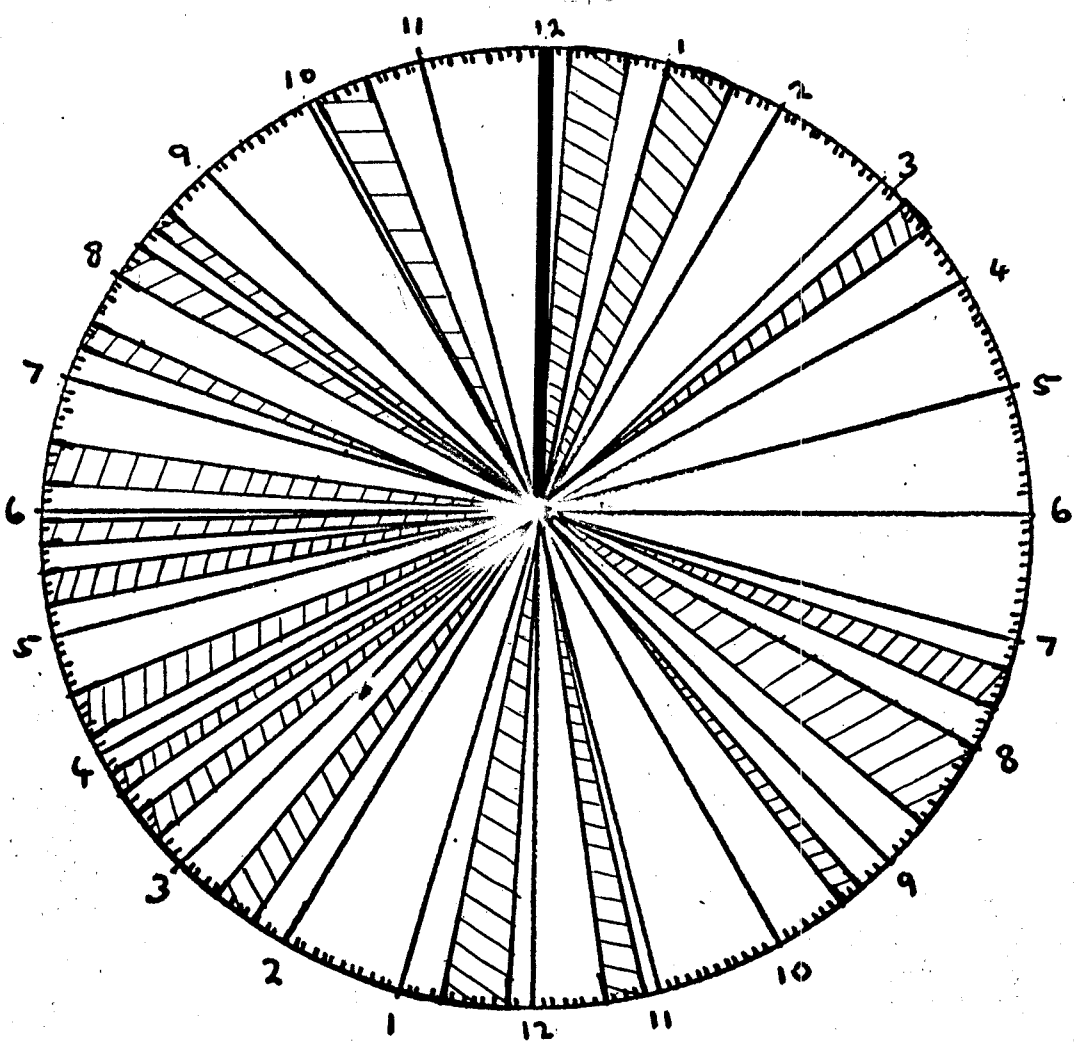


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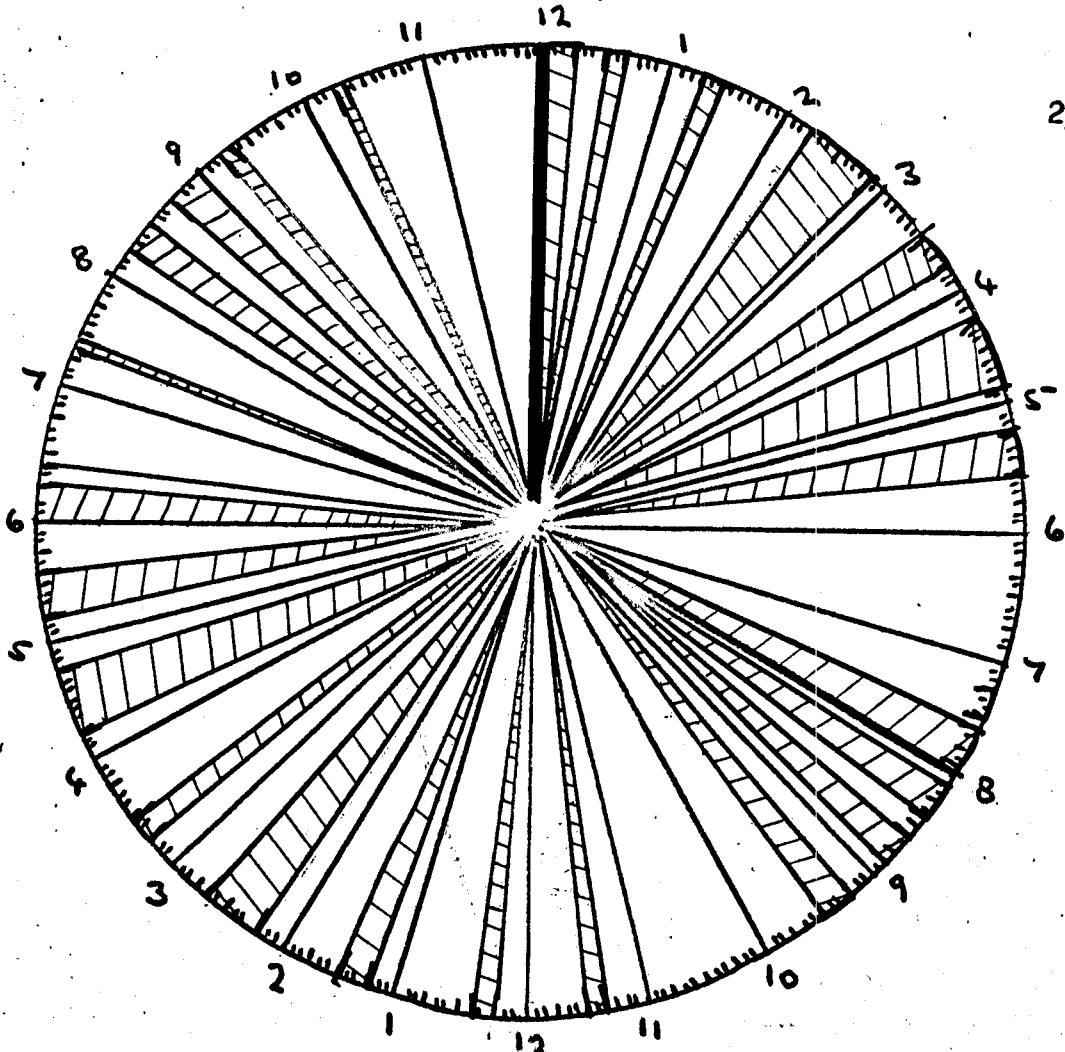
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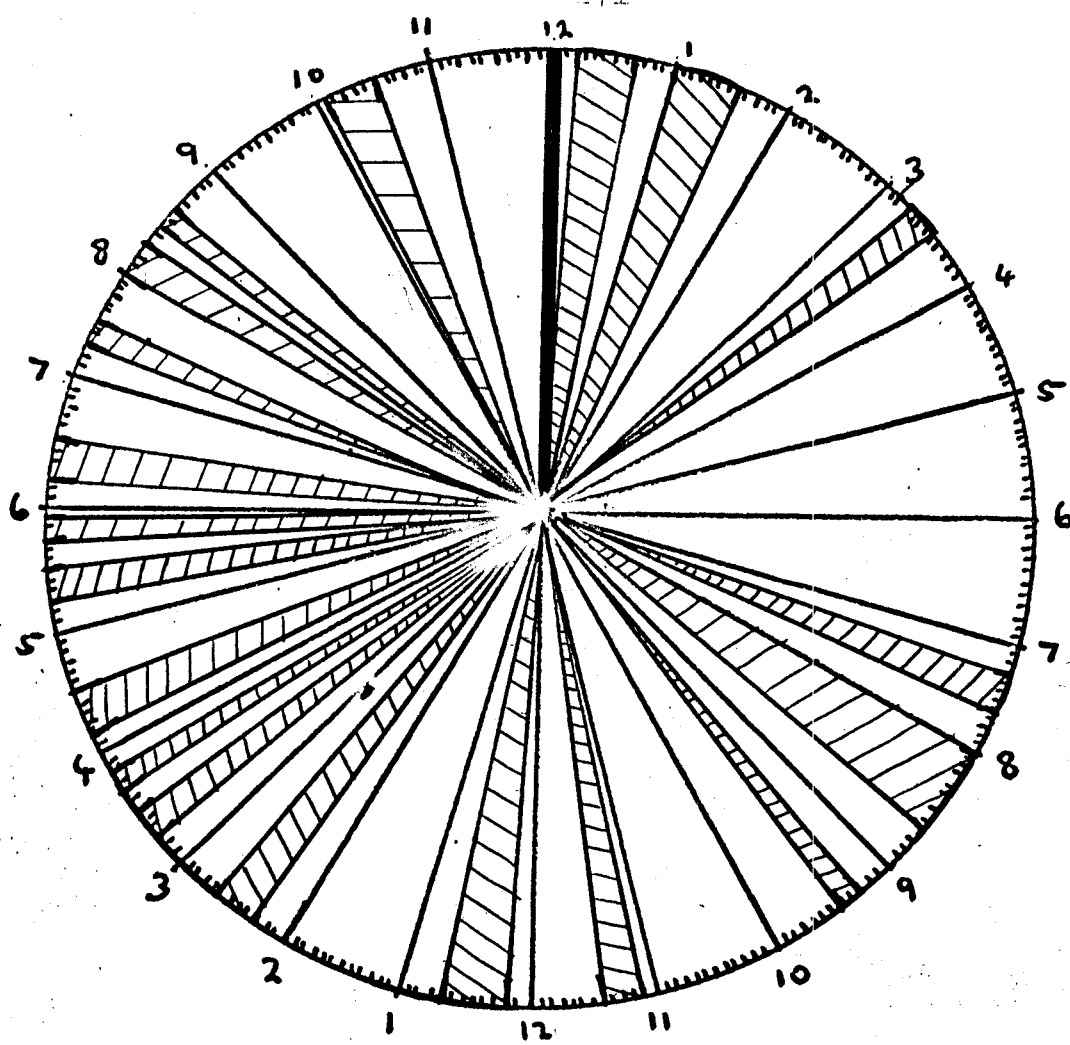


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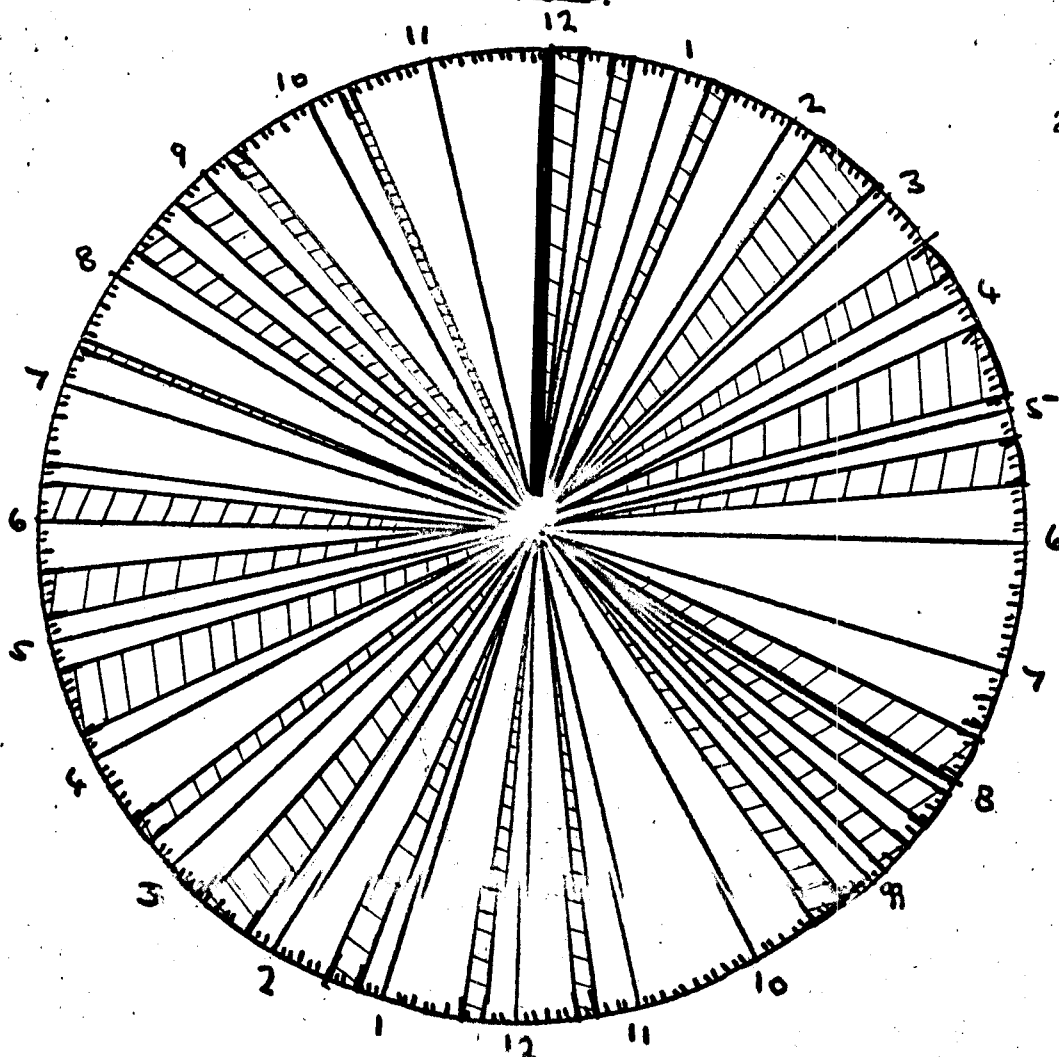
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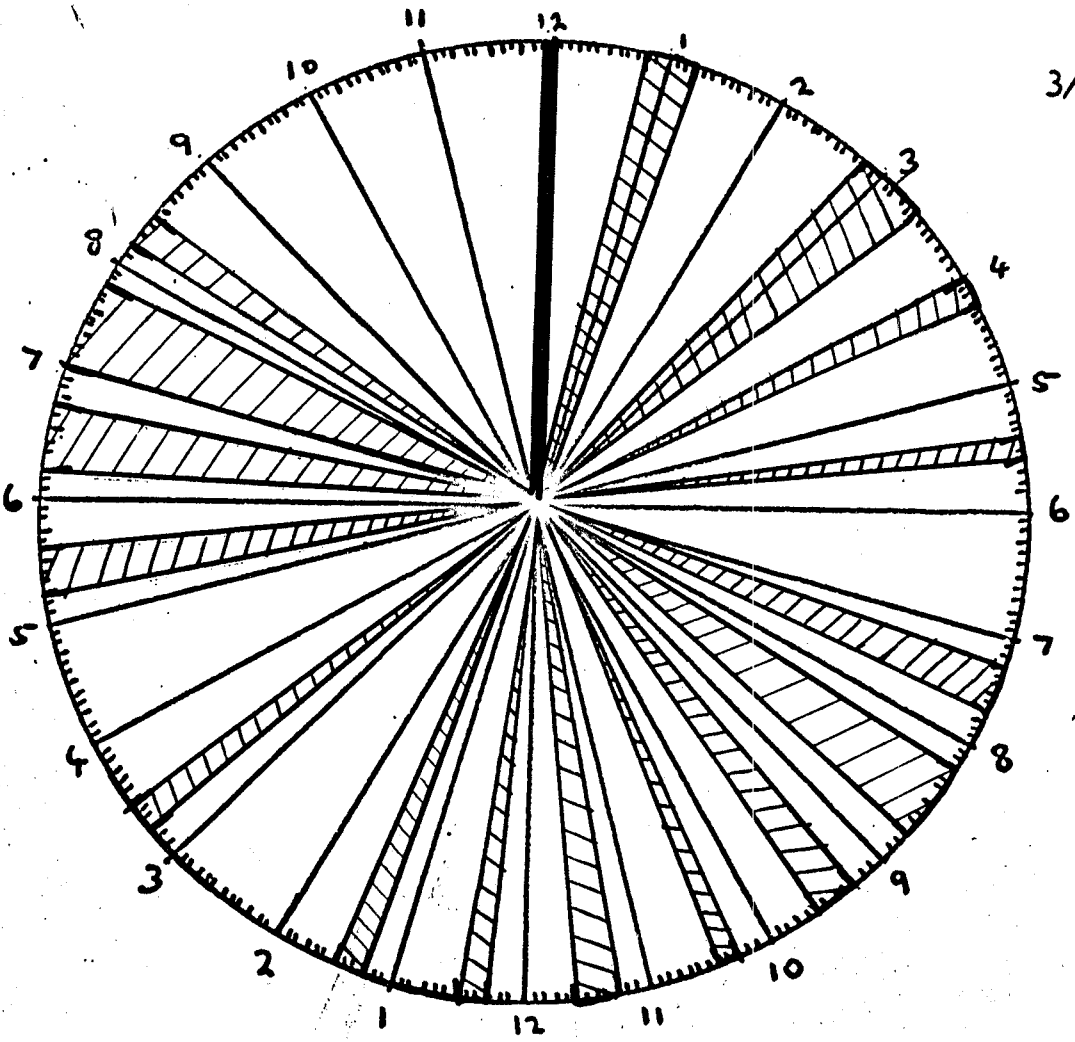


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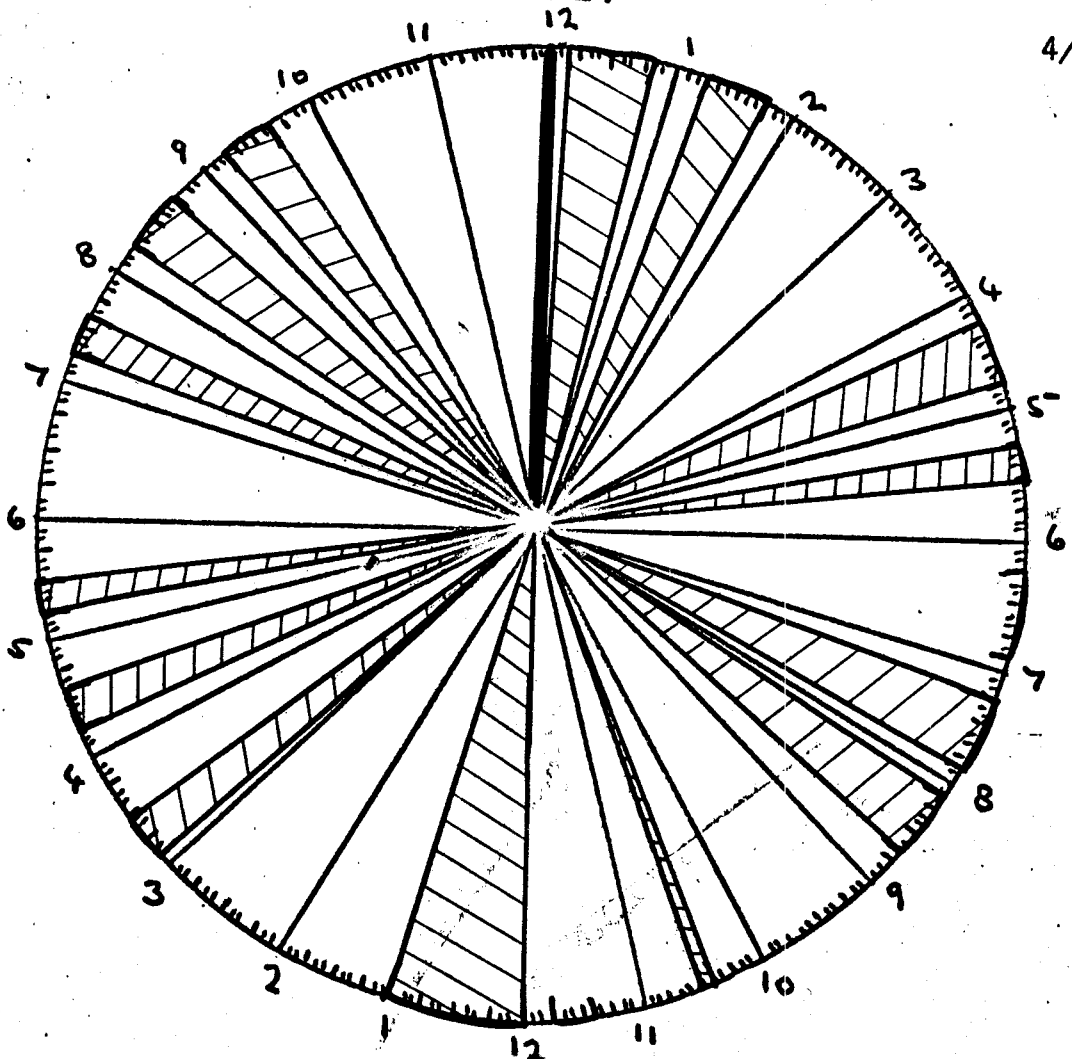


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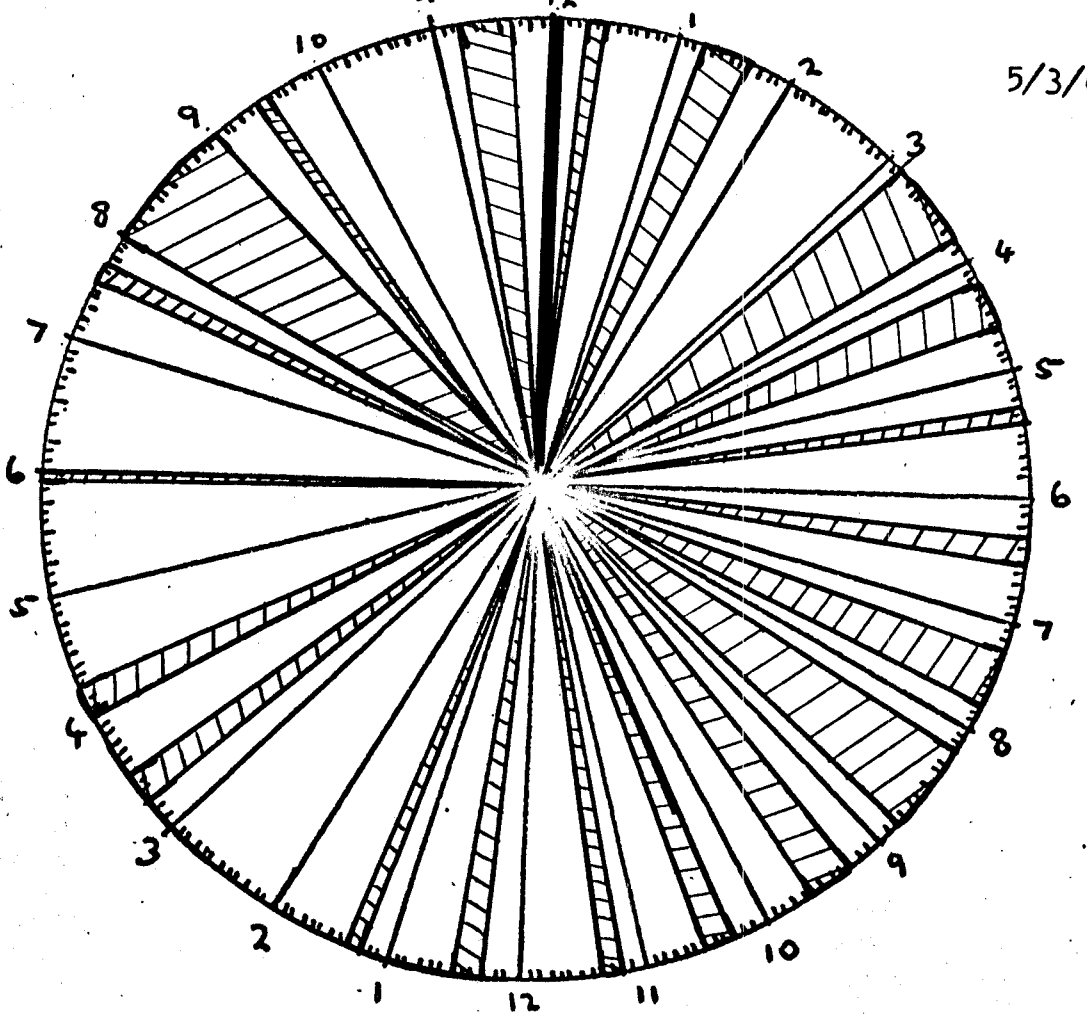


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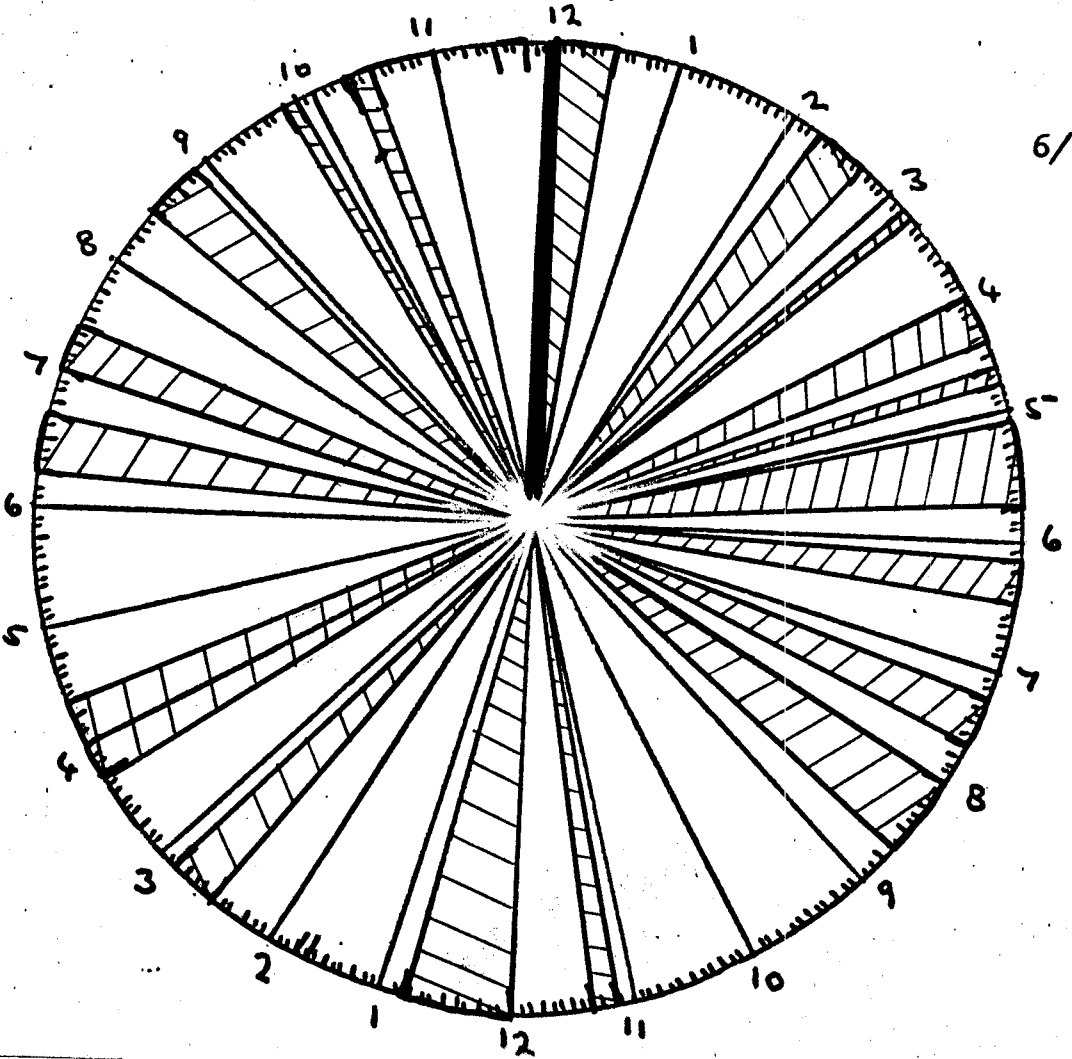


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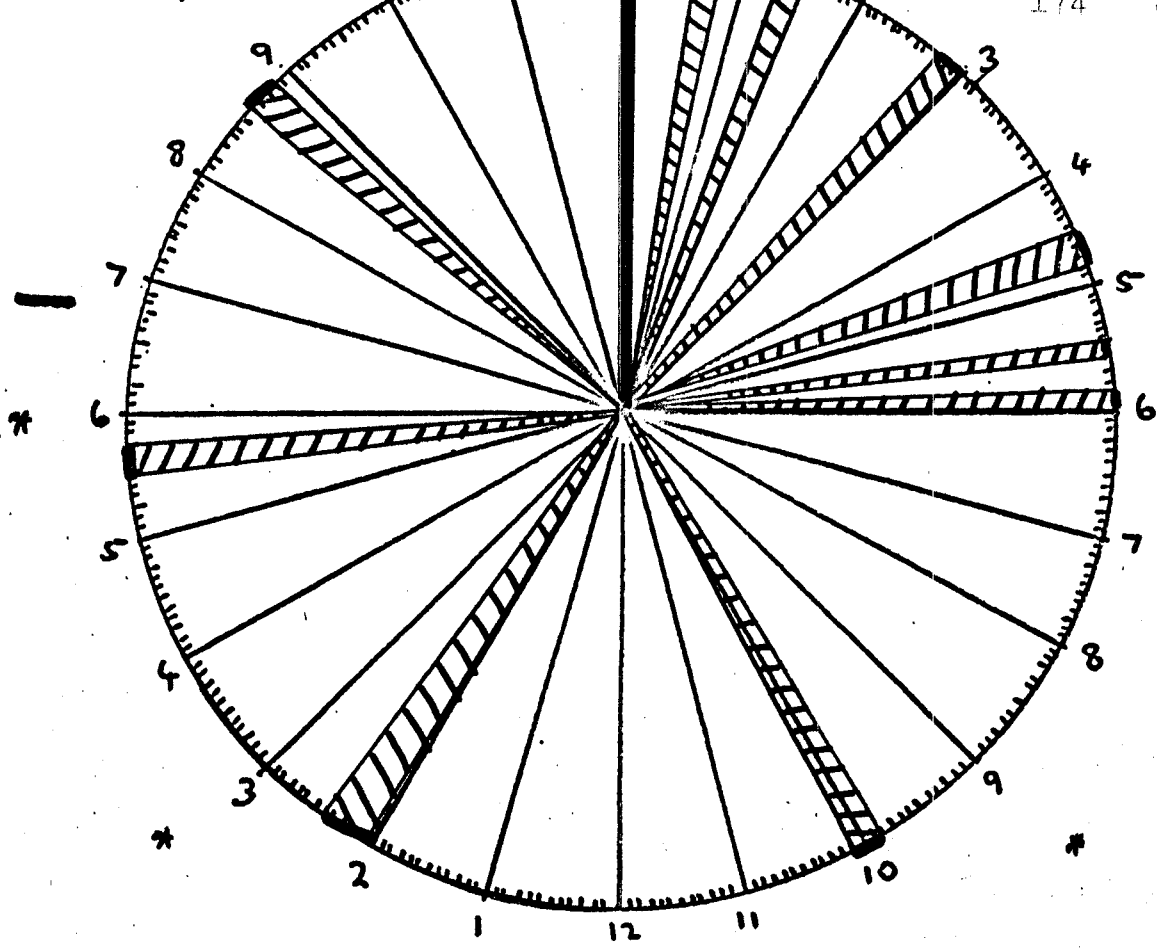


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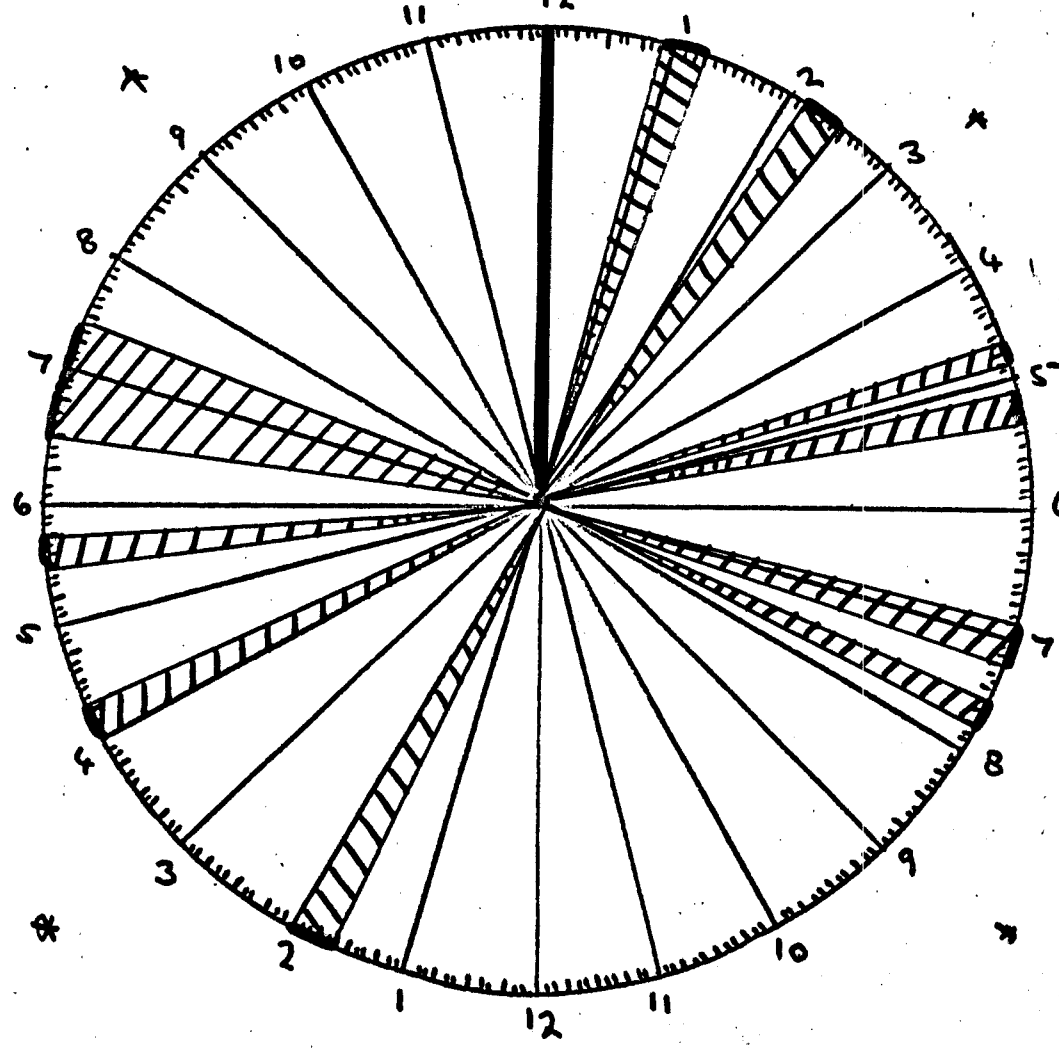
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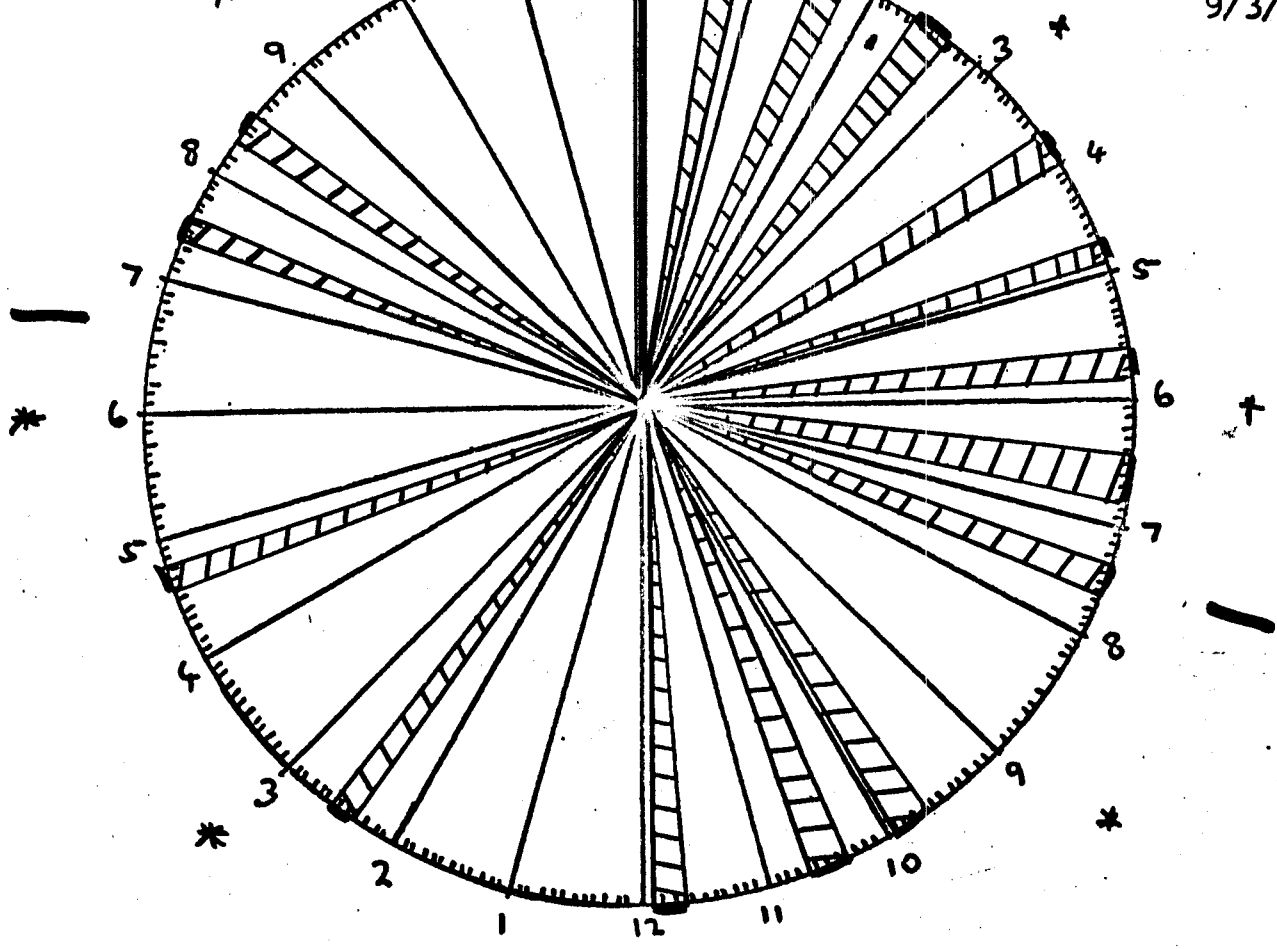
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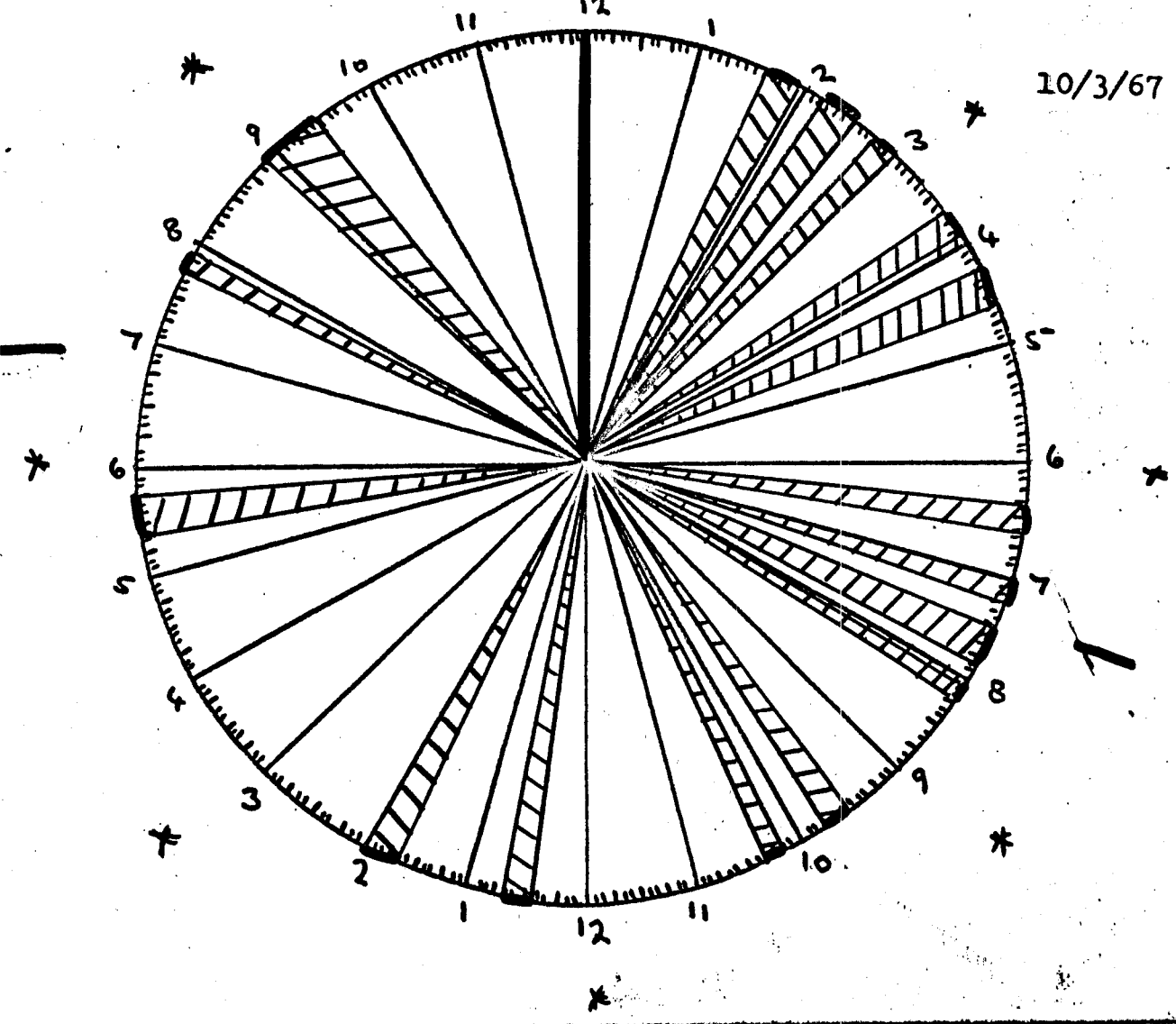


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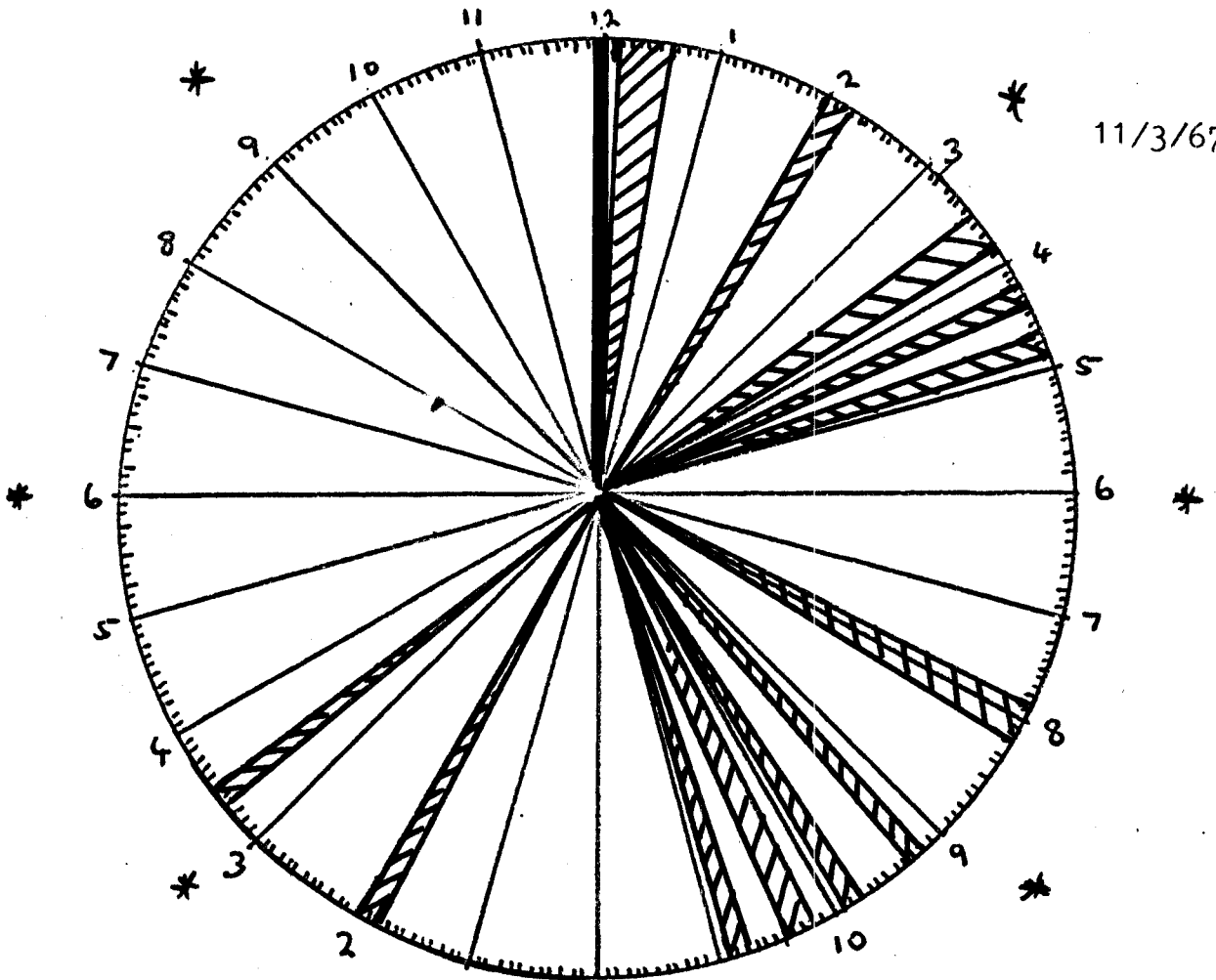
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February.

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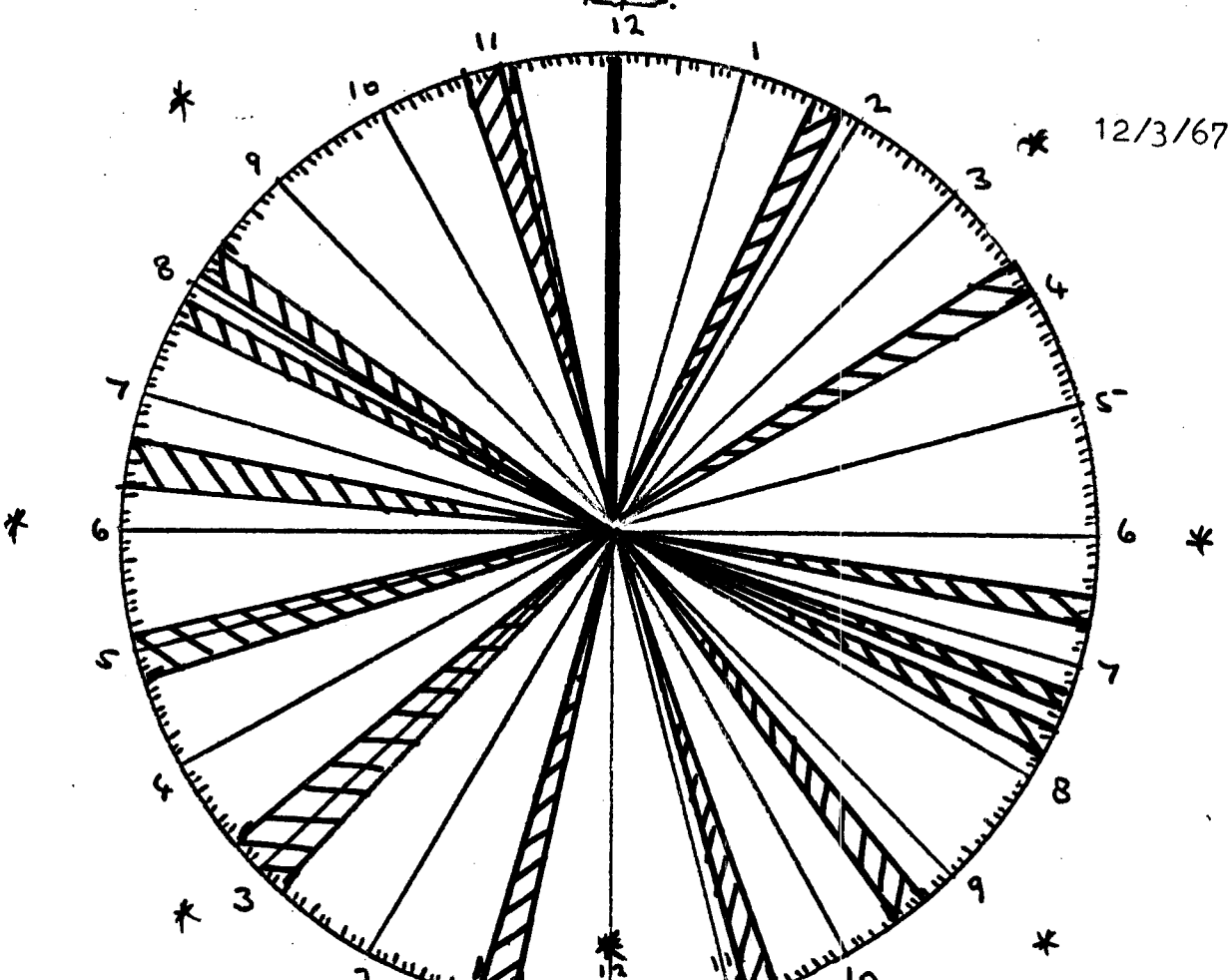
MIDNIGHT 175a.

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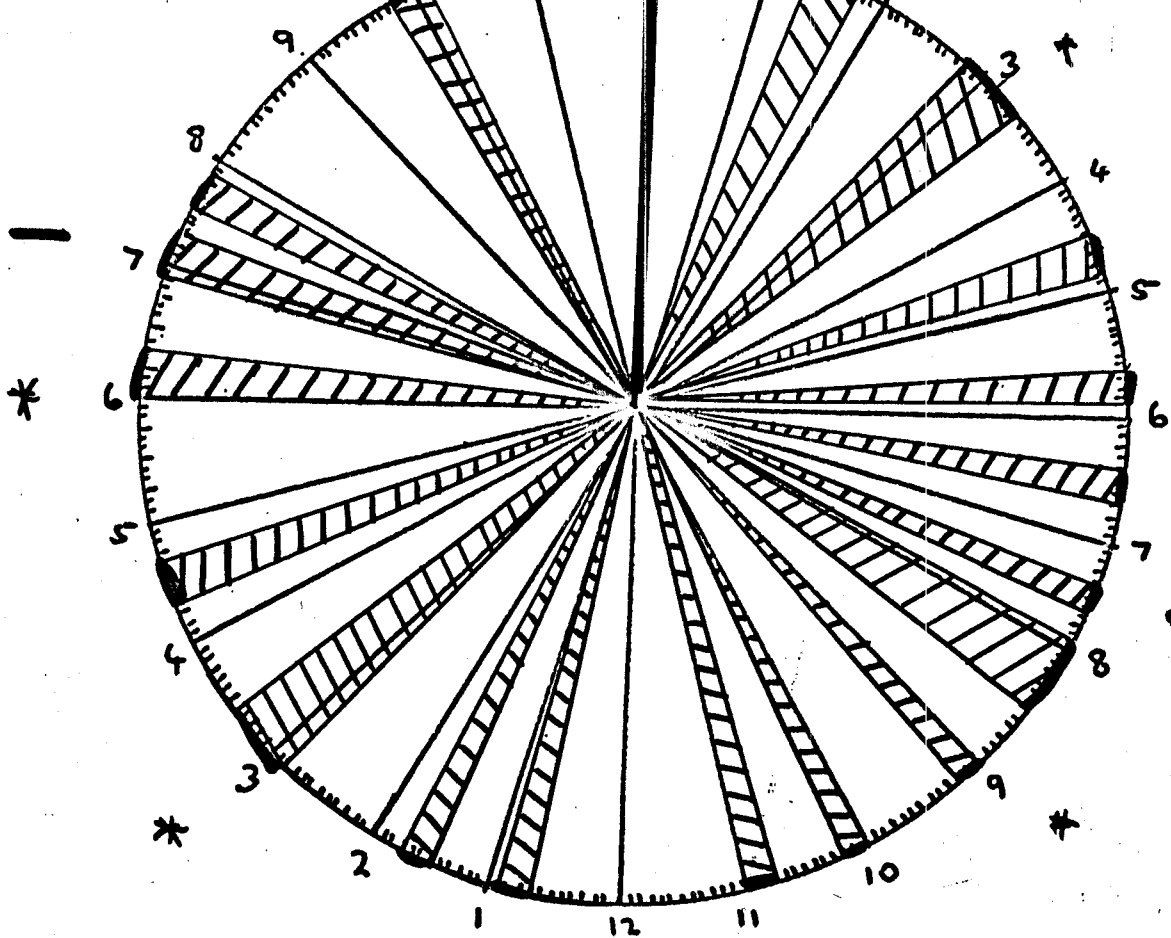


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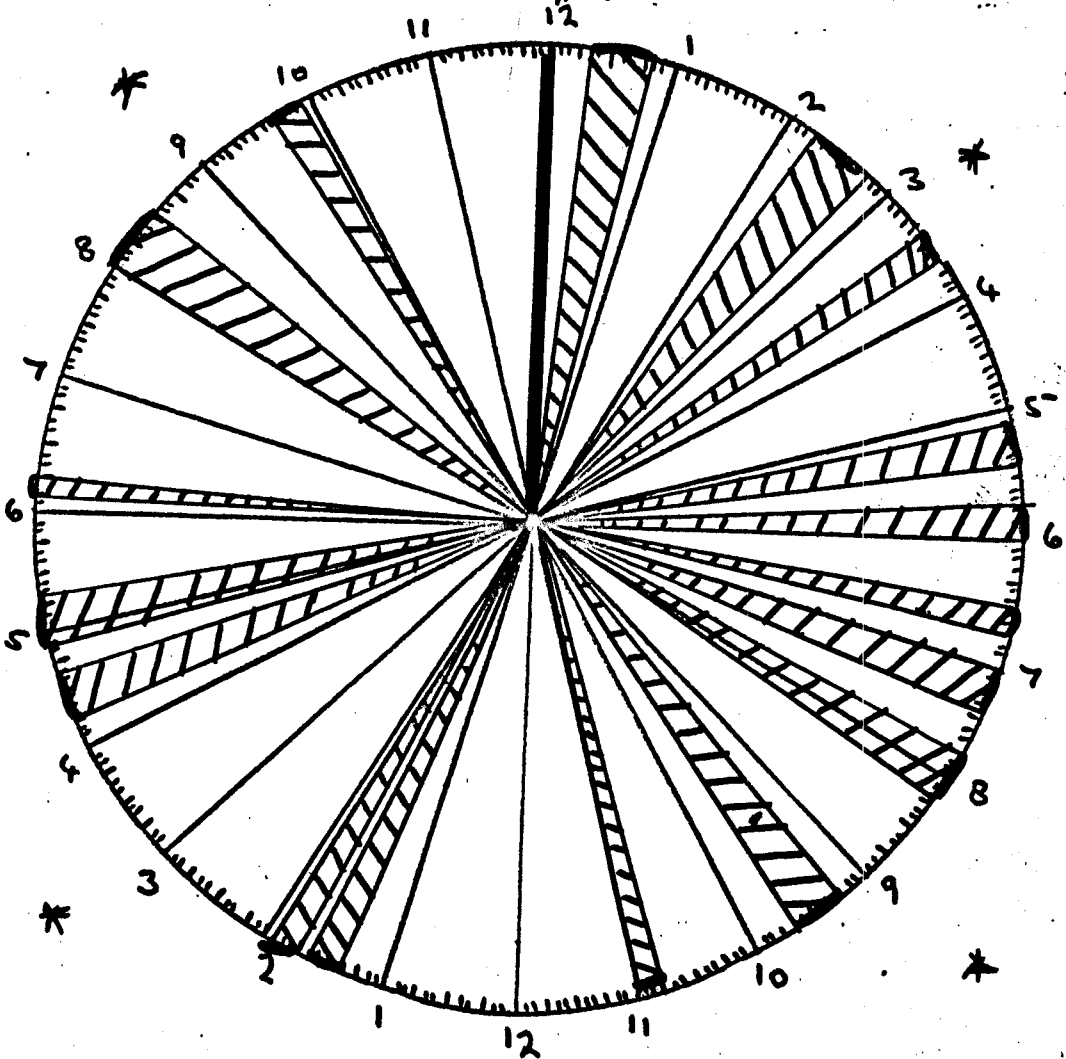


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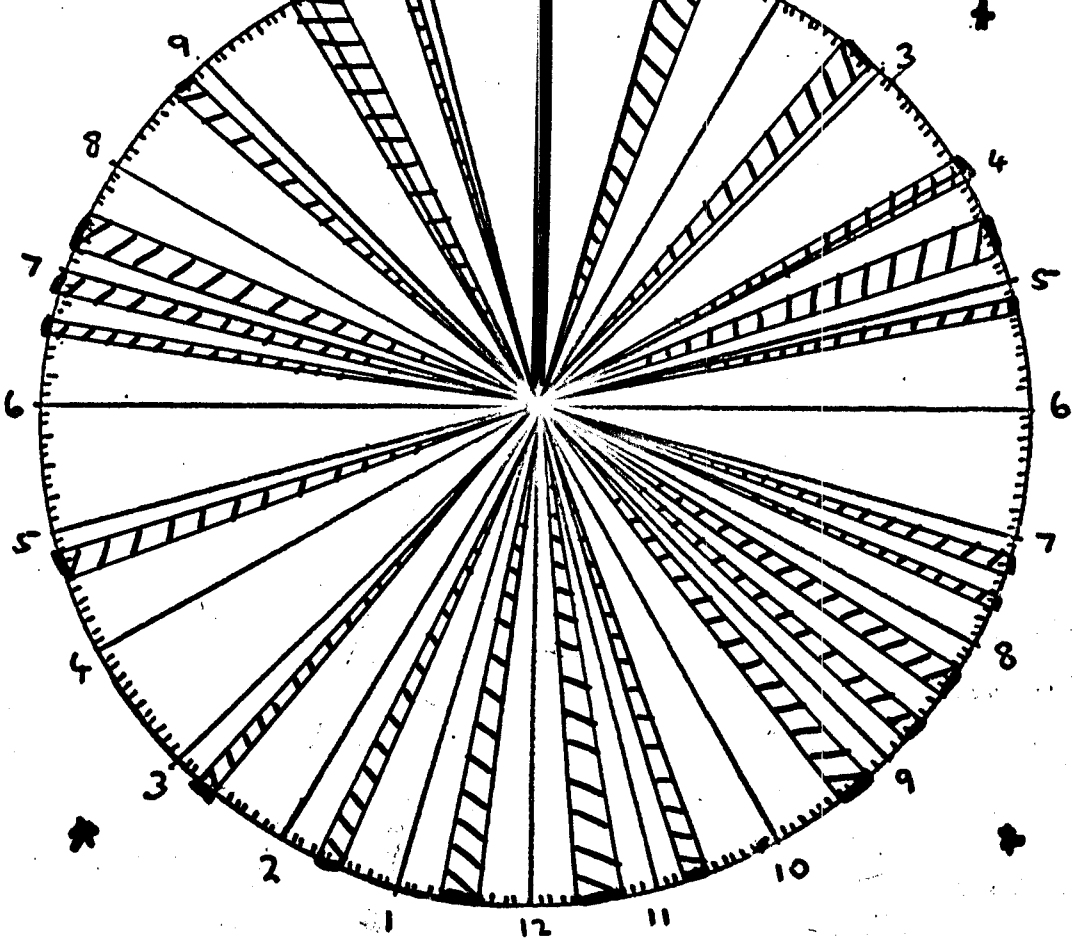


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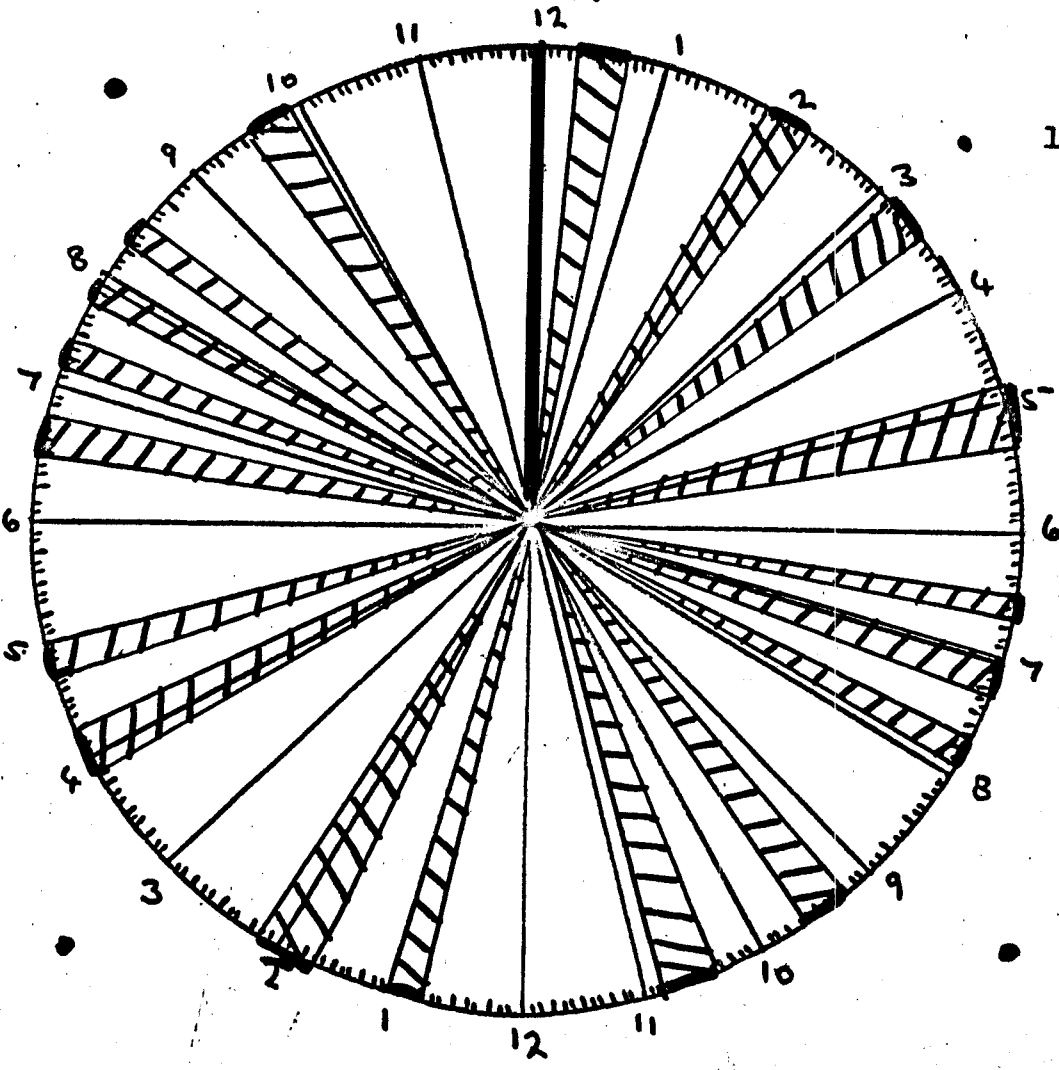


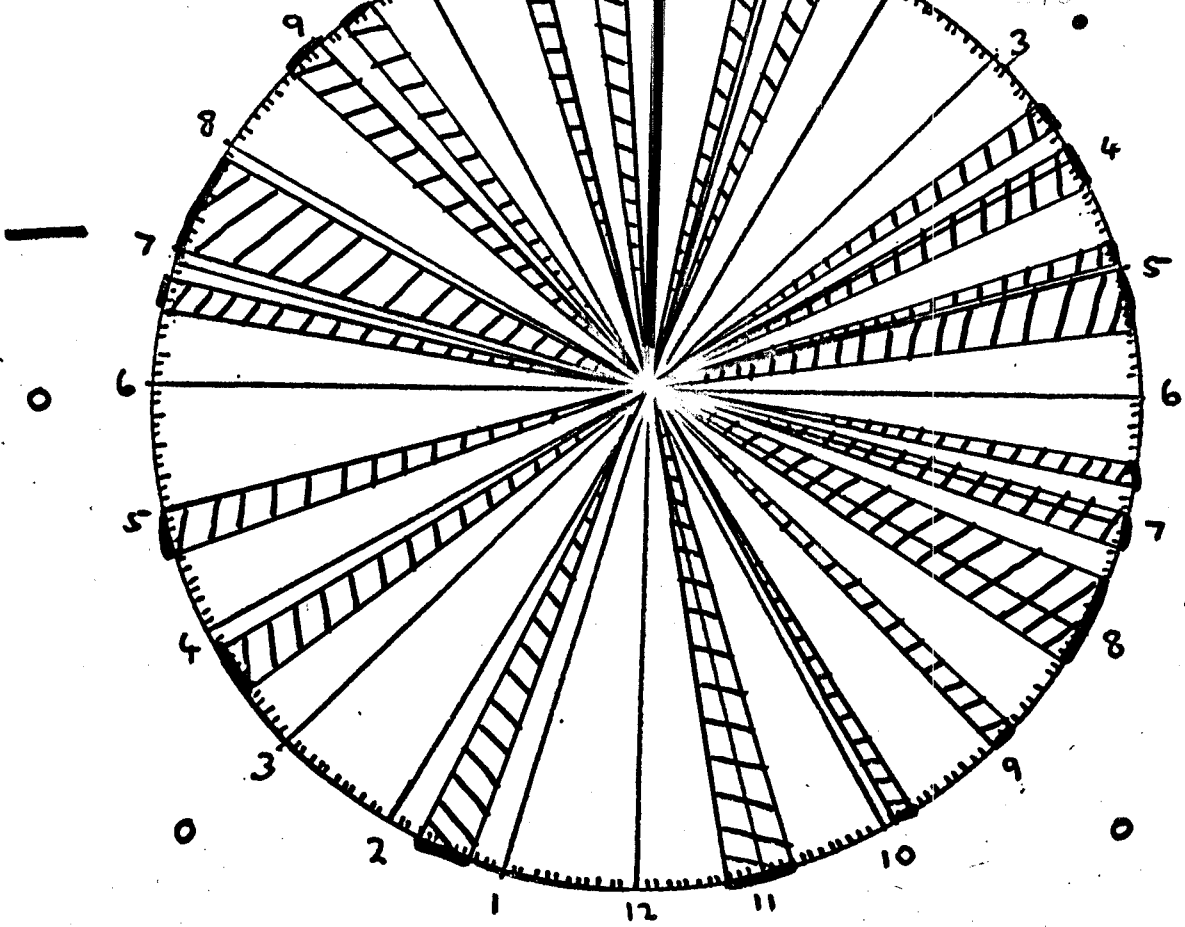
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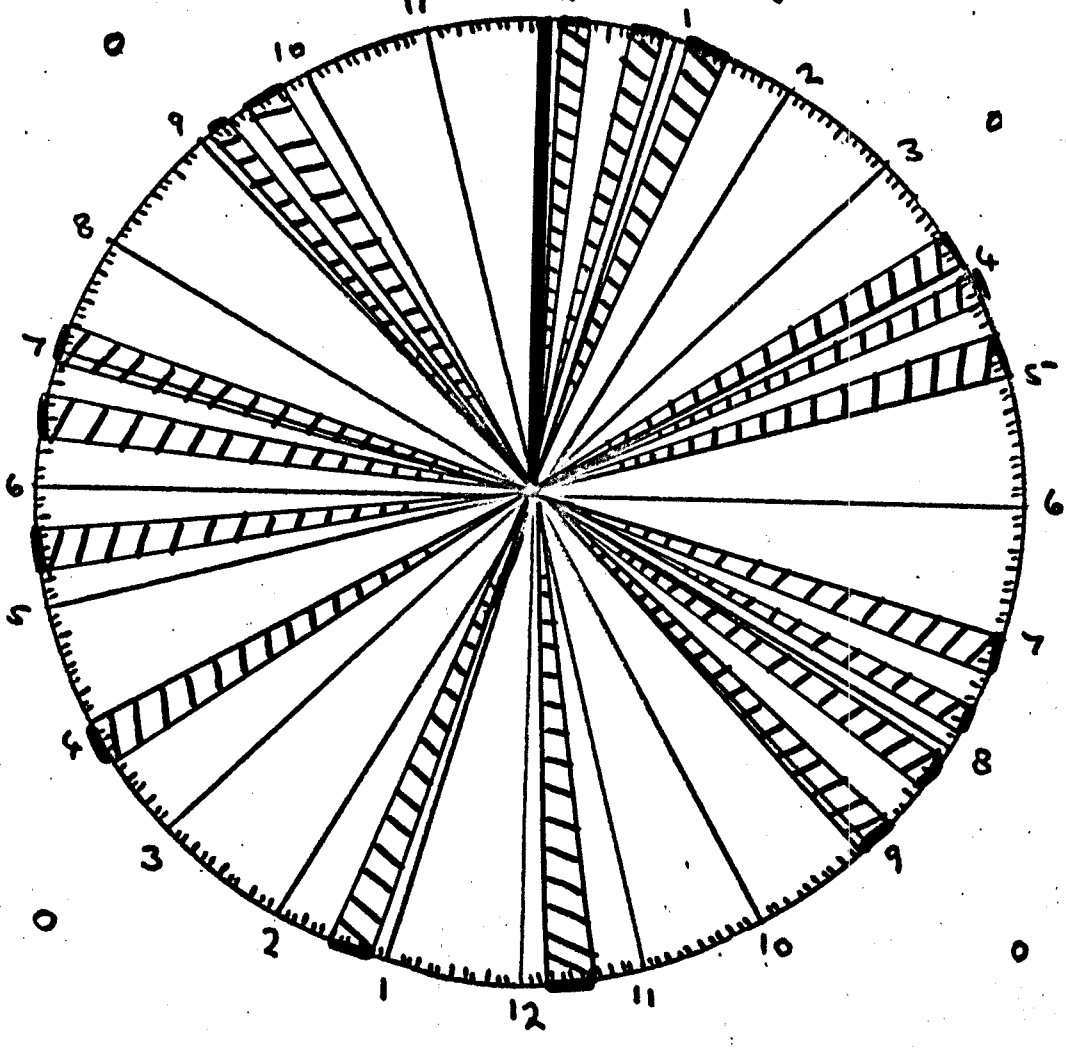
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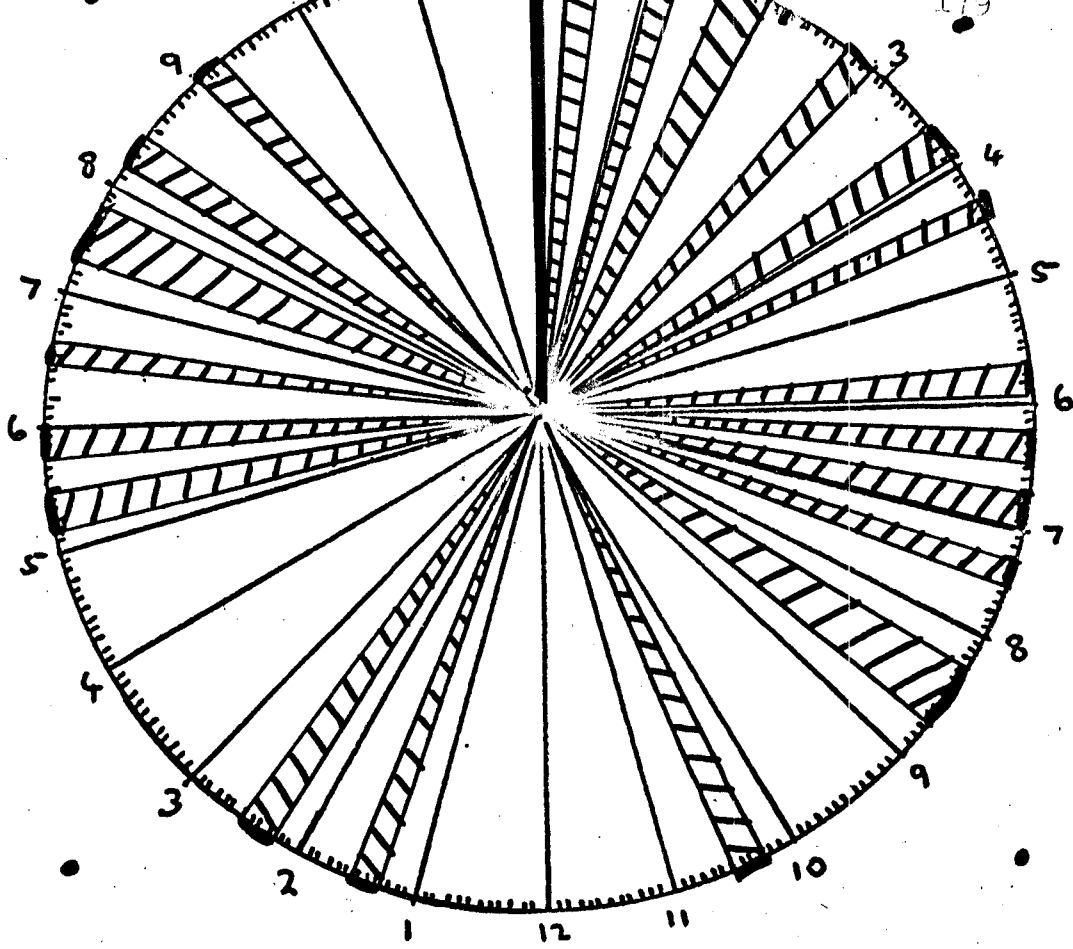
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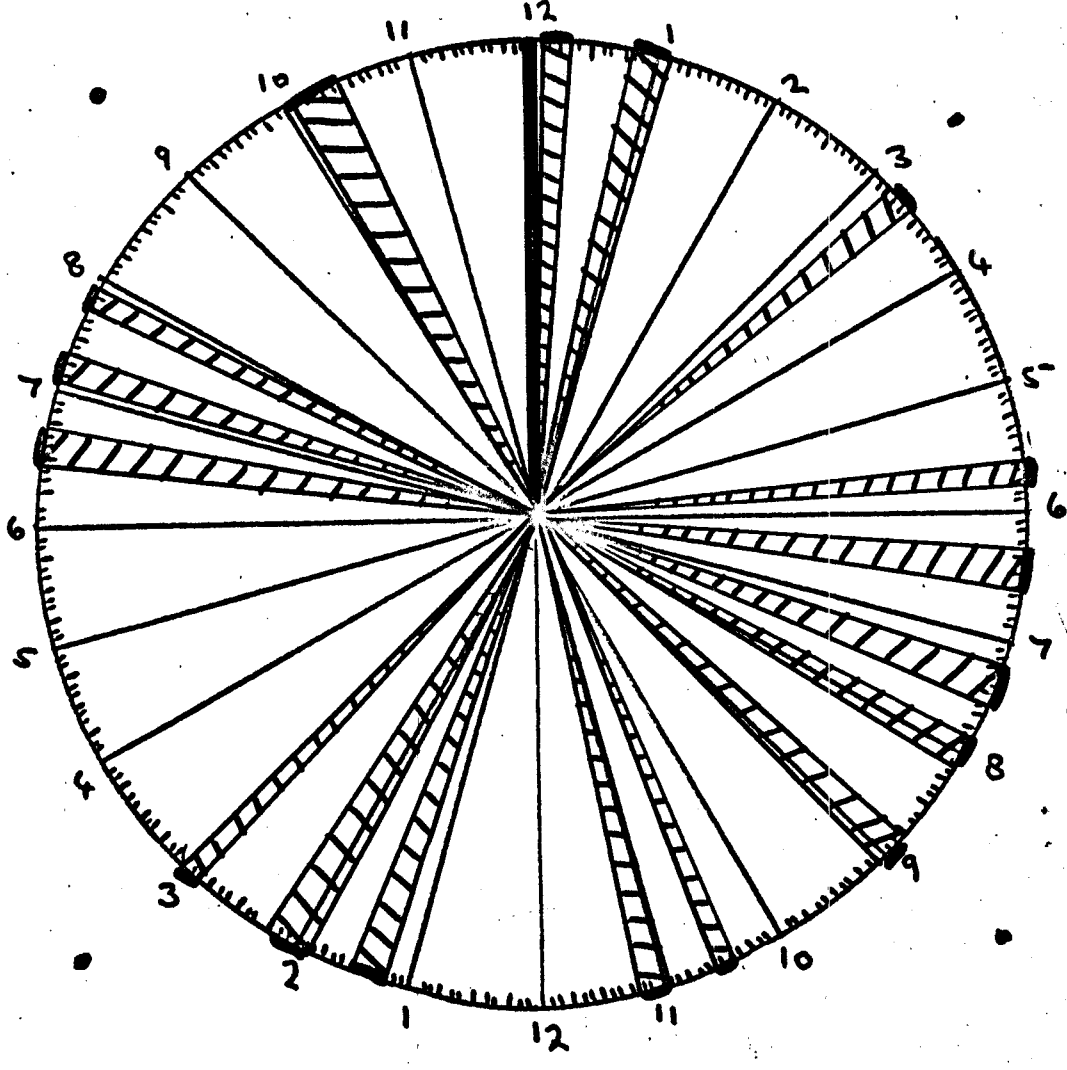


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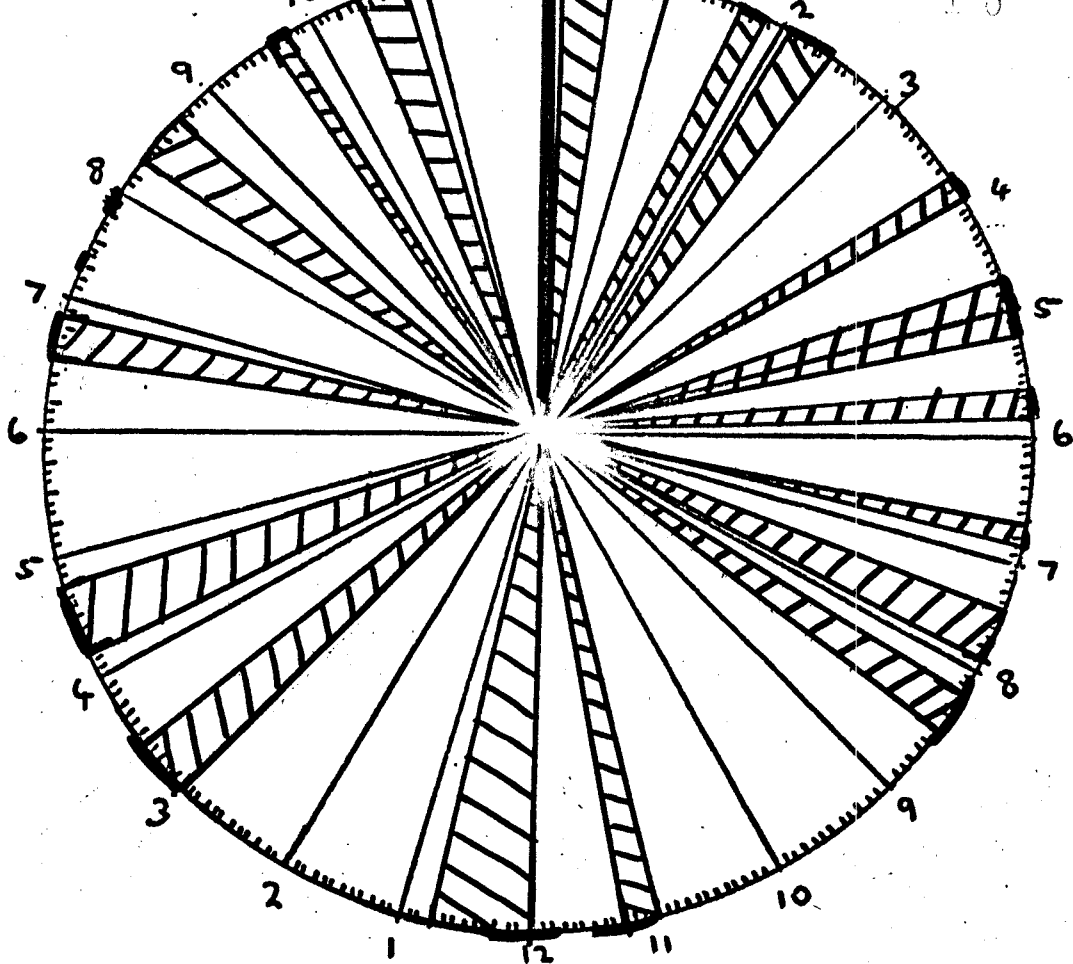


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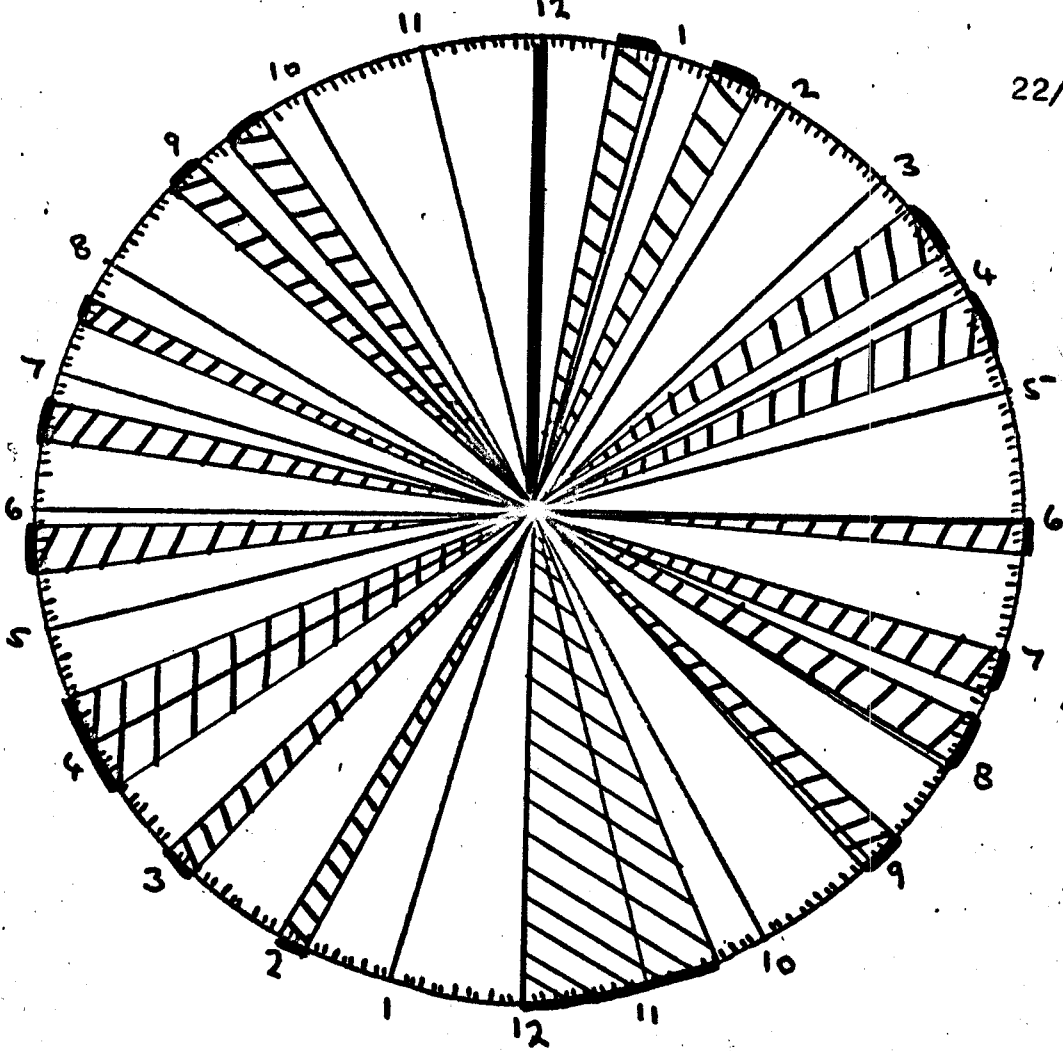
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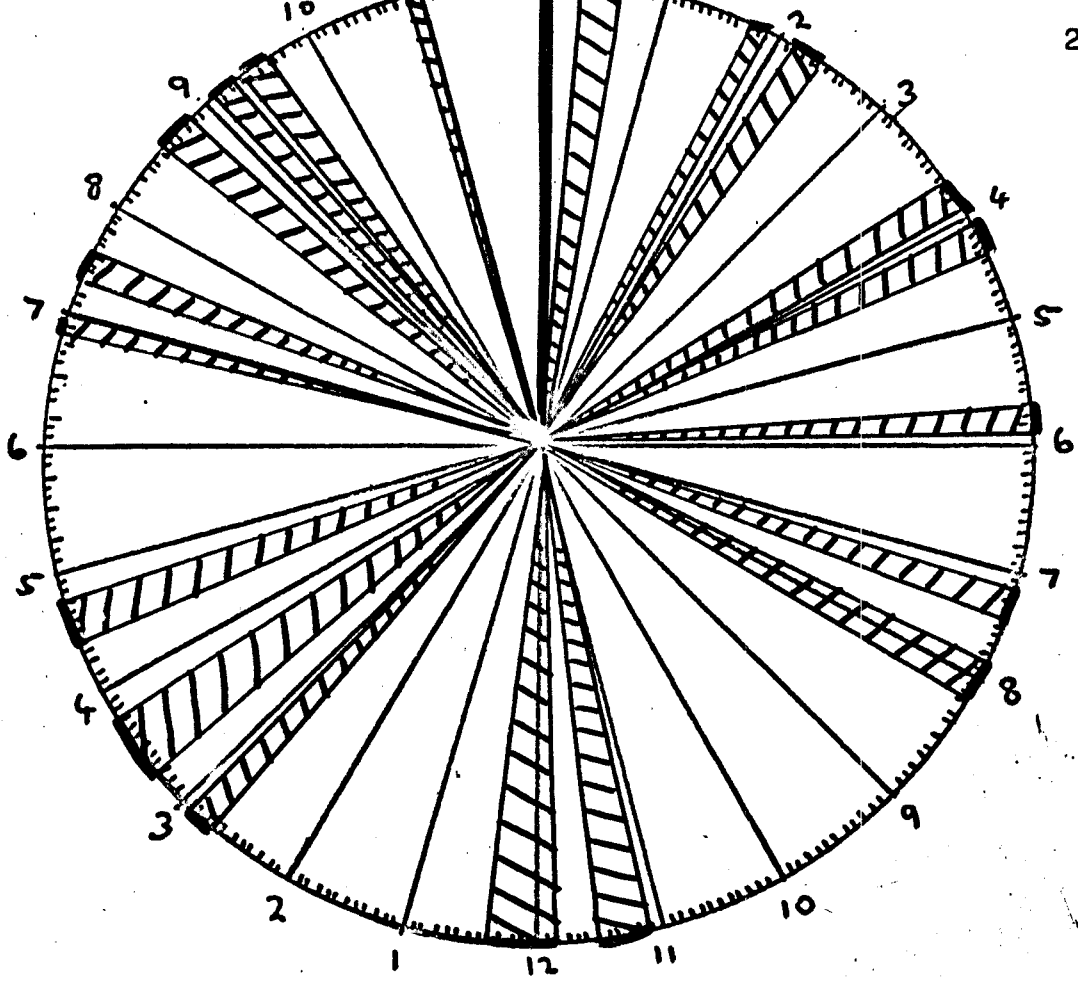


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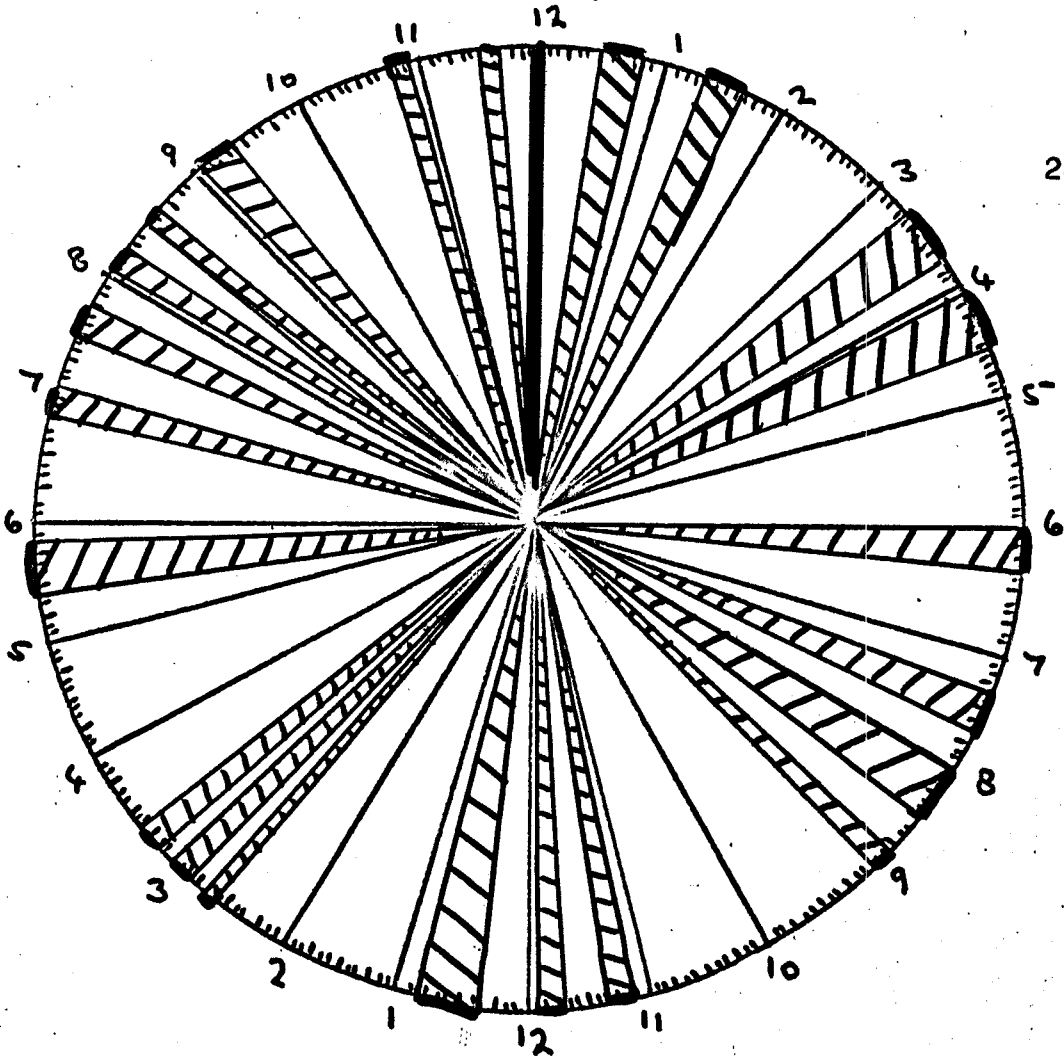
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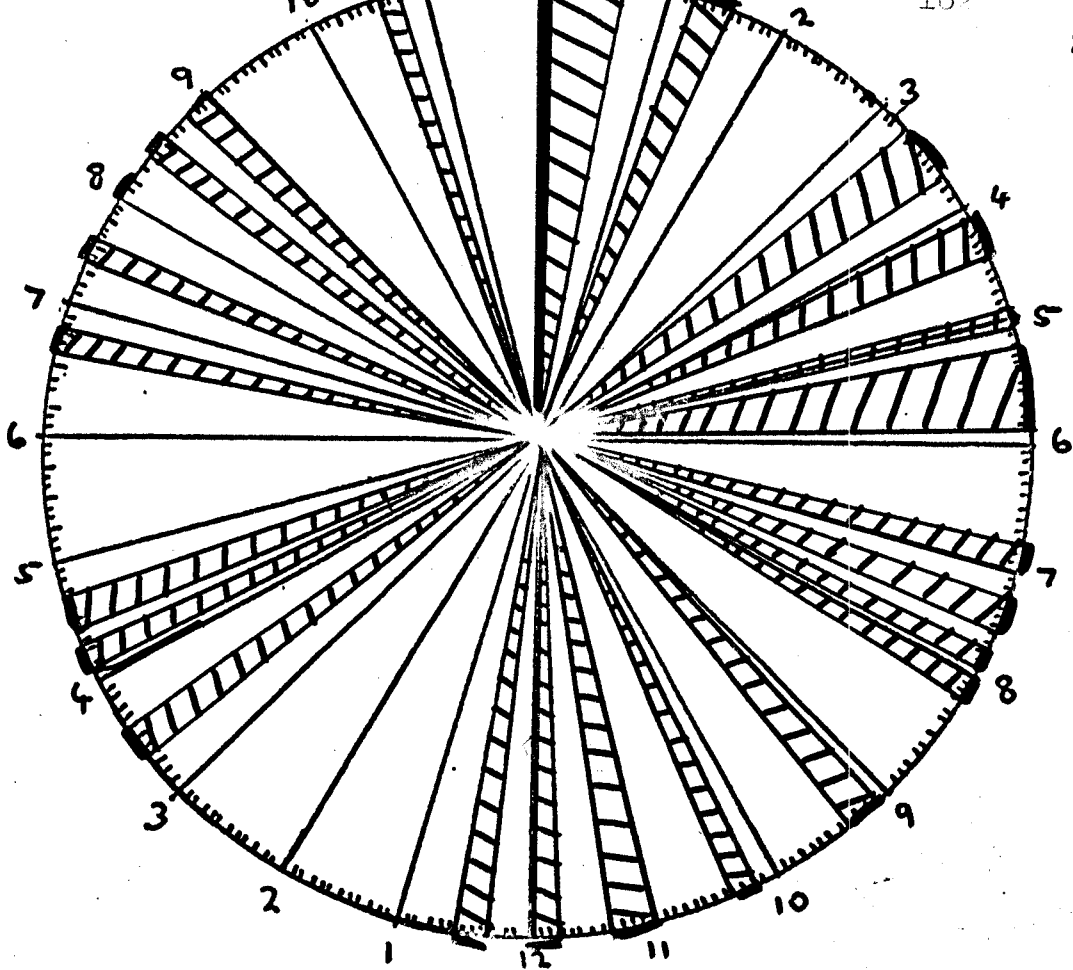


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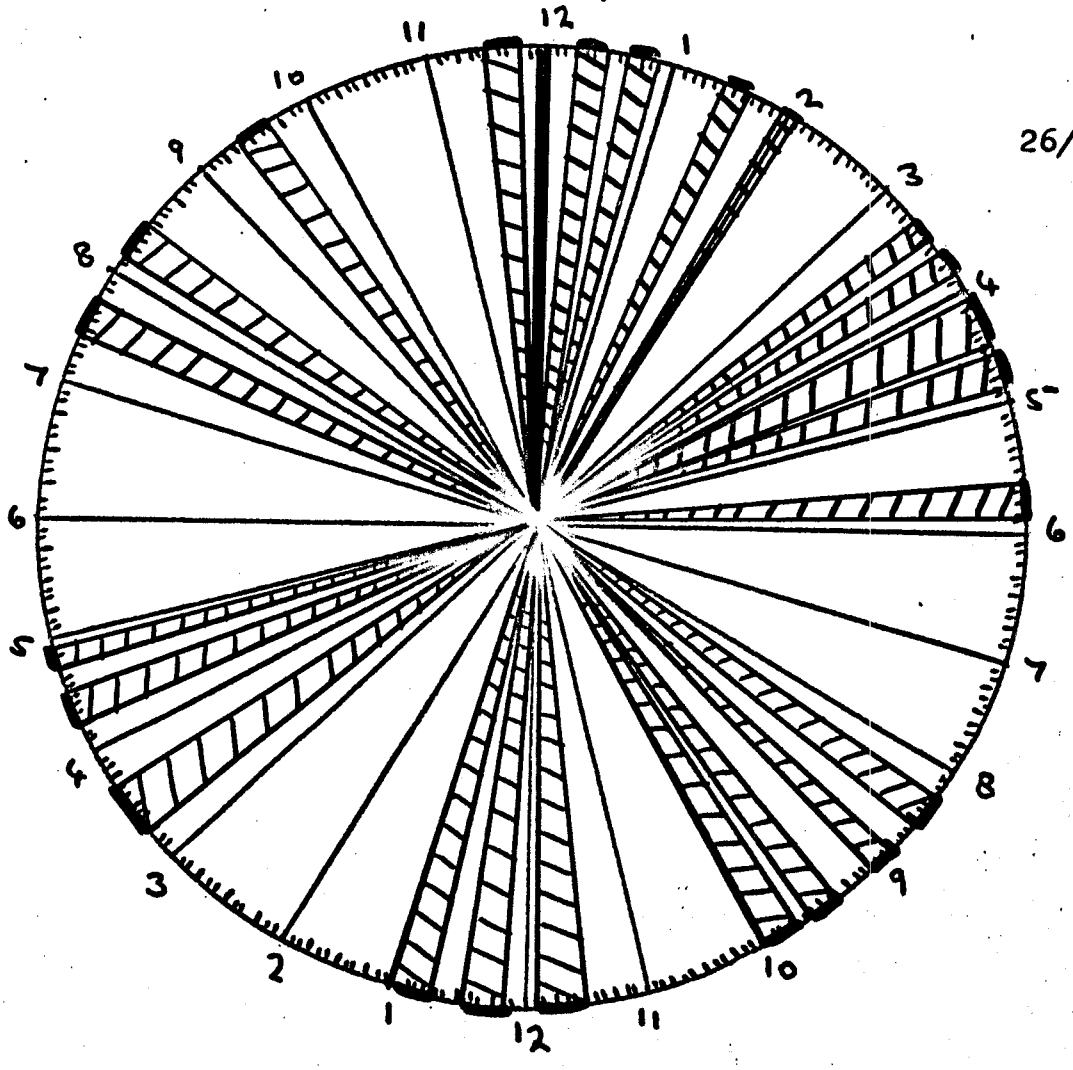
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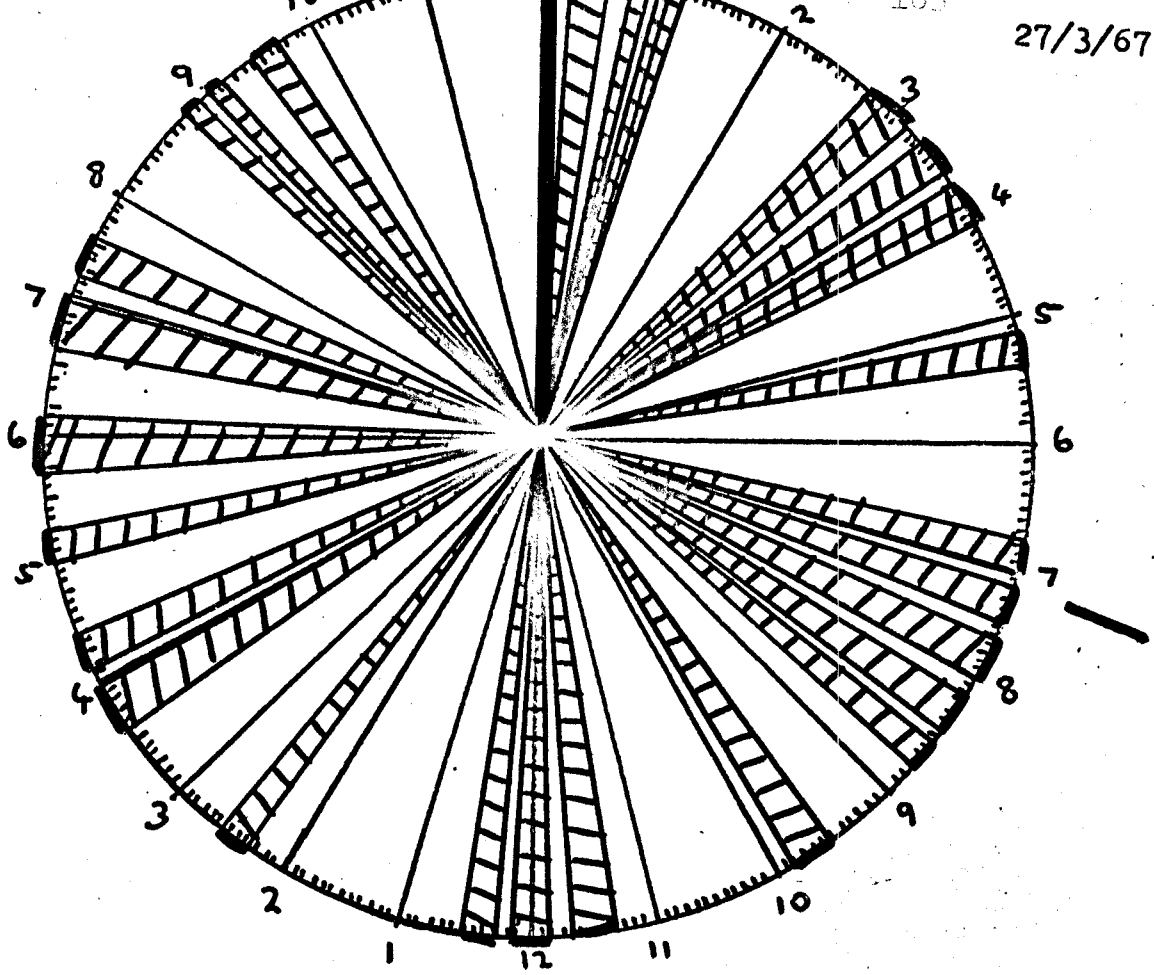


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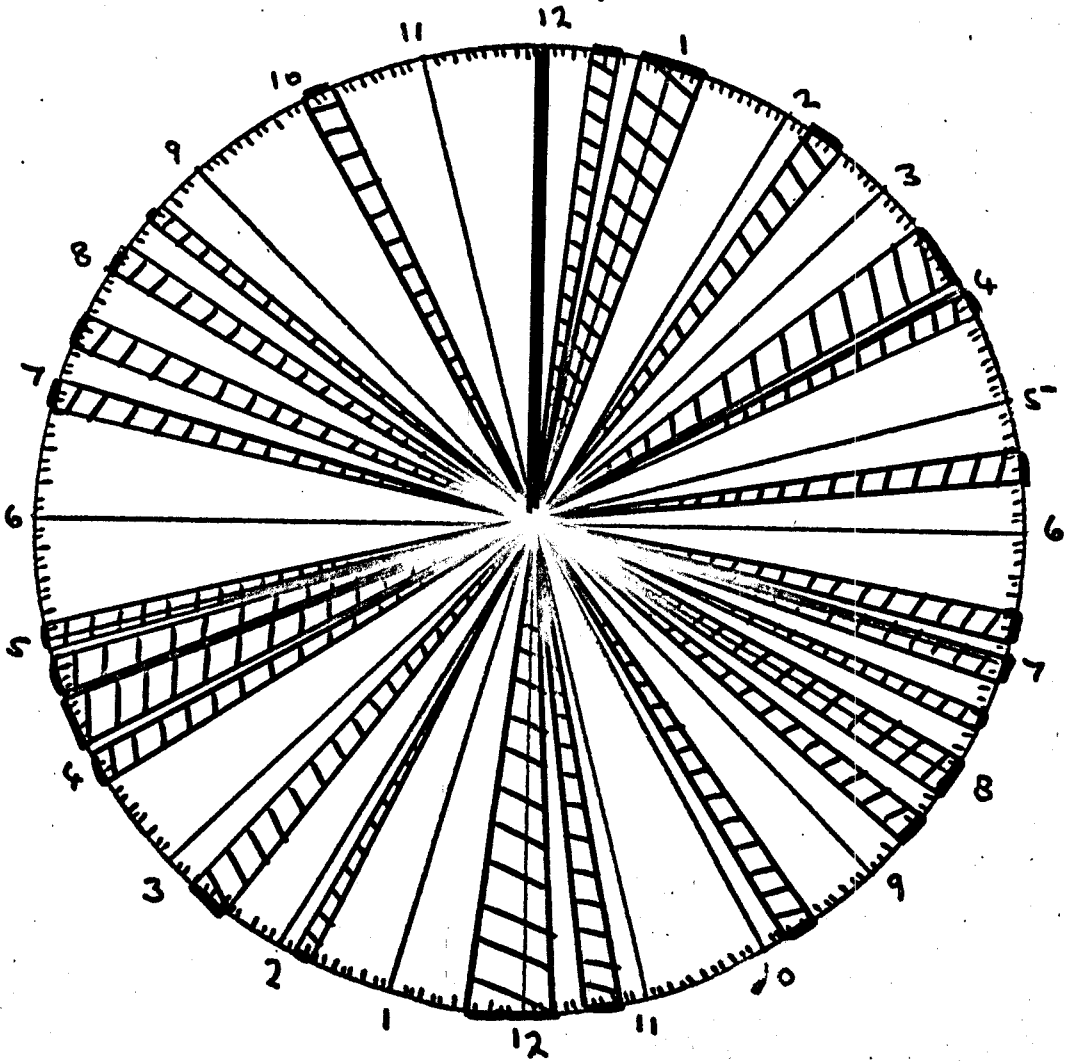
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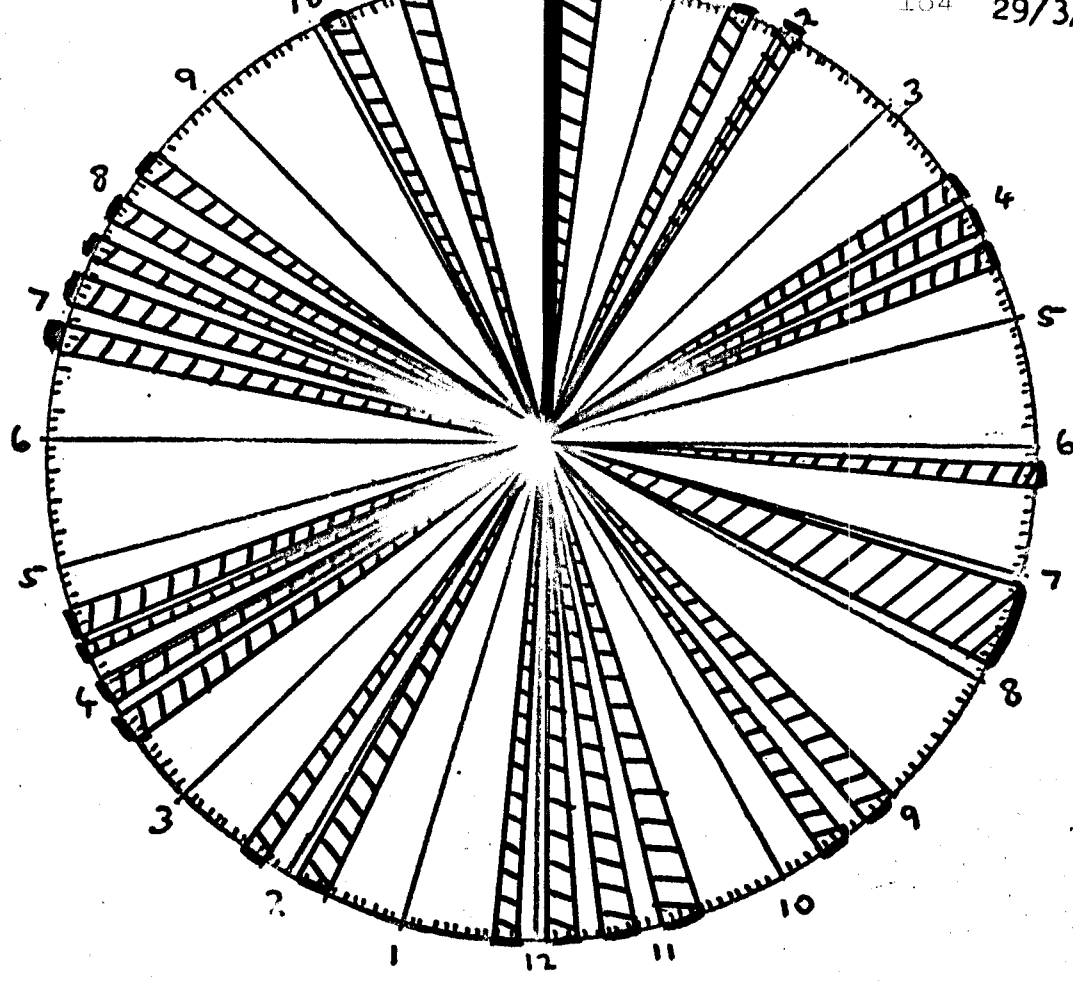
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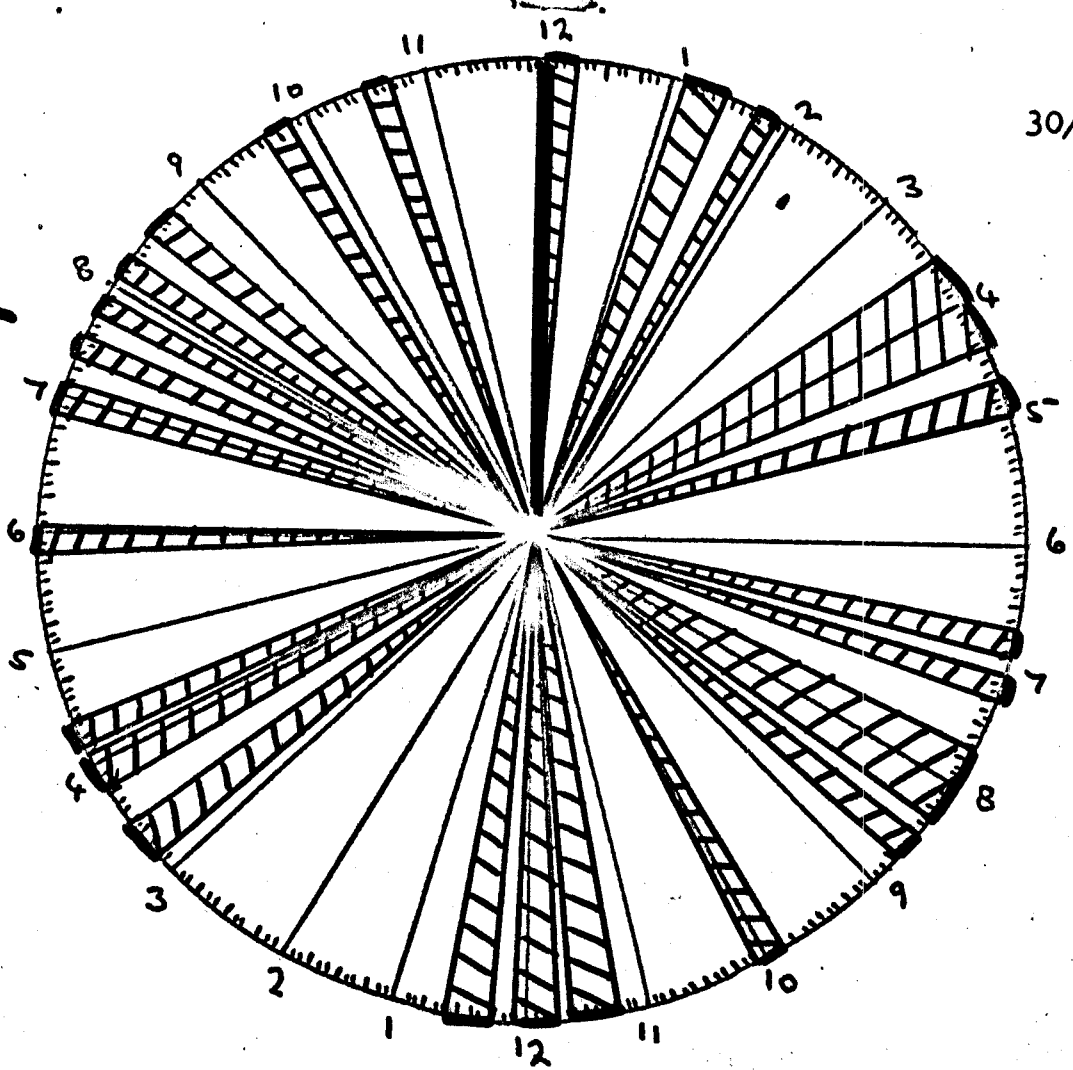
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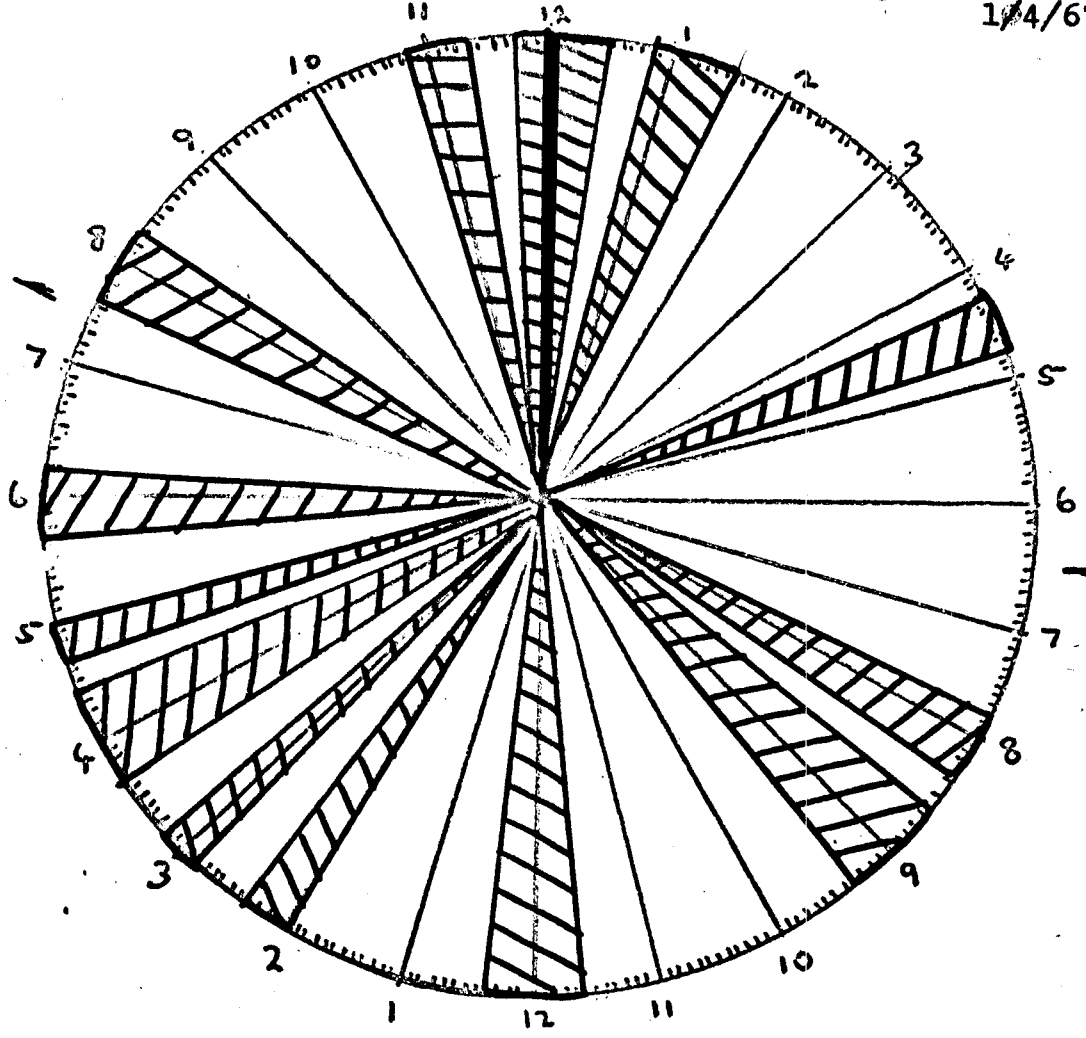
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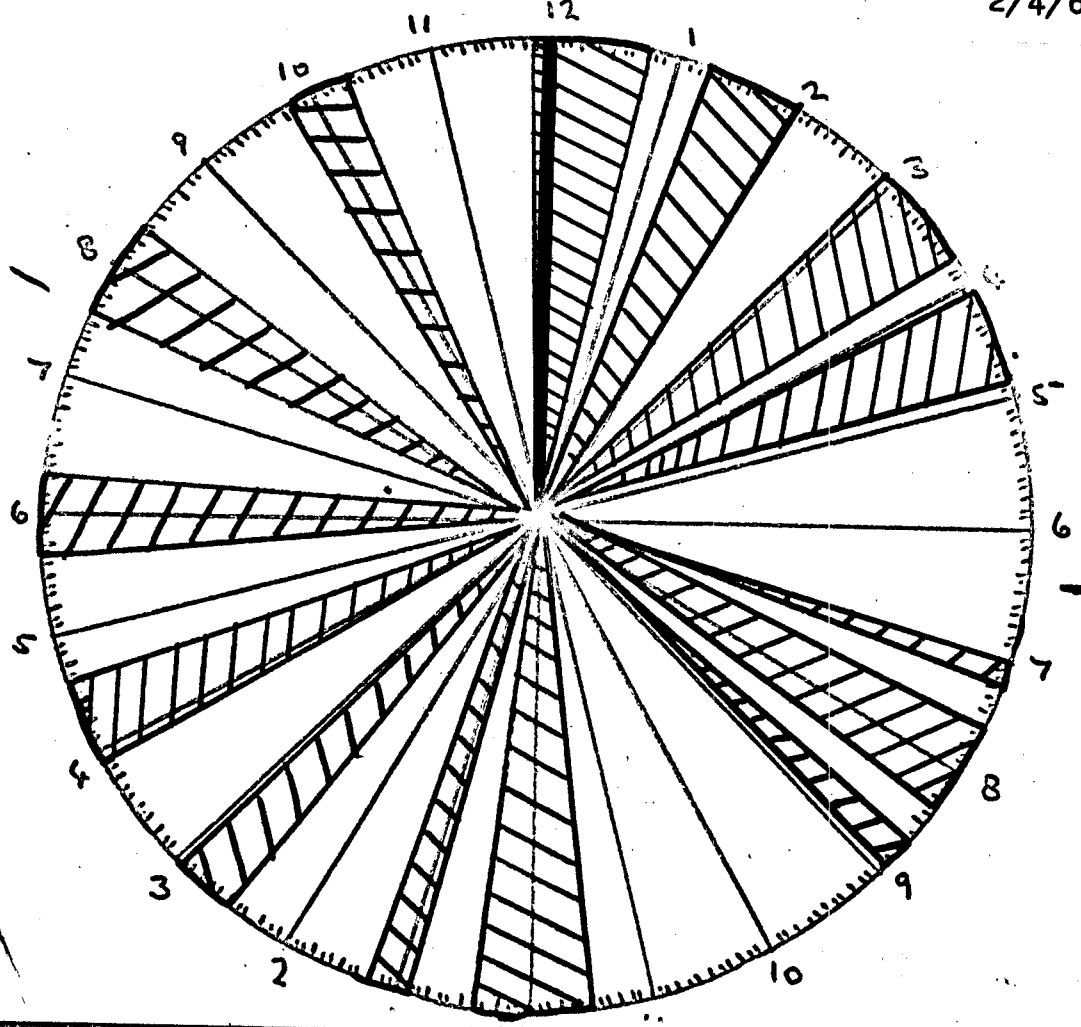


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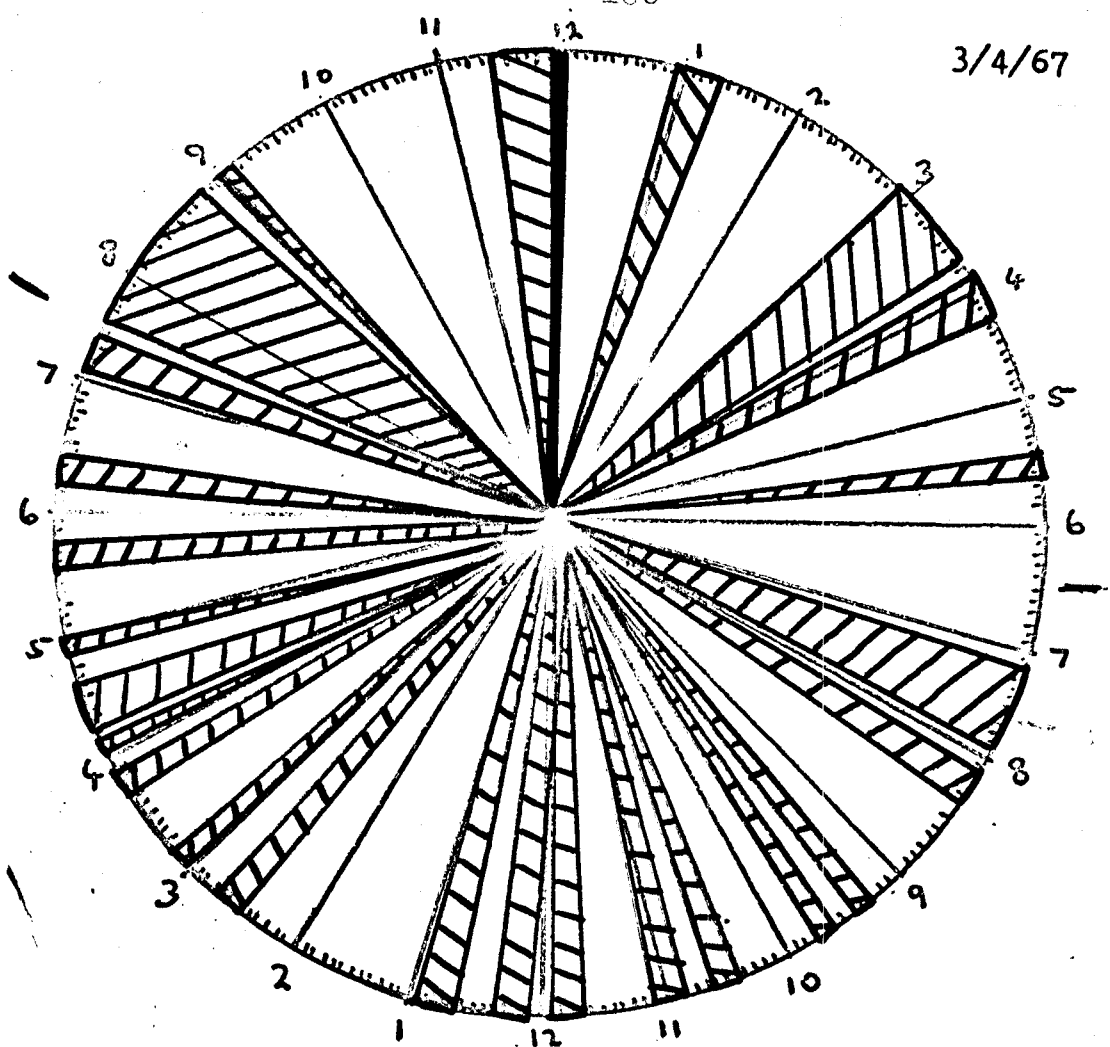


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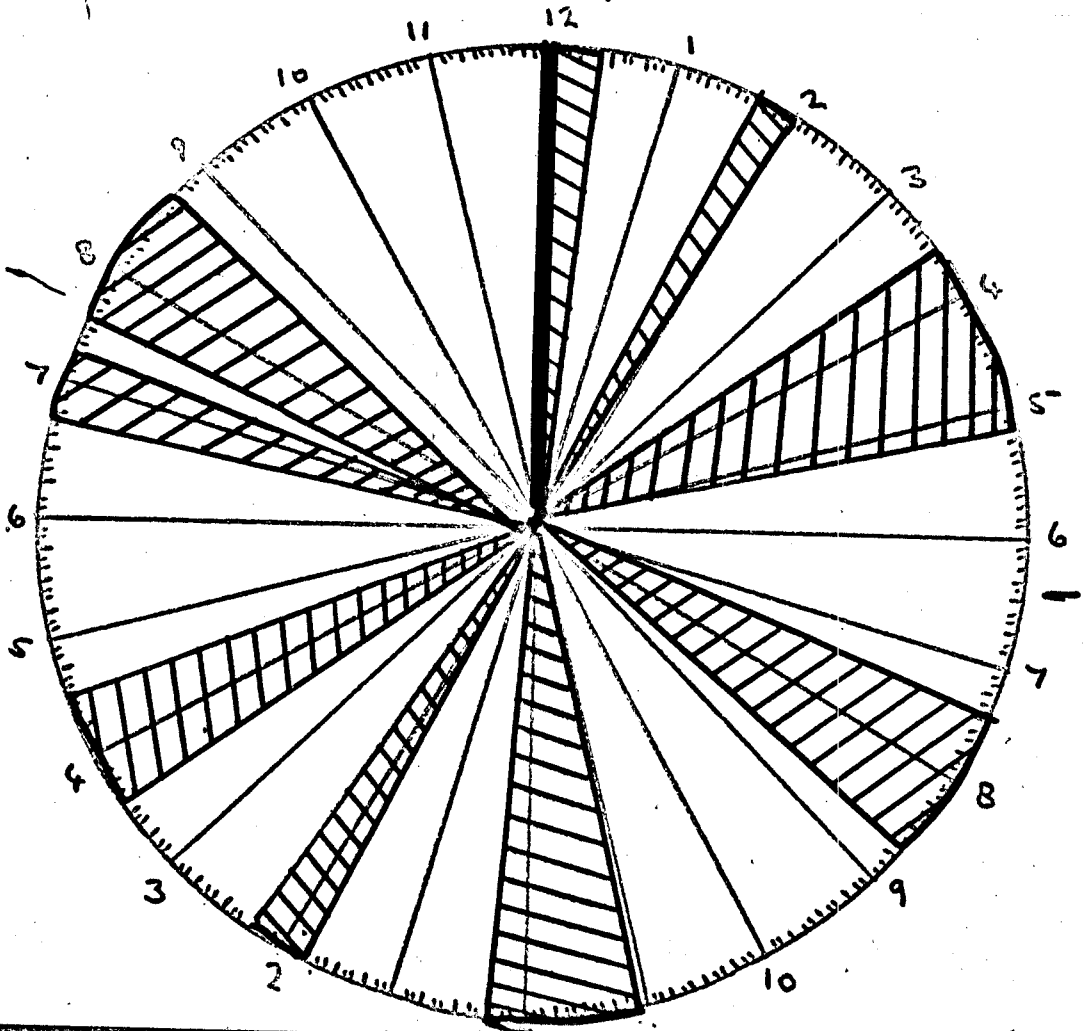


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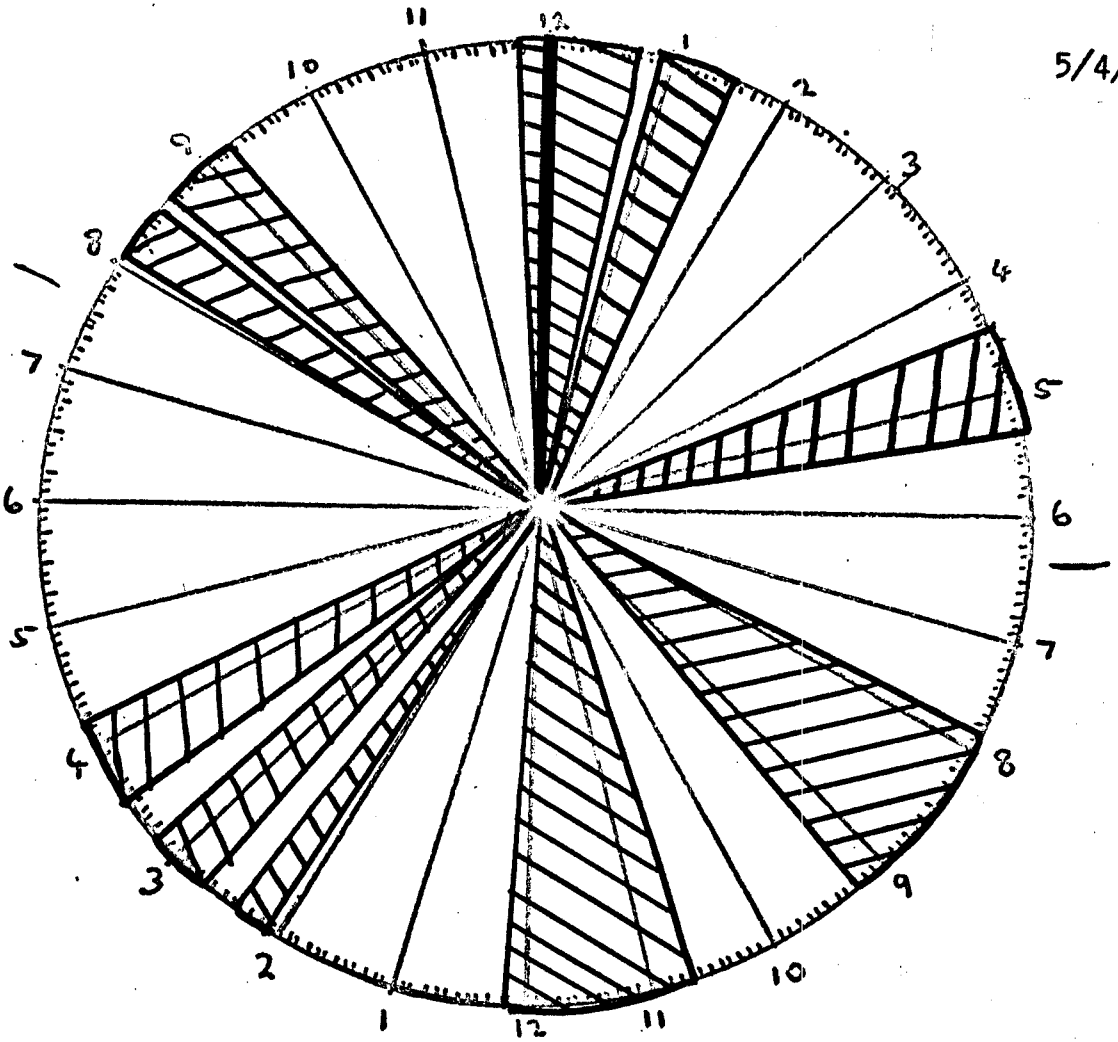


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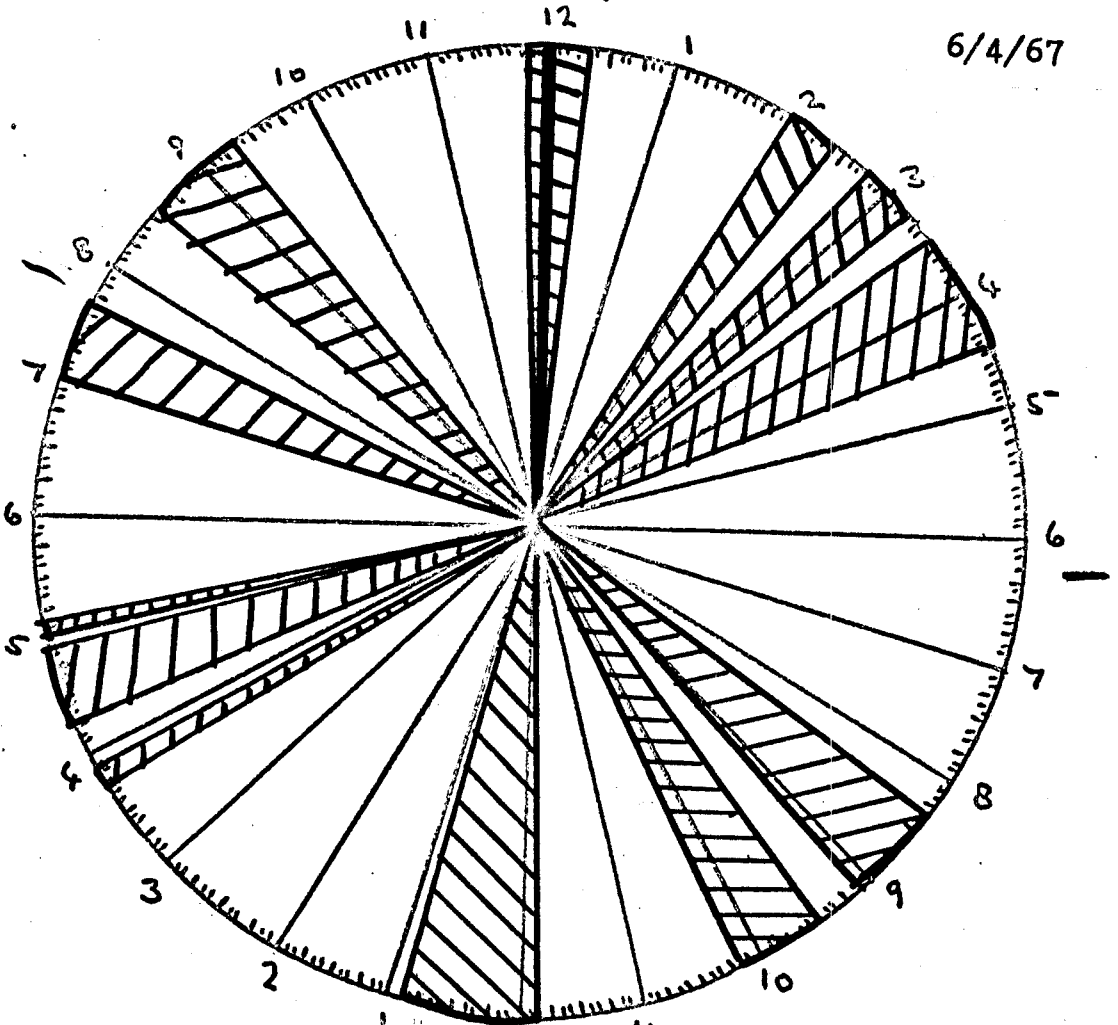


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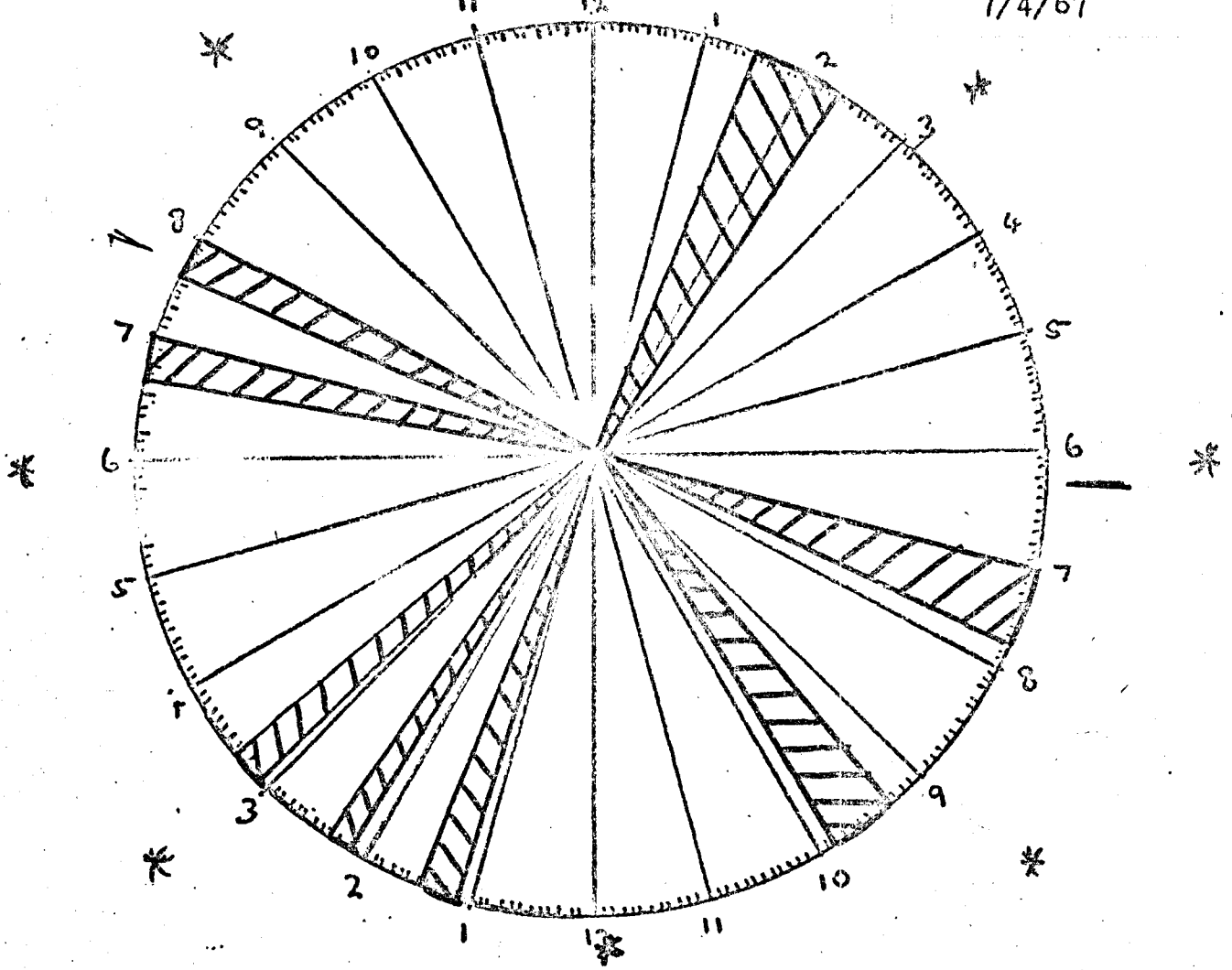


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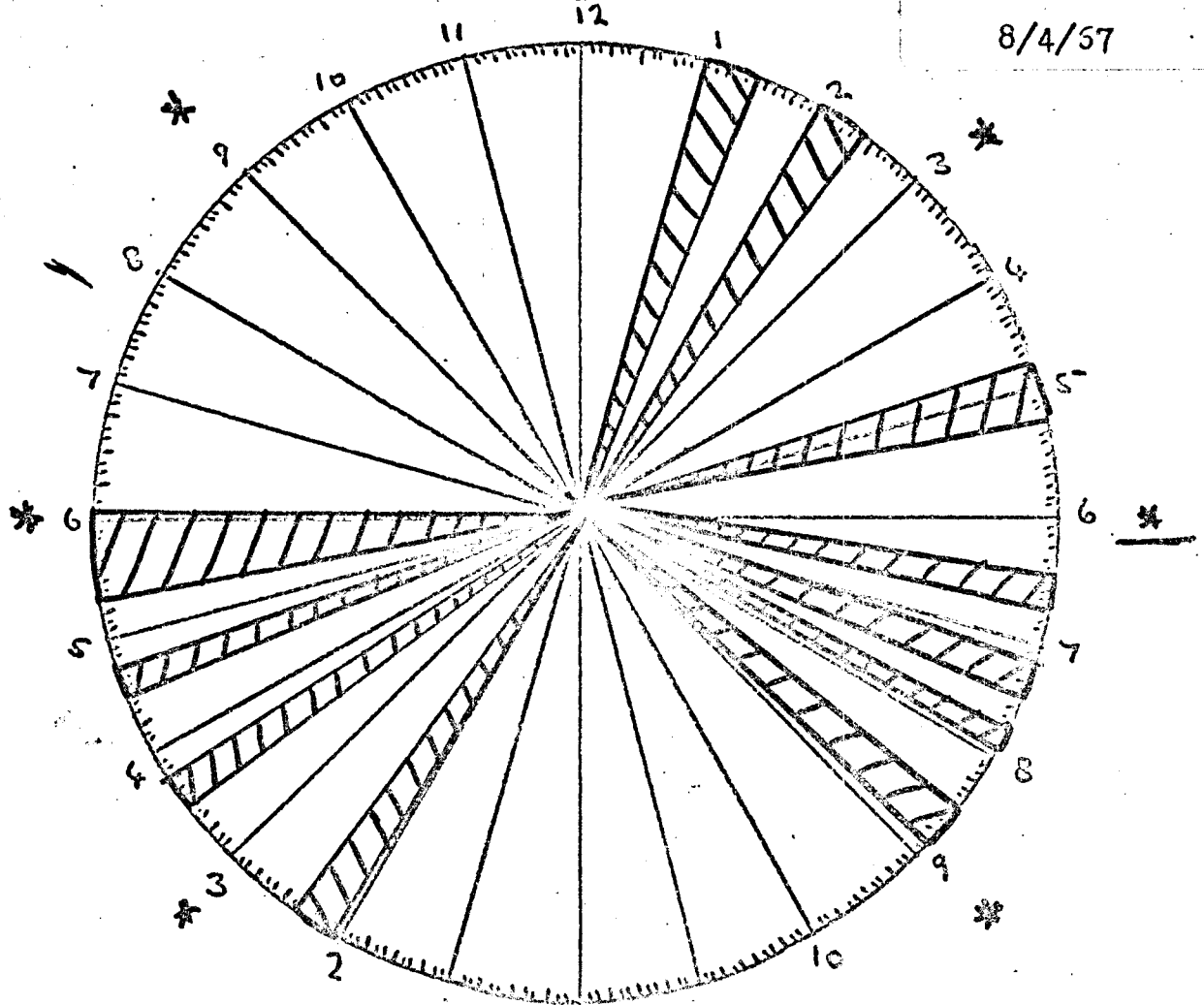


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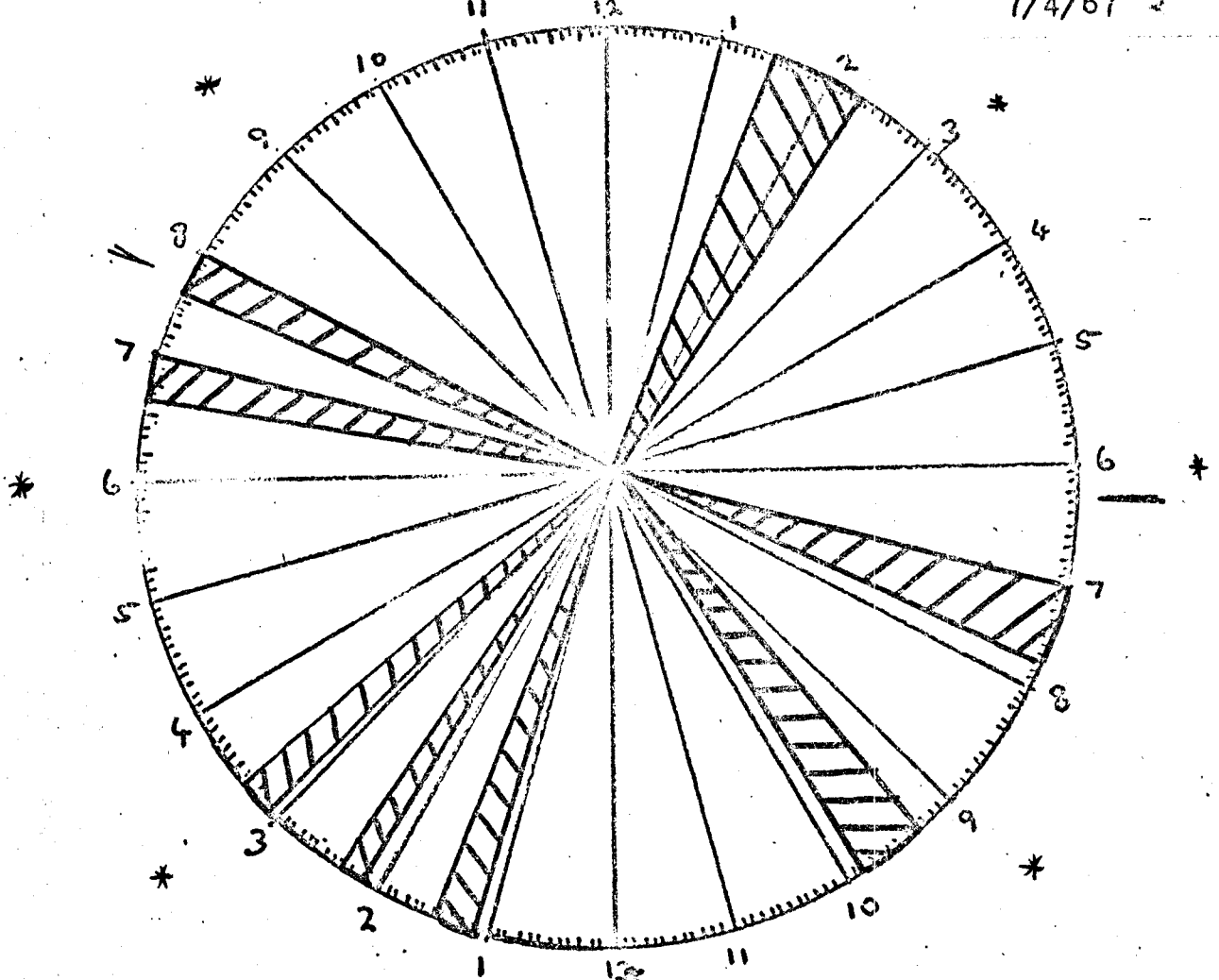


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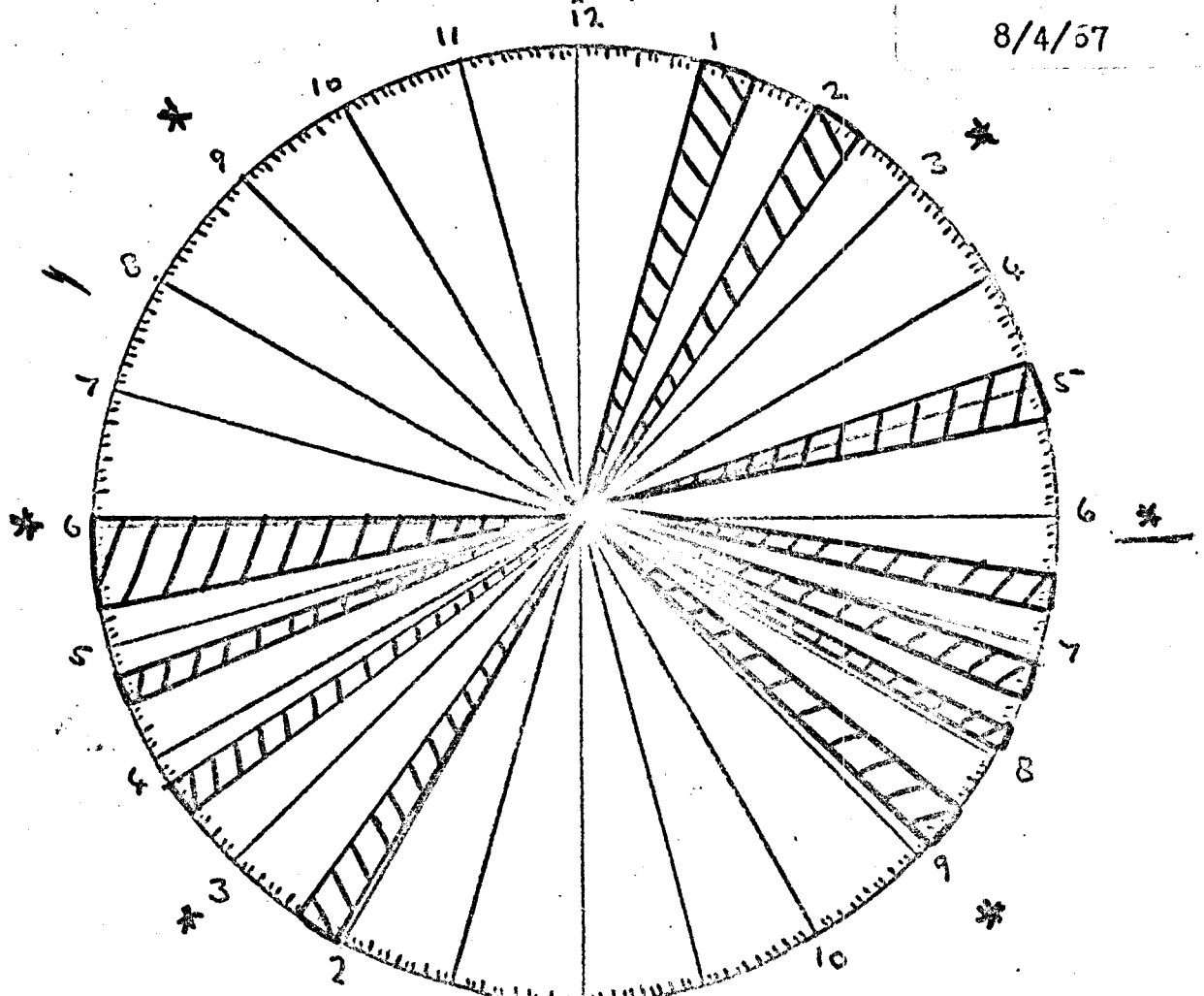


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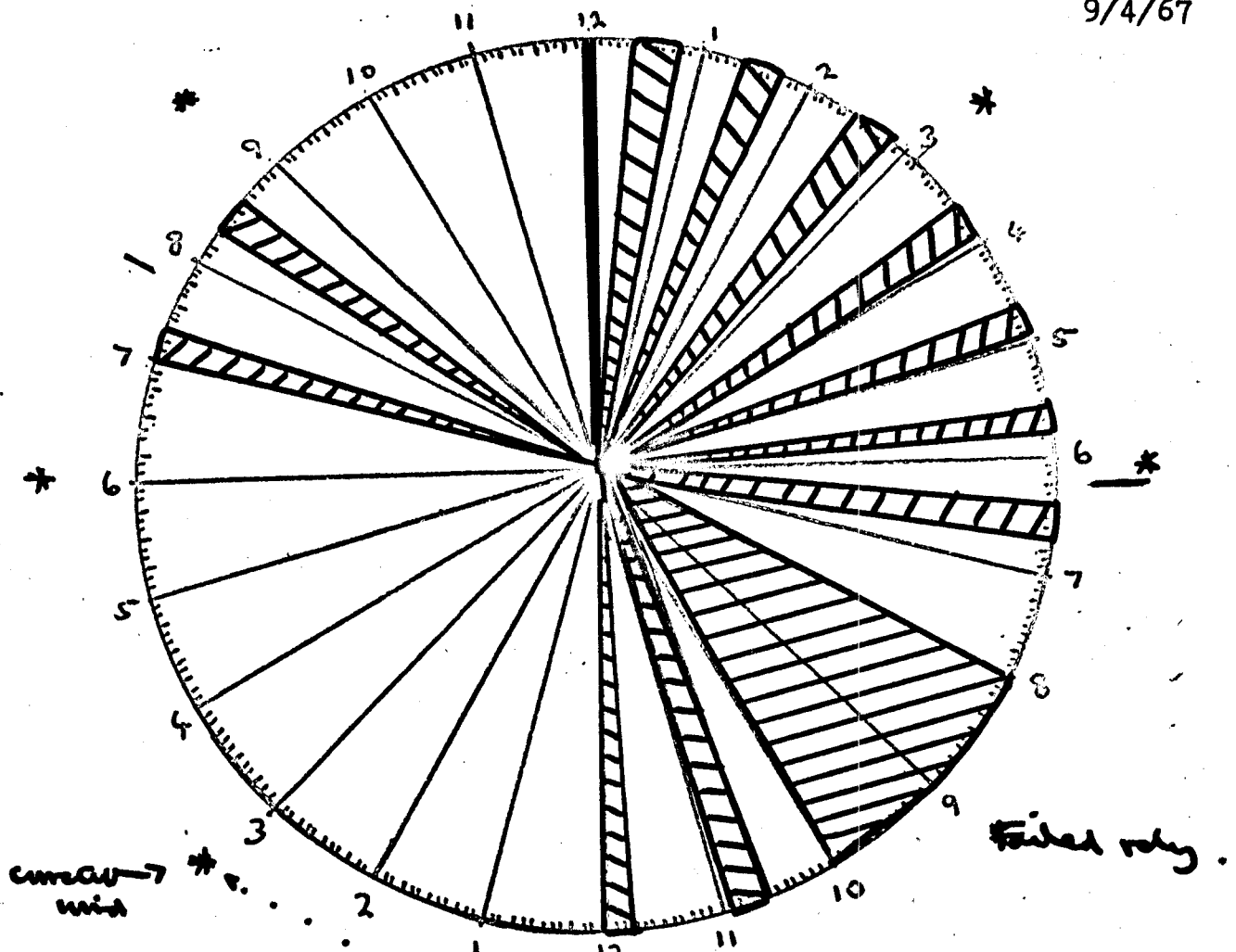


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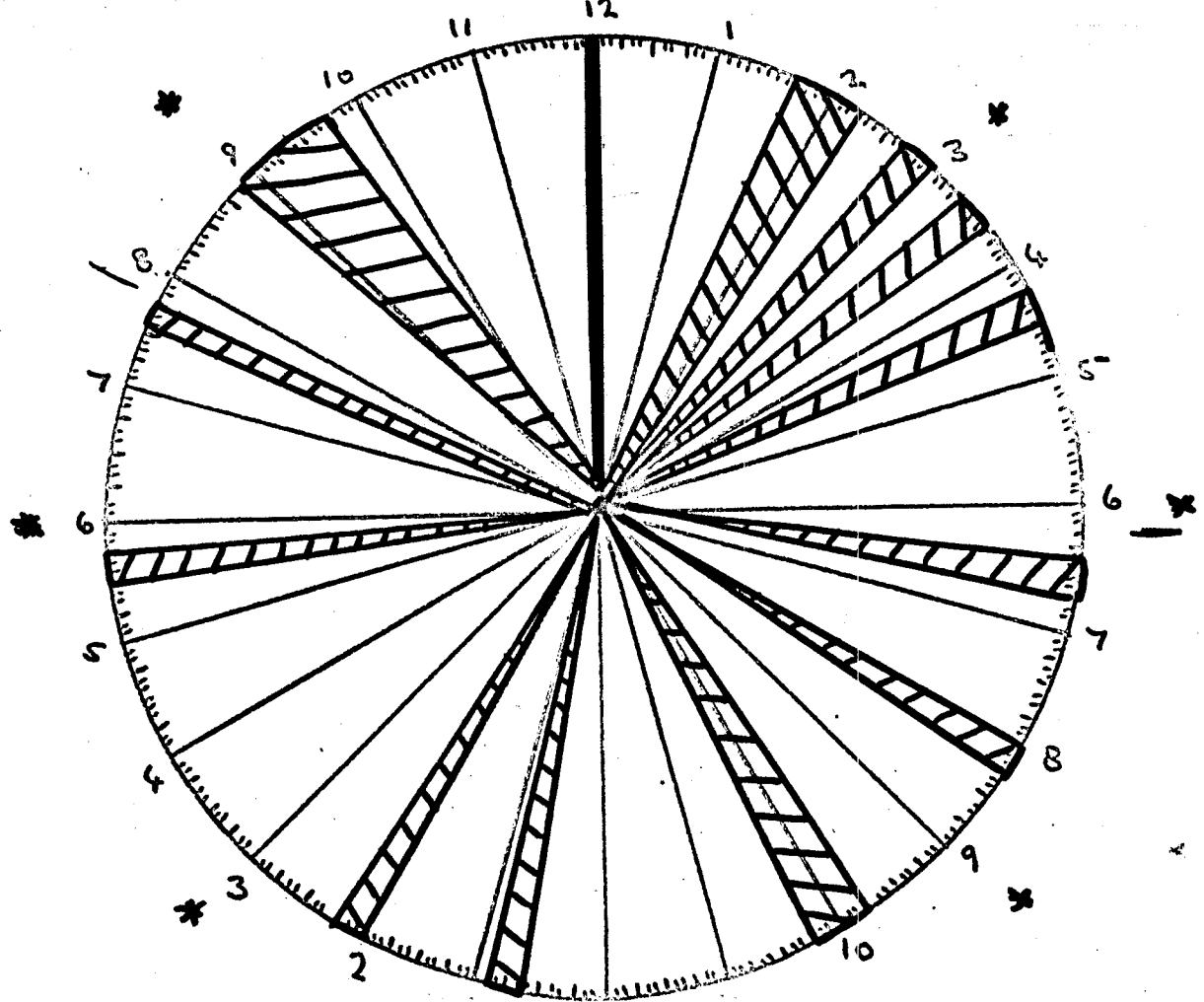
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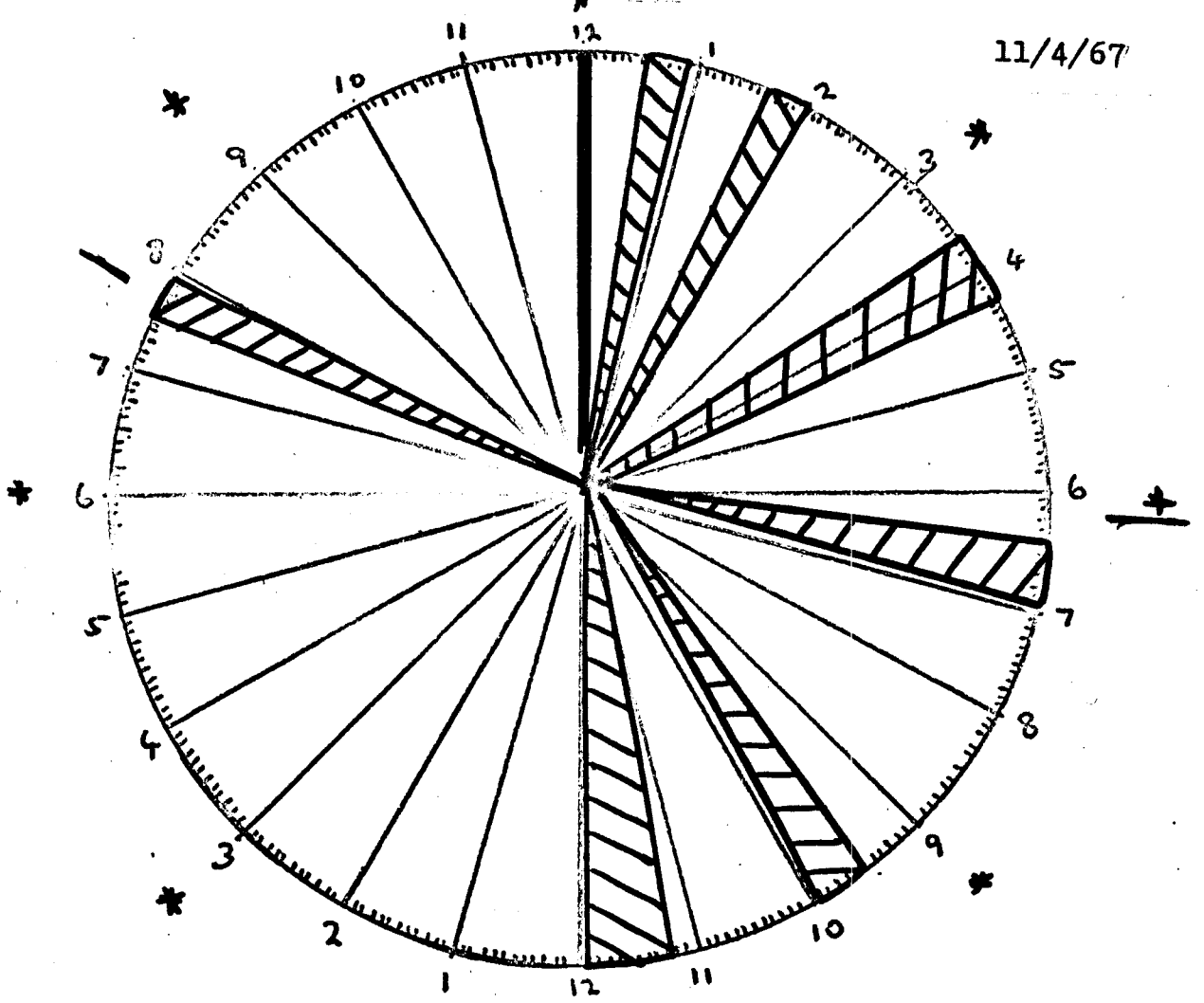
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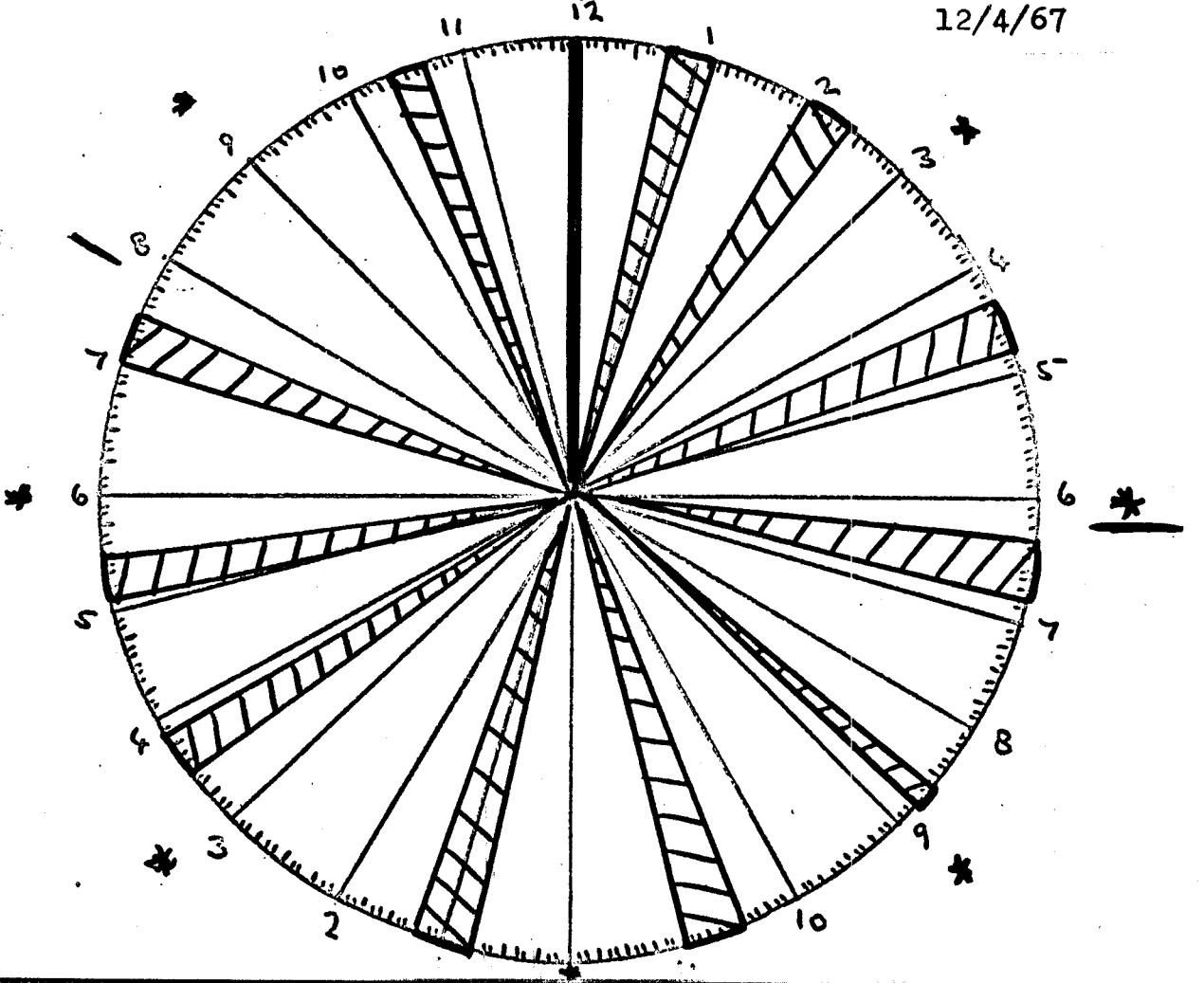


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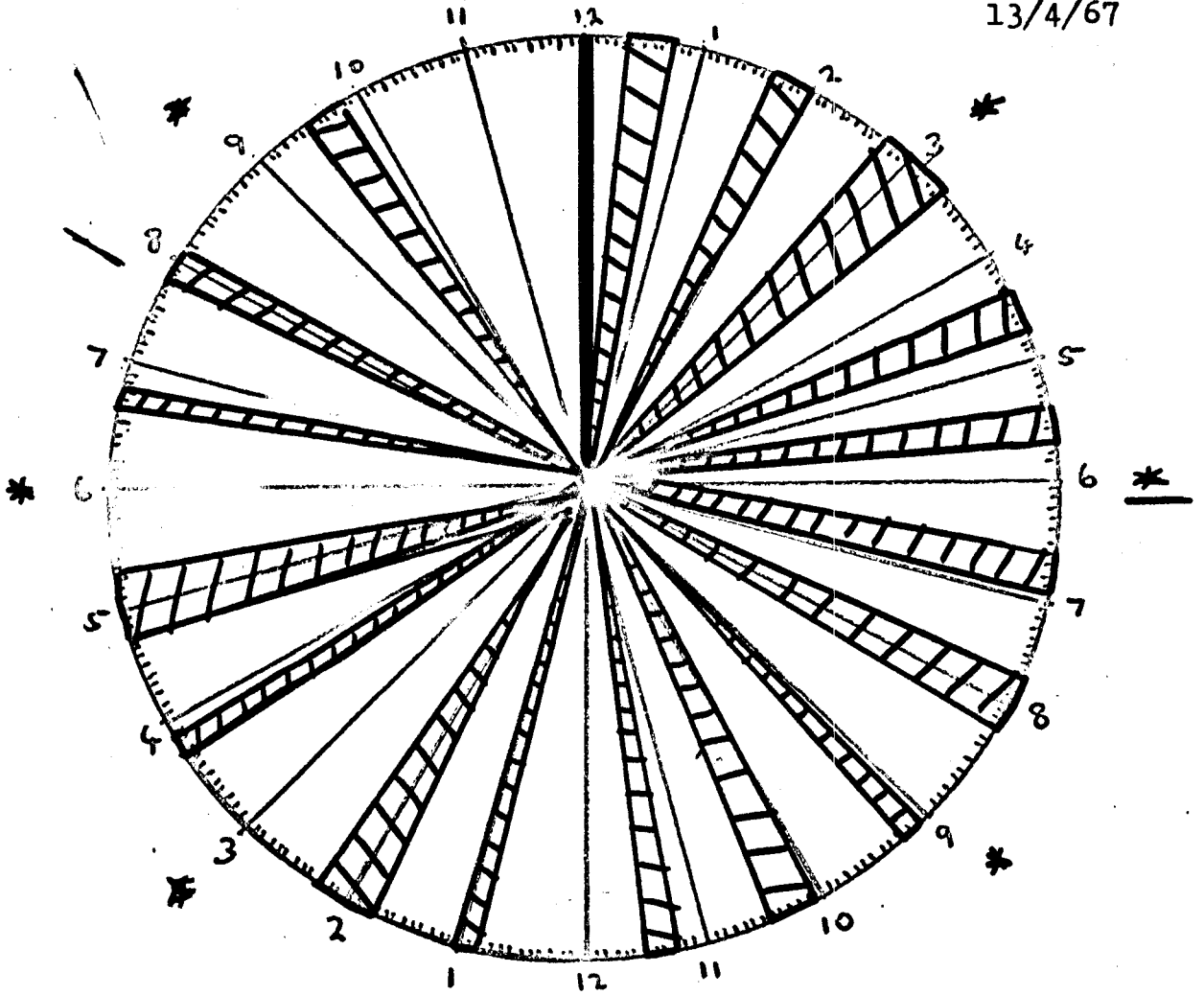


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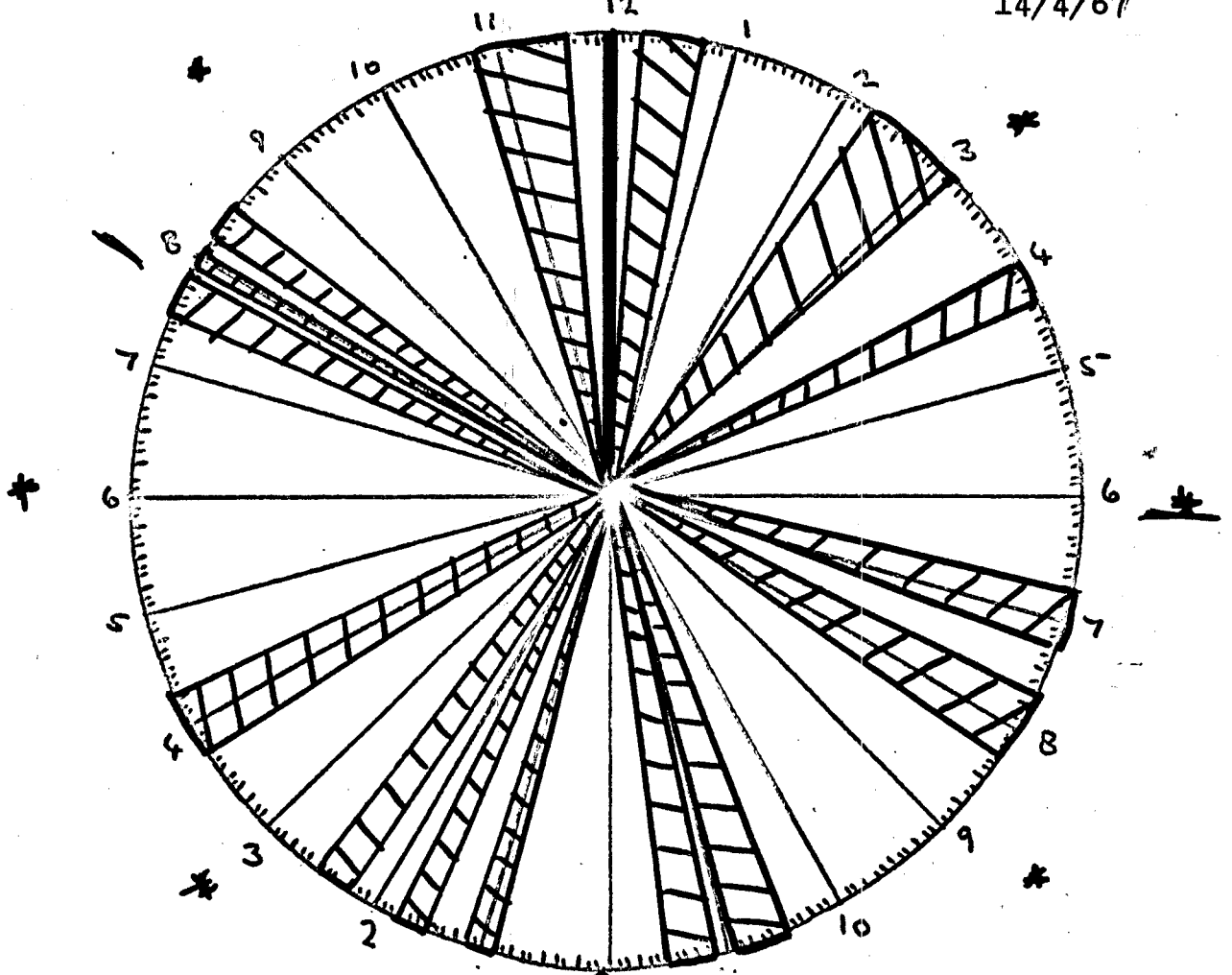


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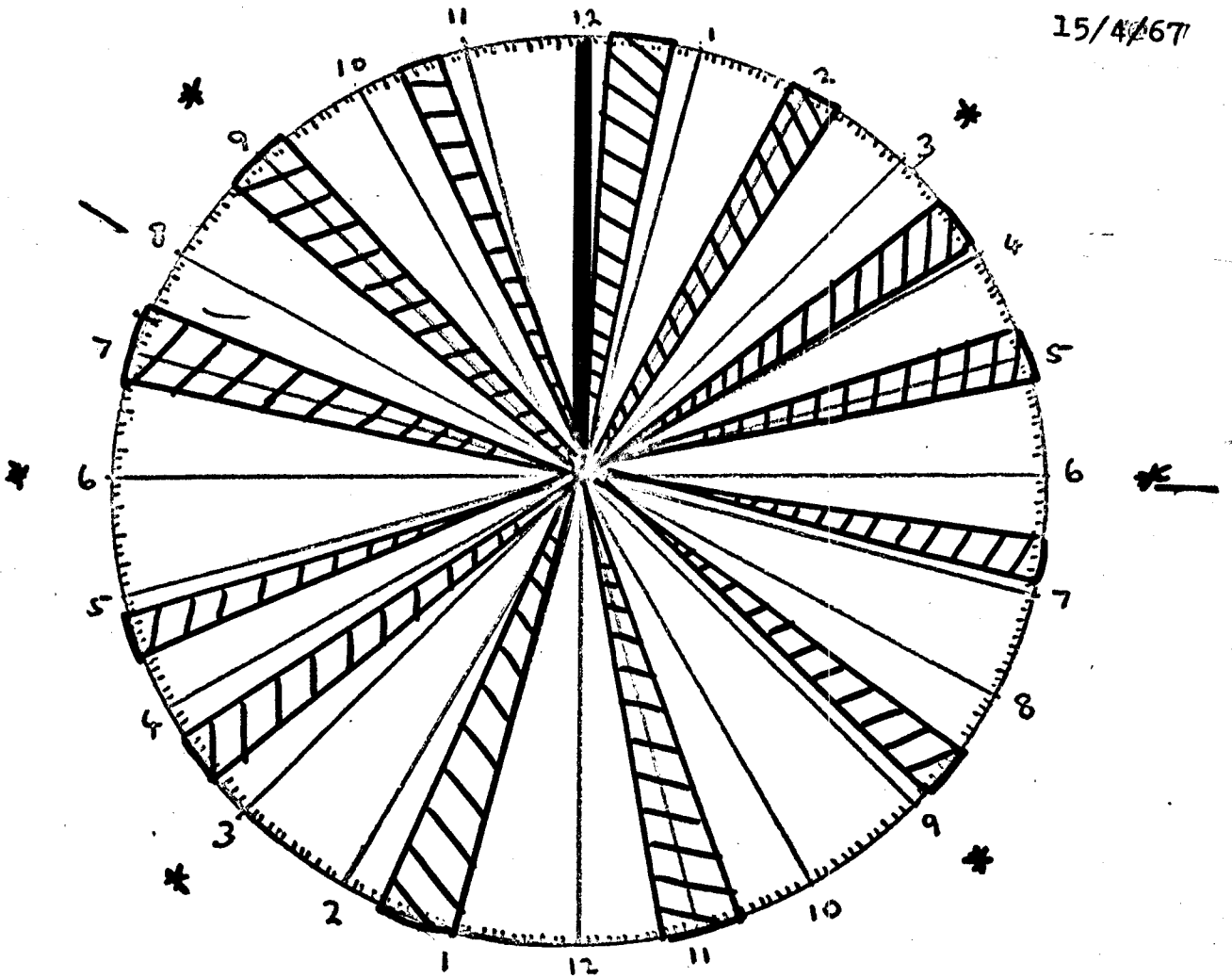


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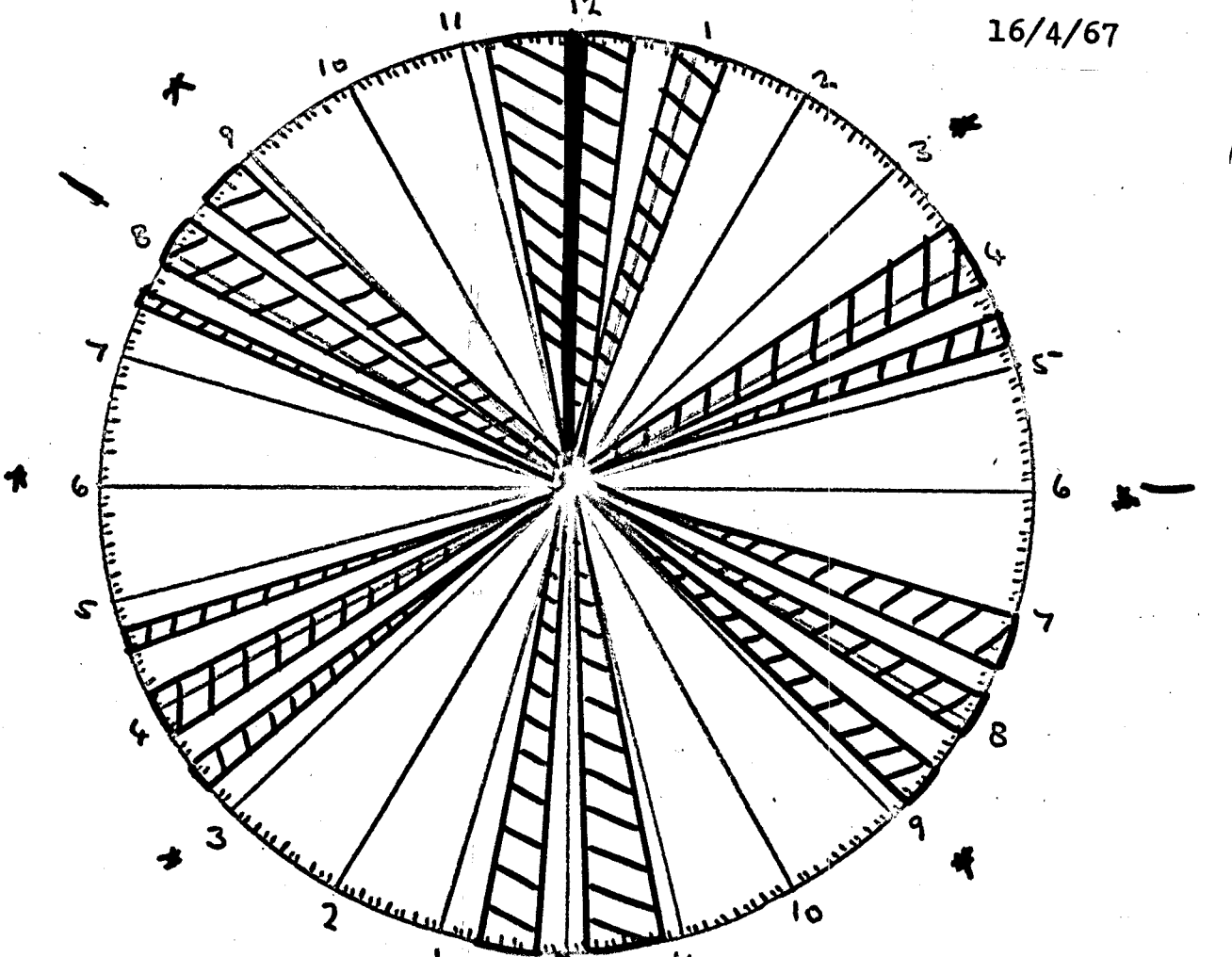


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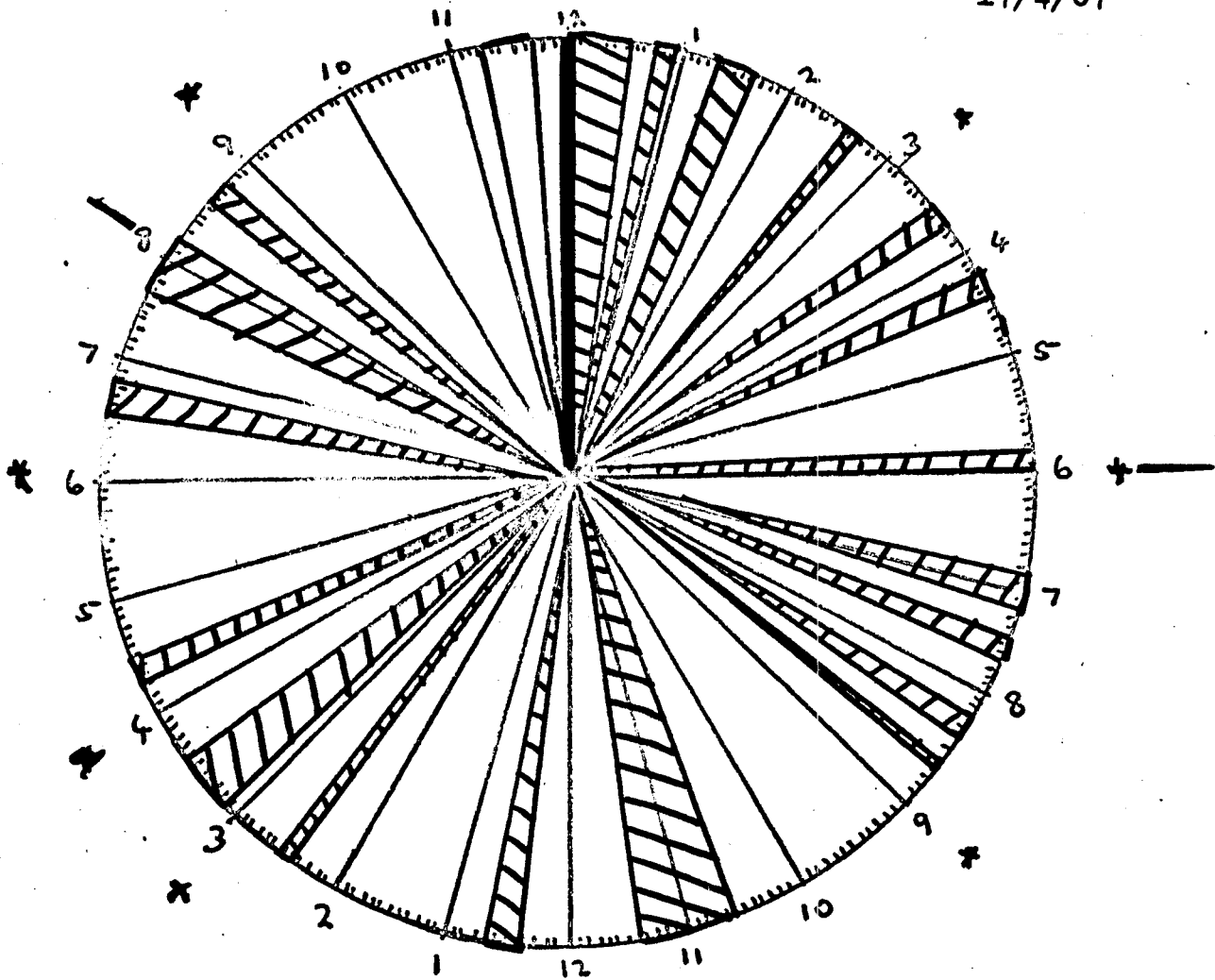


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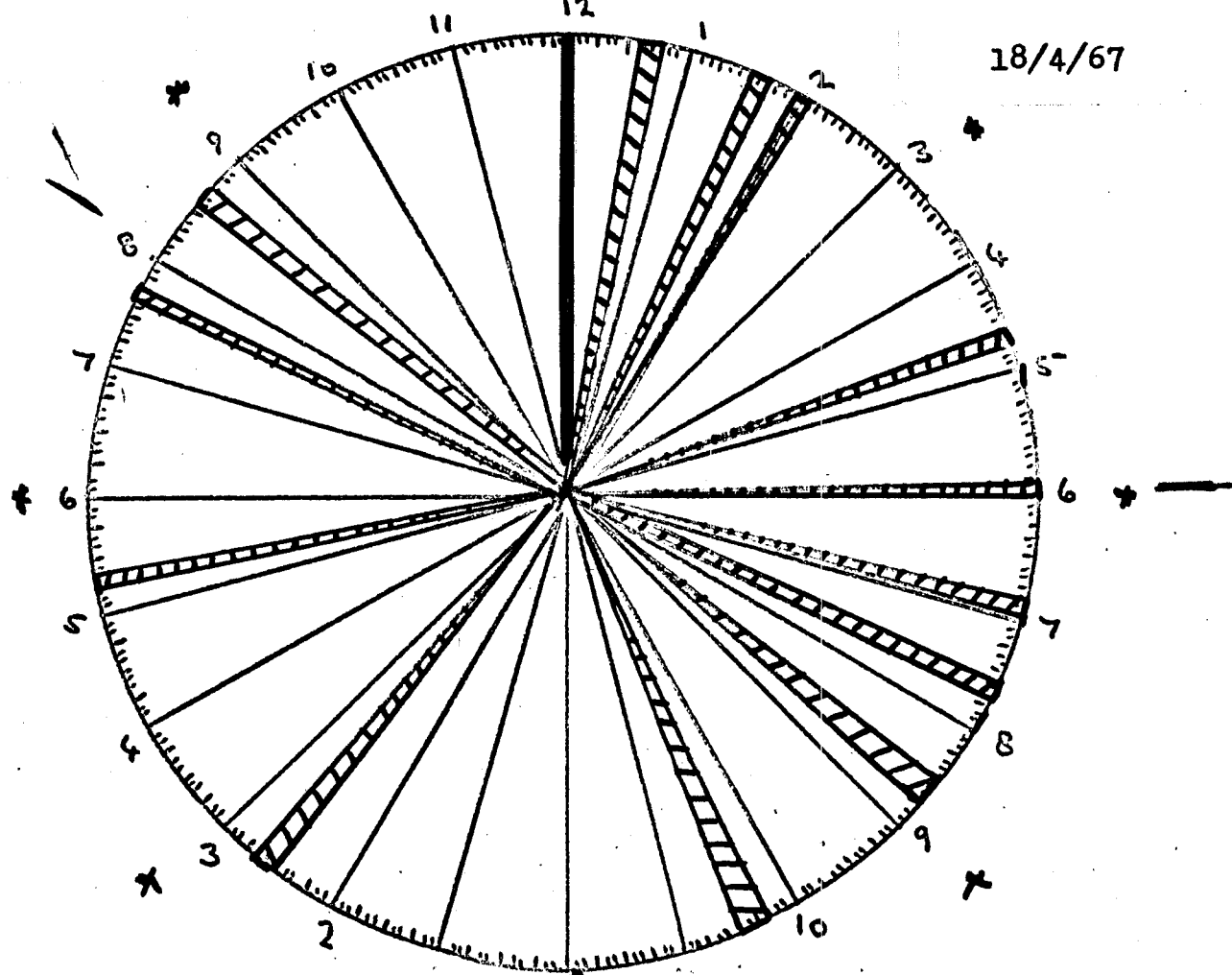


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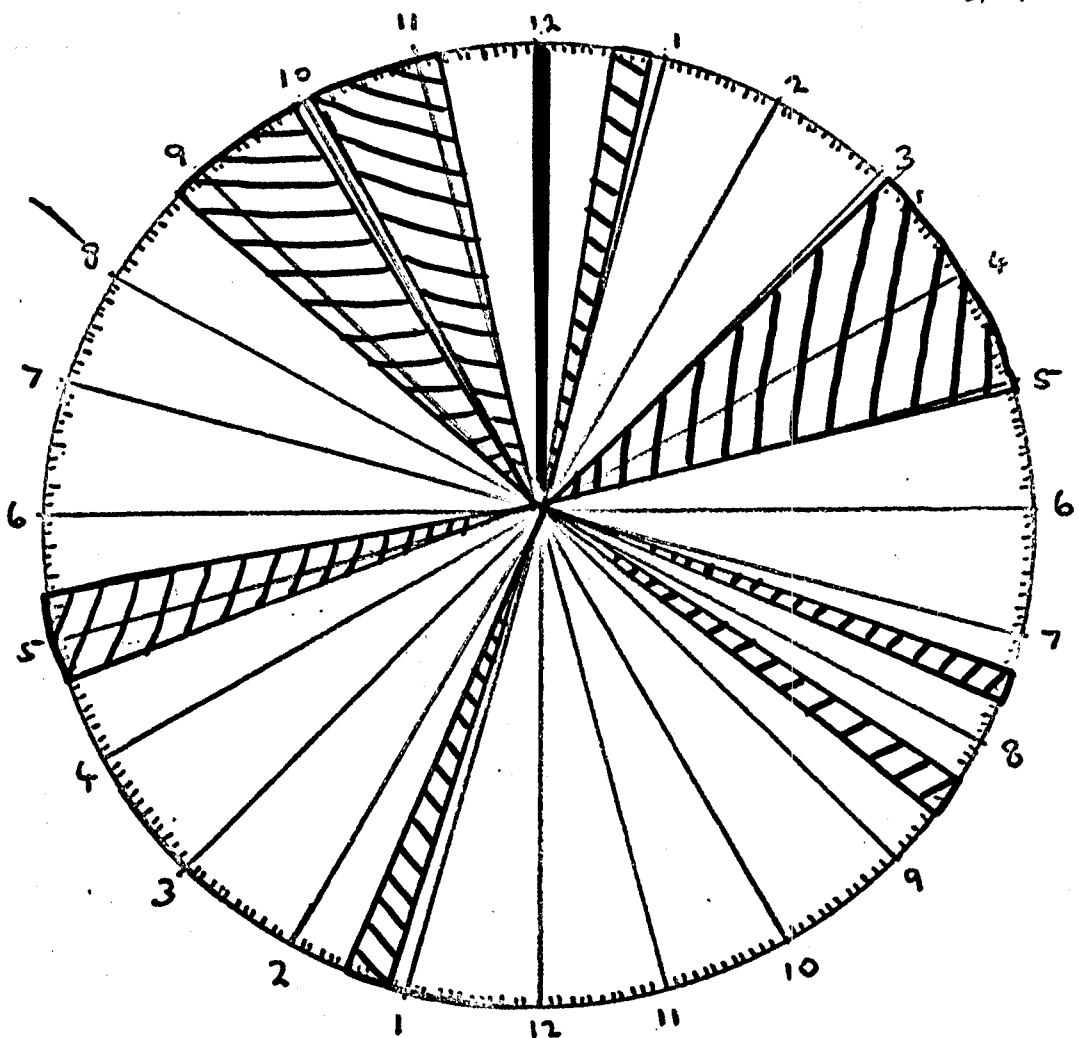


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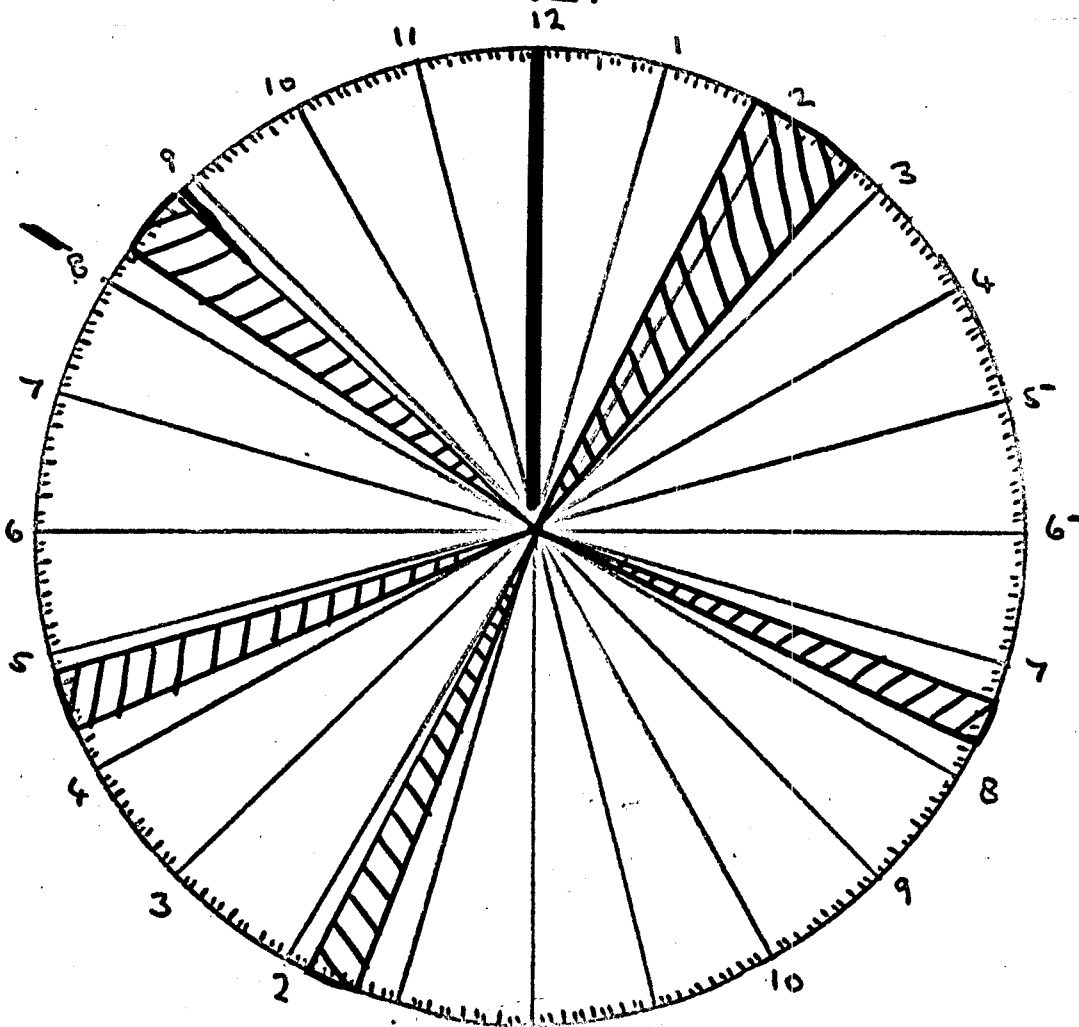


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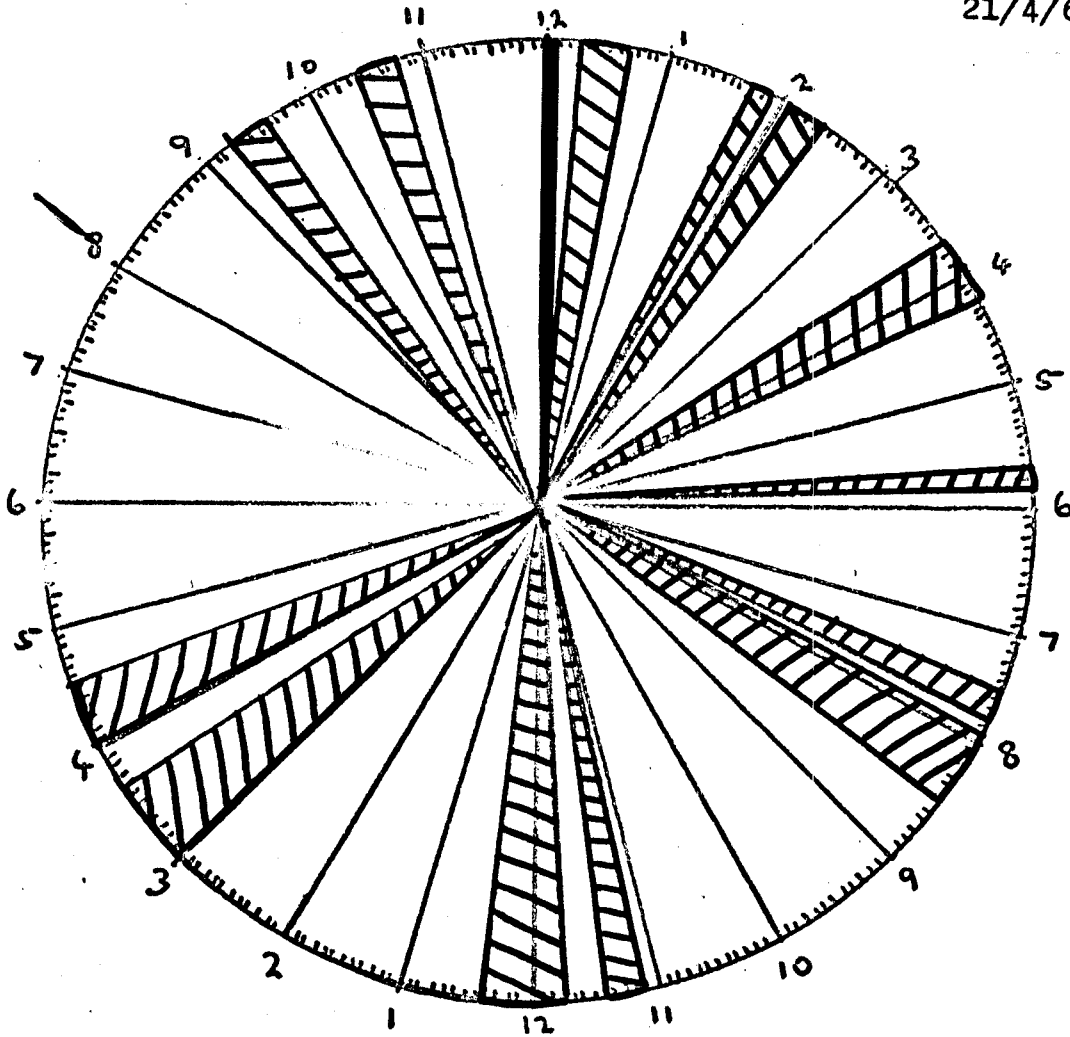


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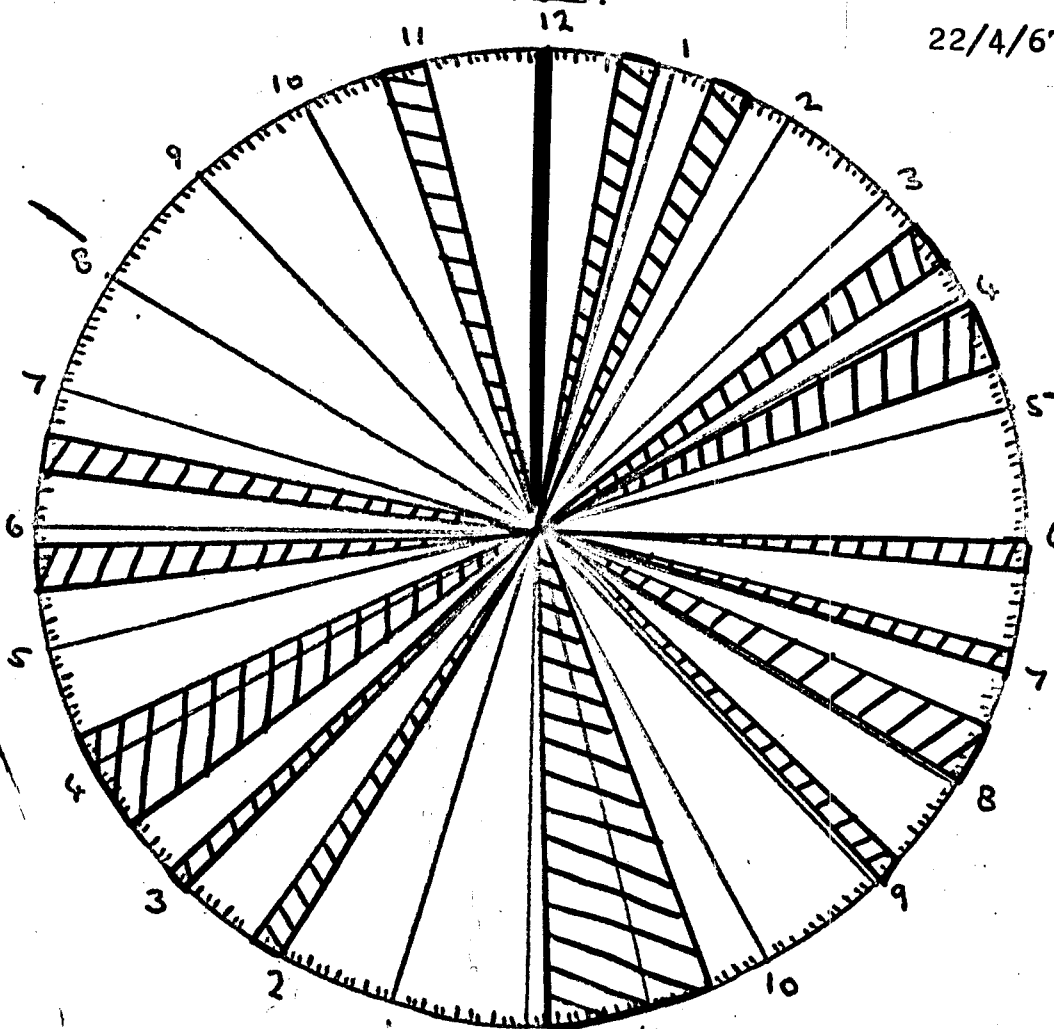


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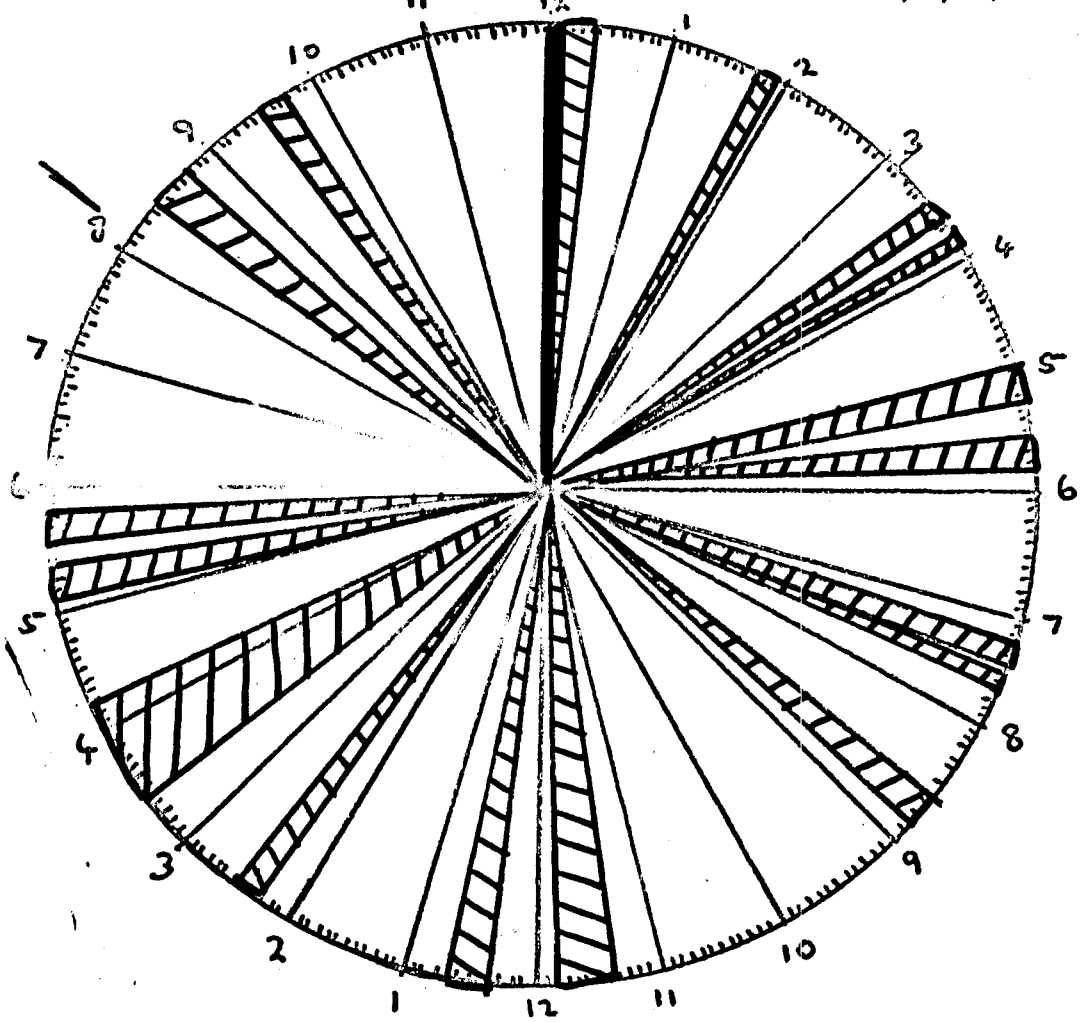


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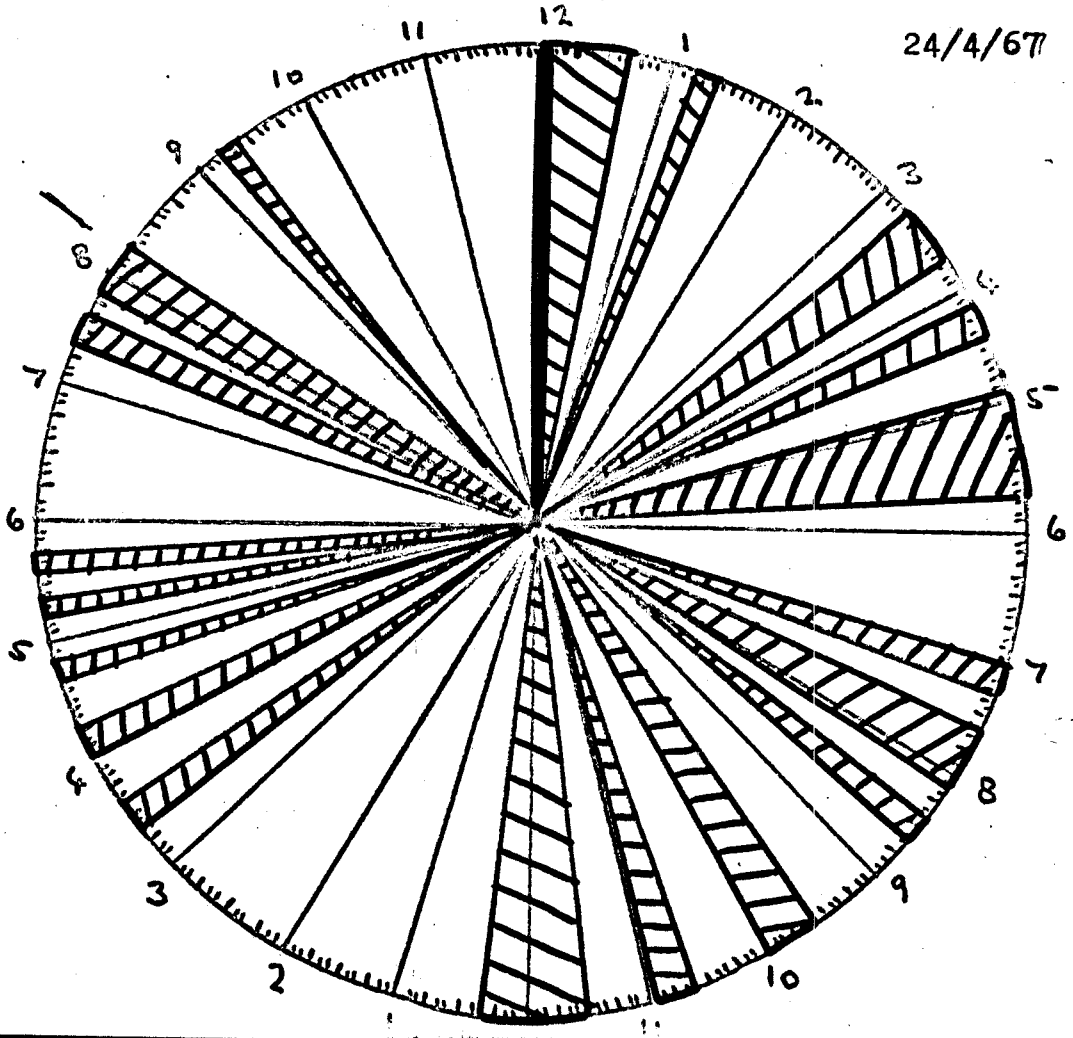


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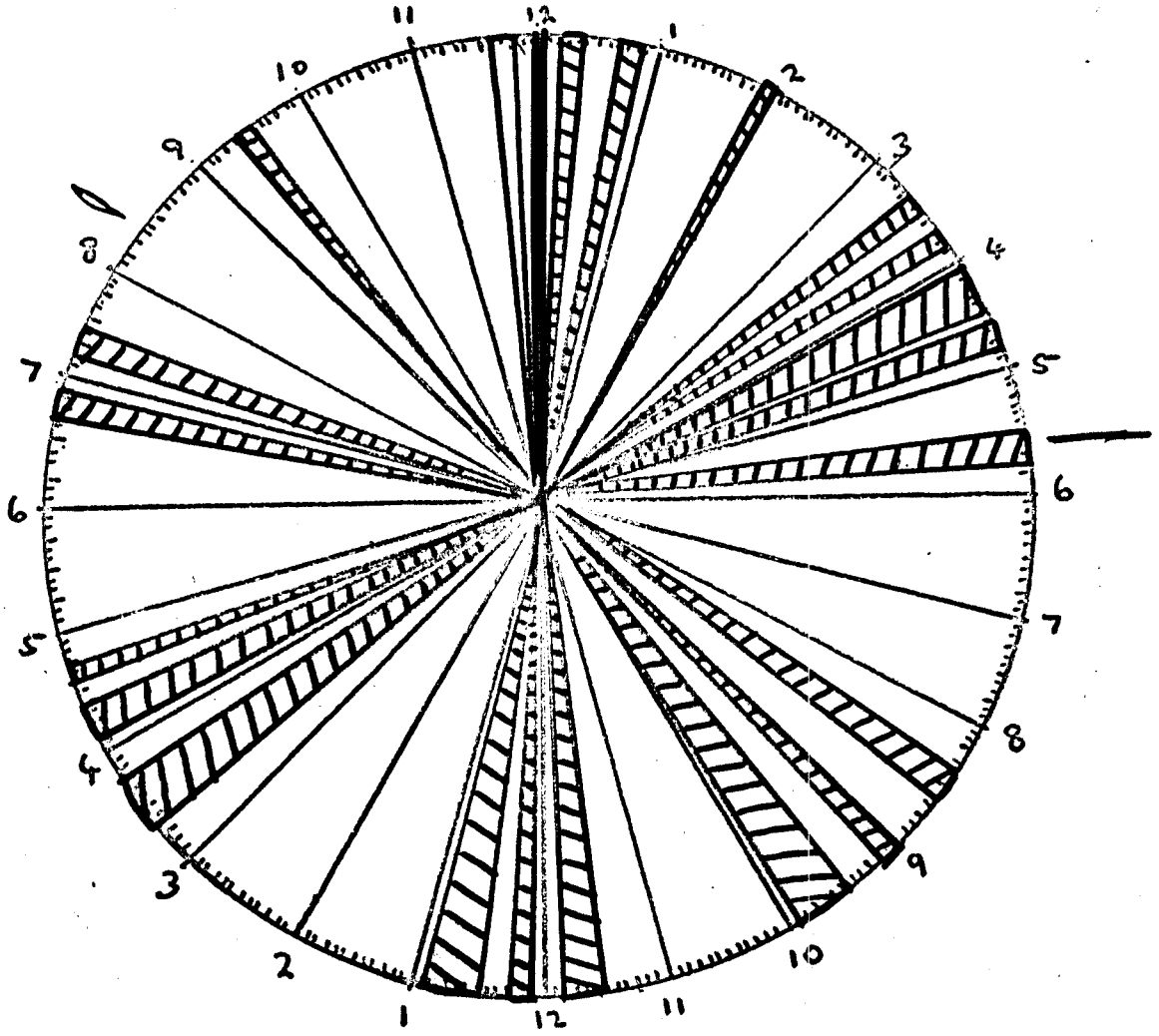


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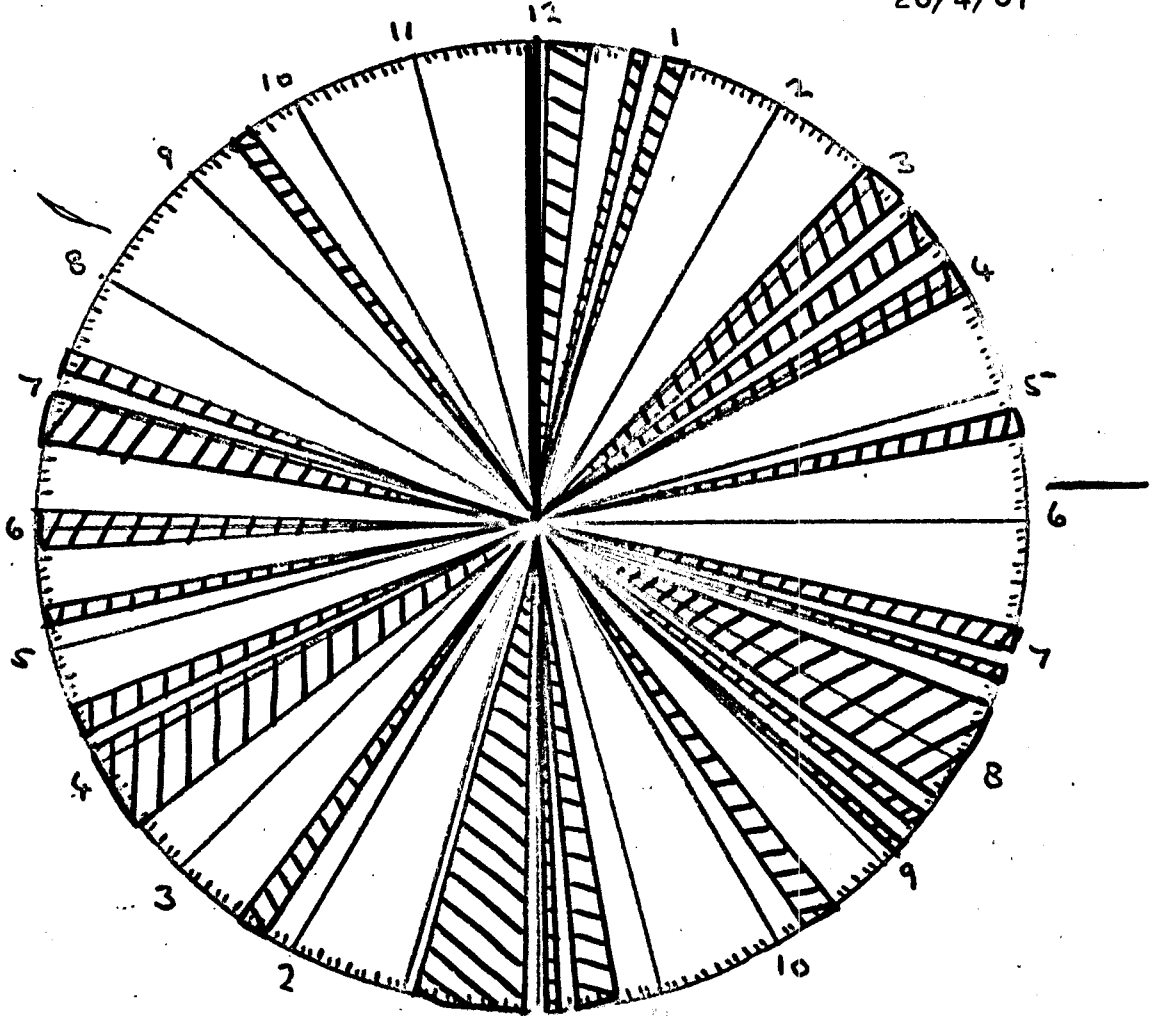


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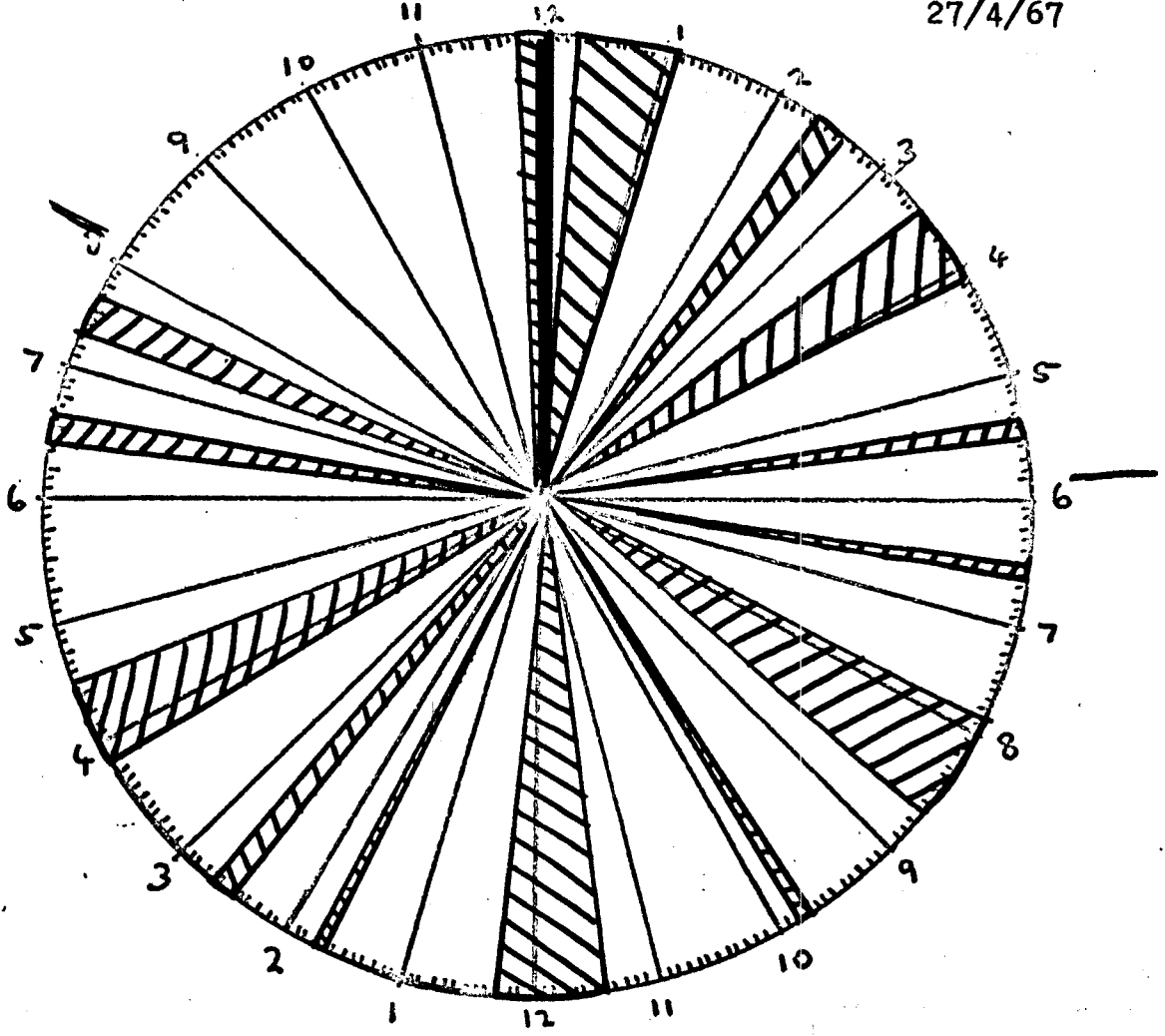


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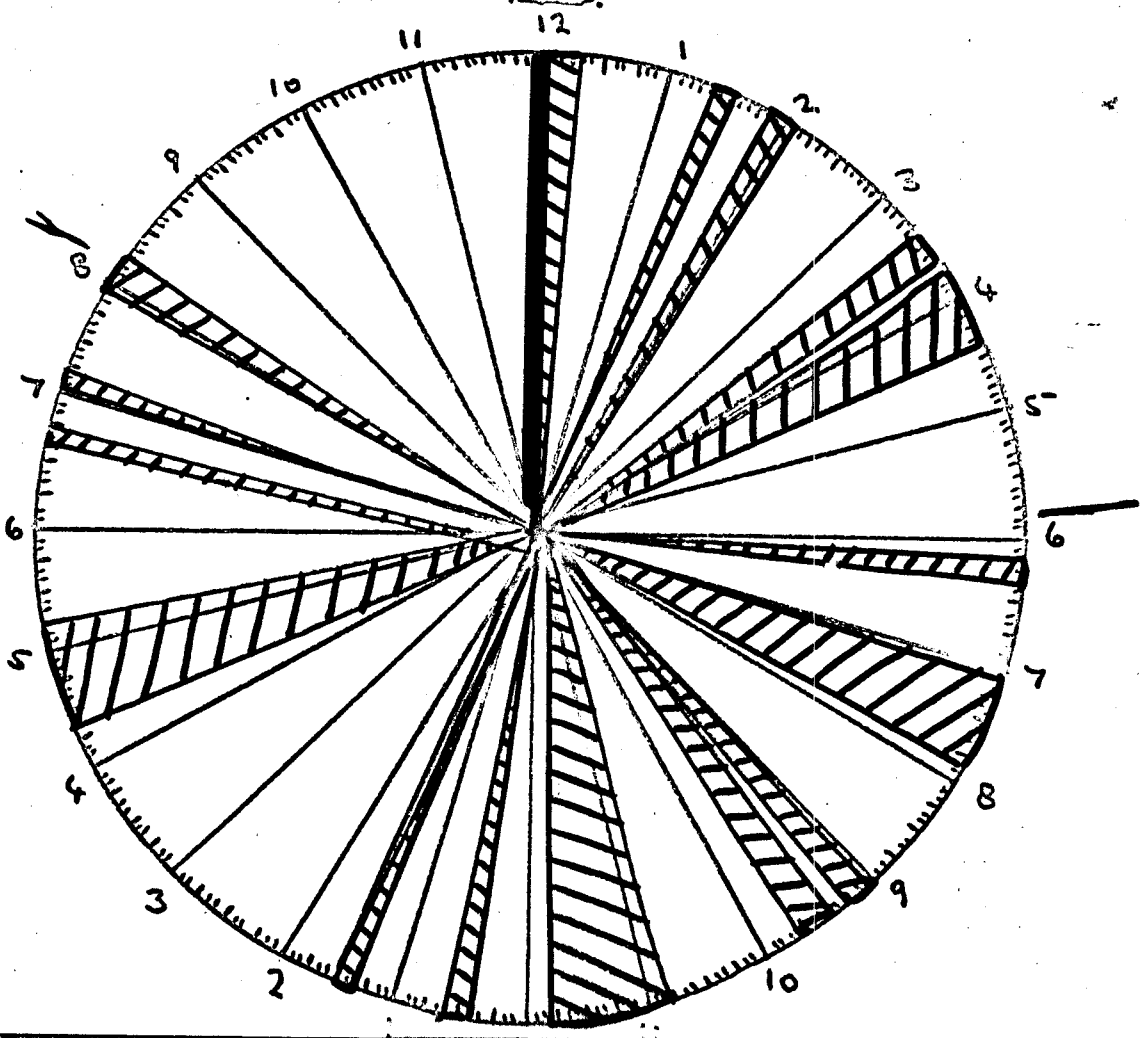


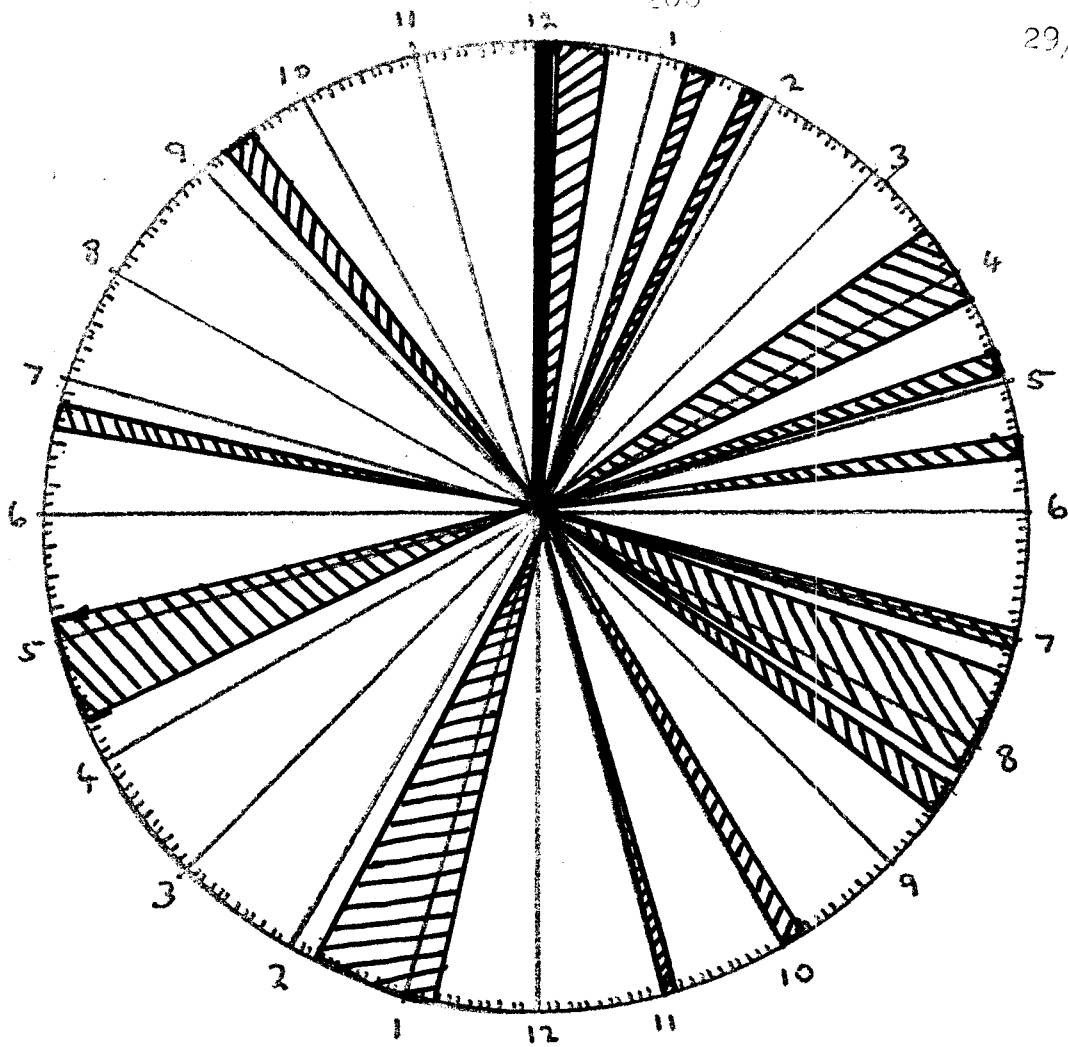
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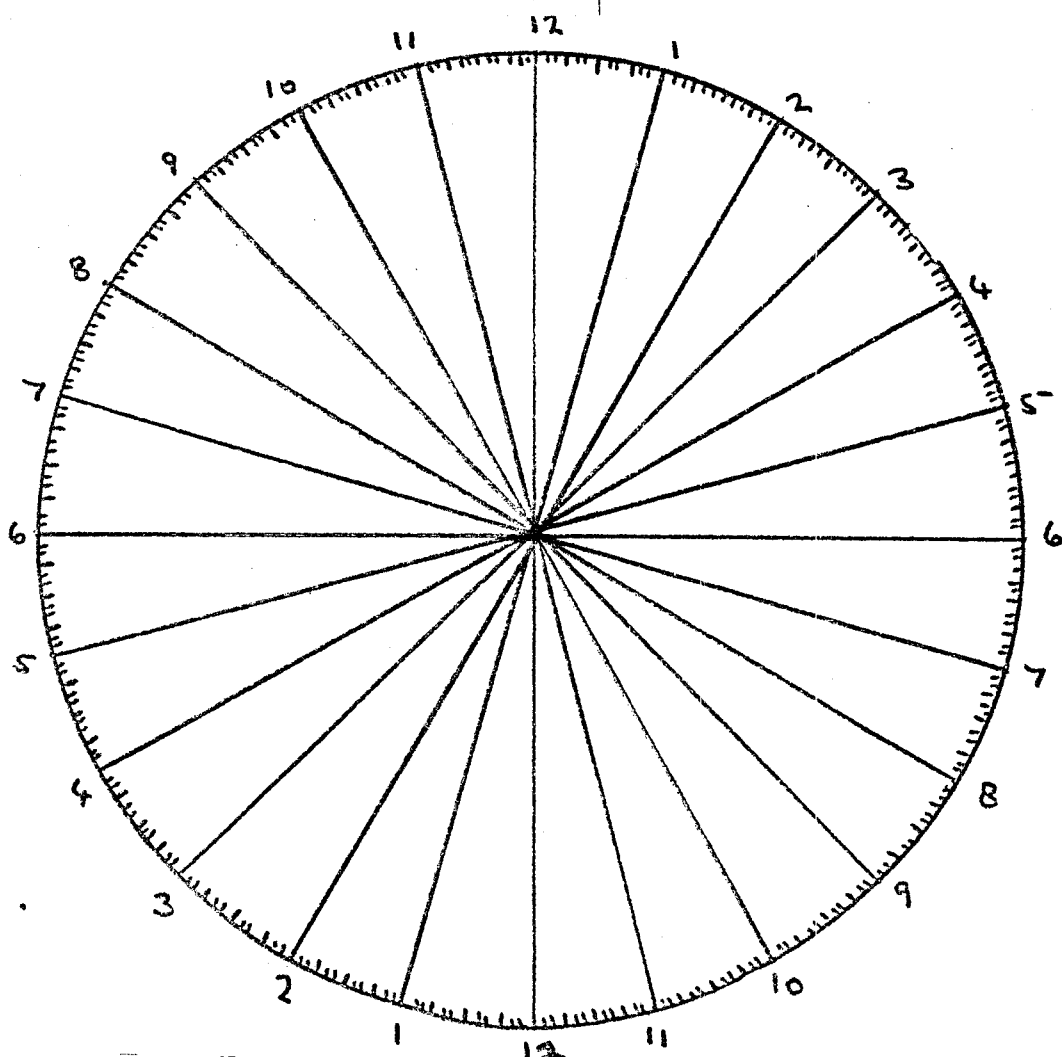
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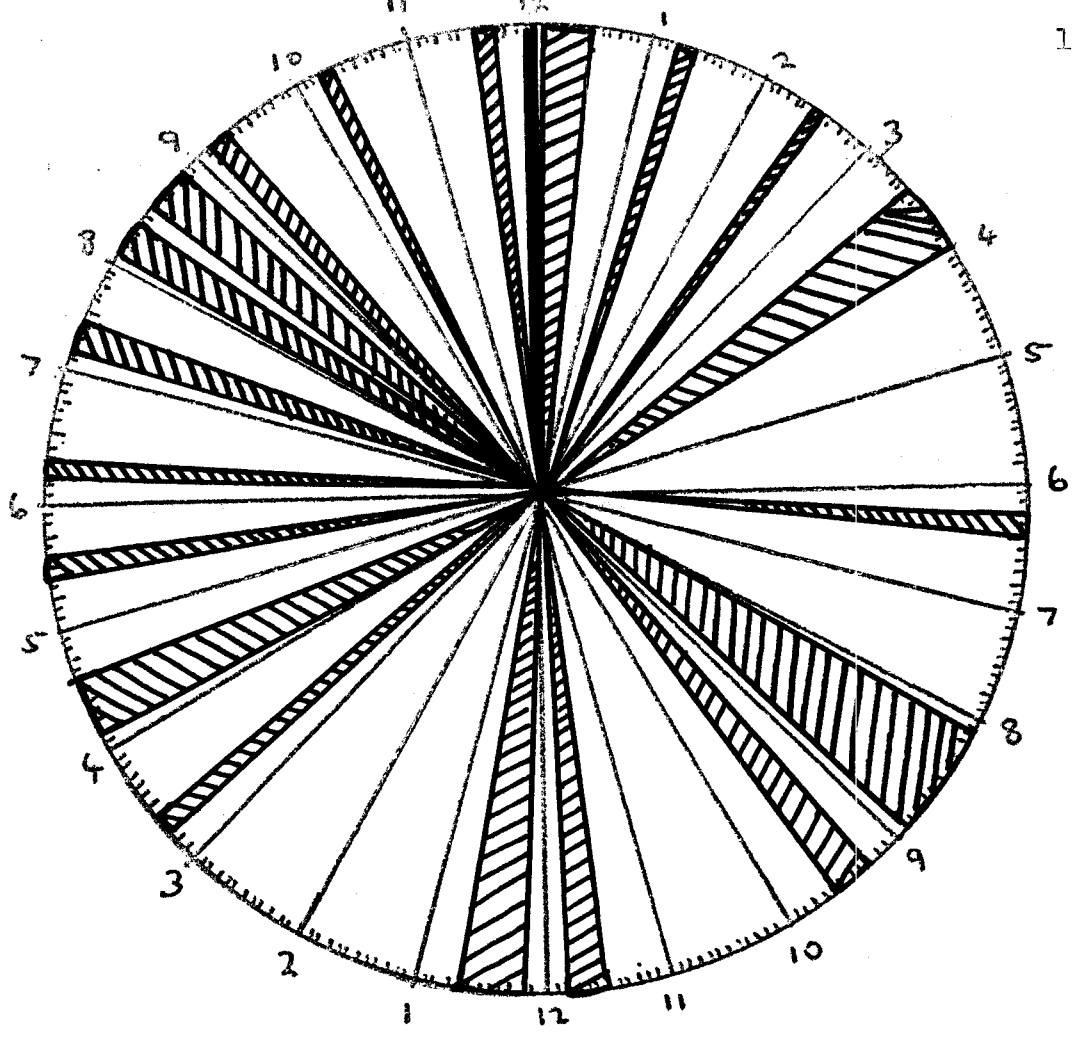




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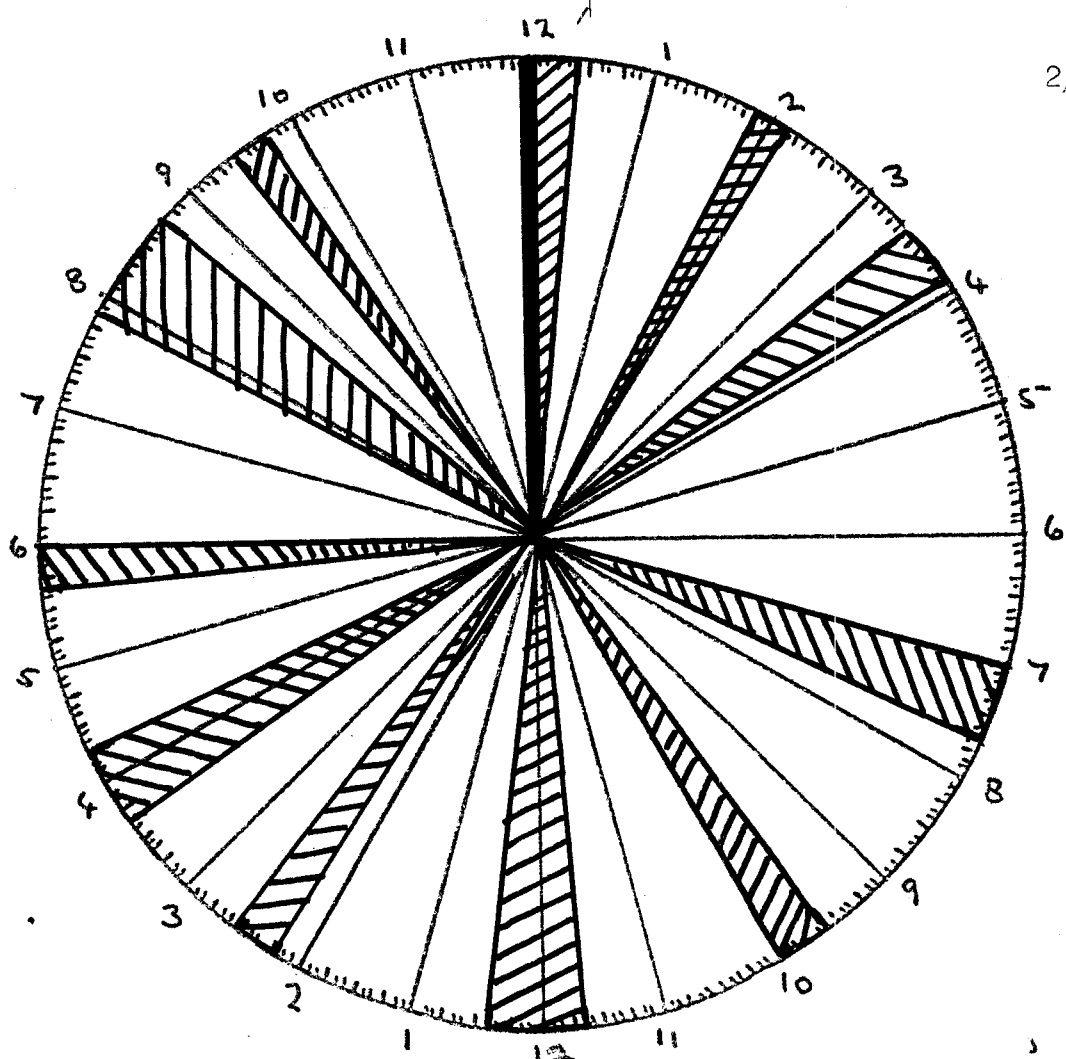


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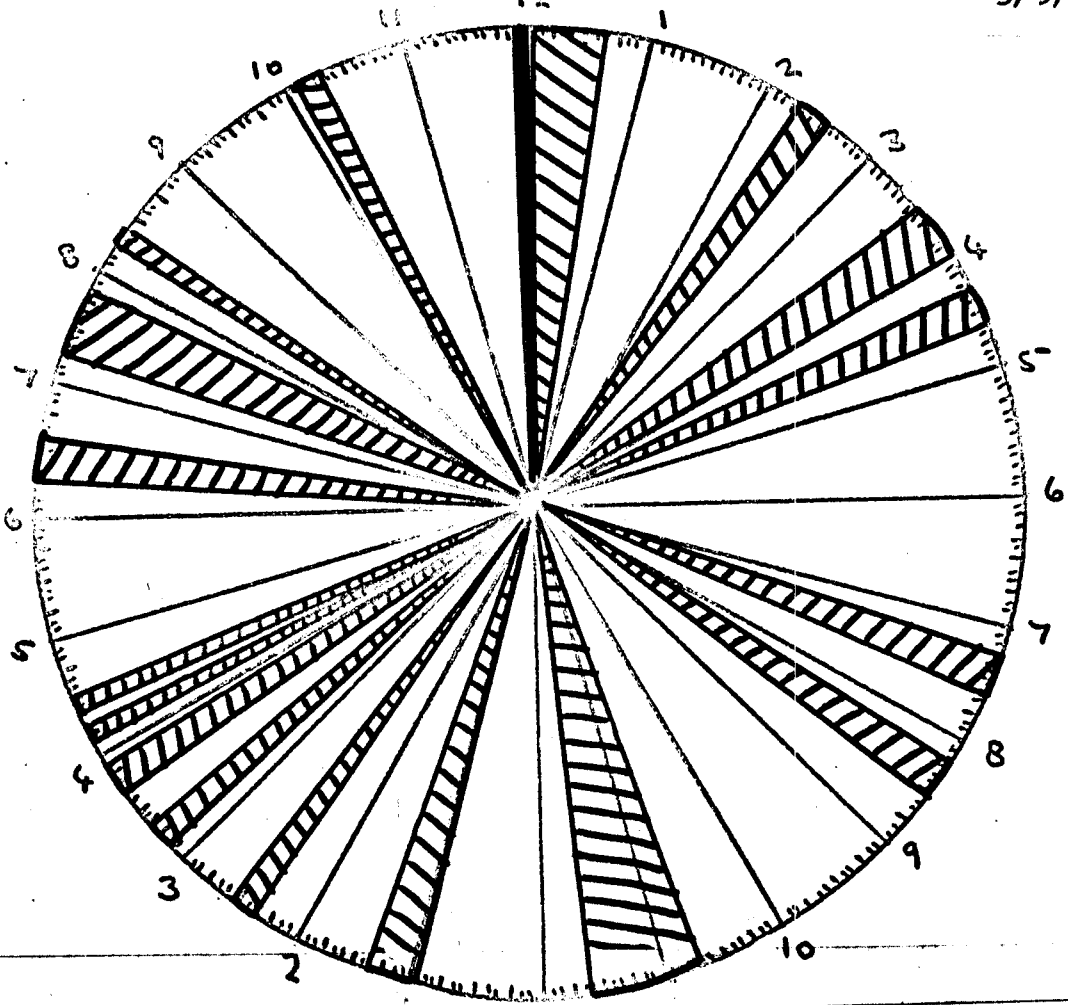


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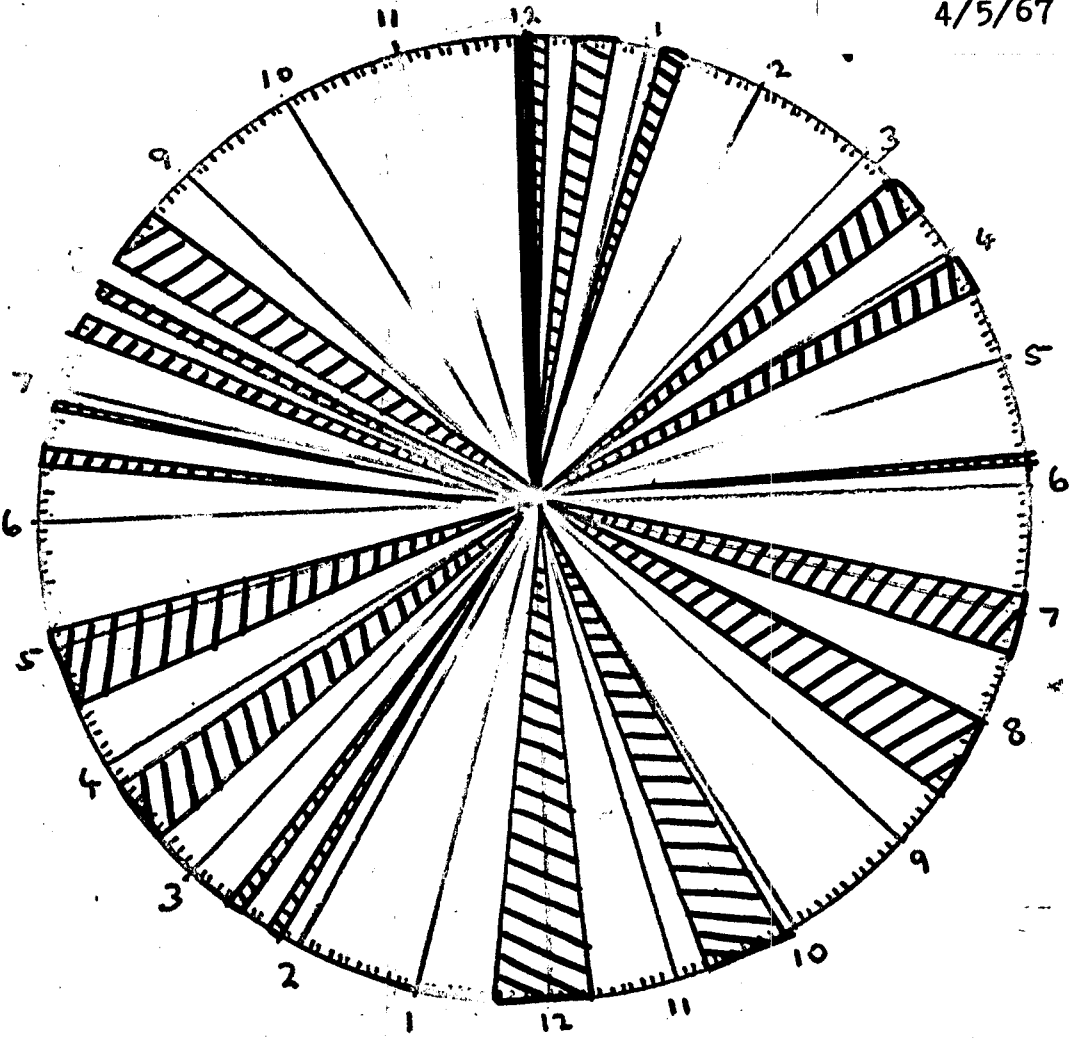


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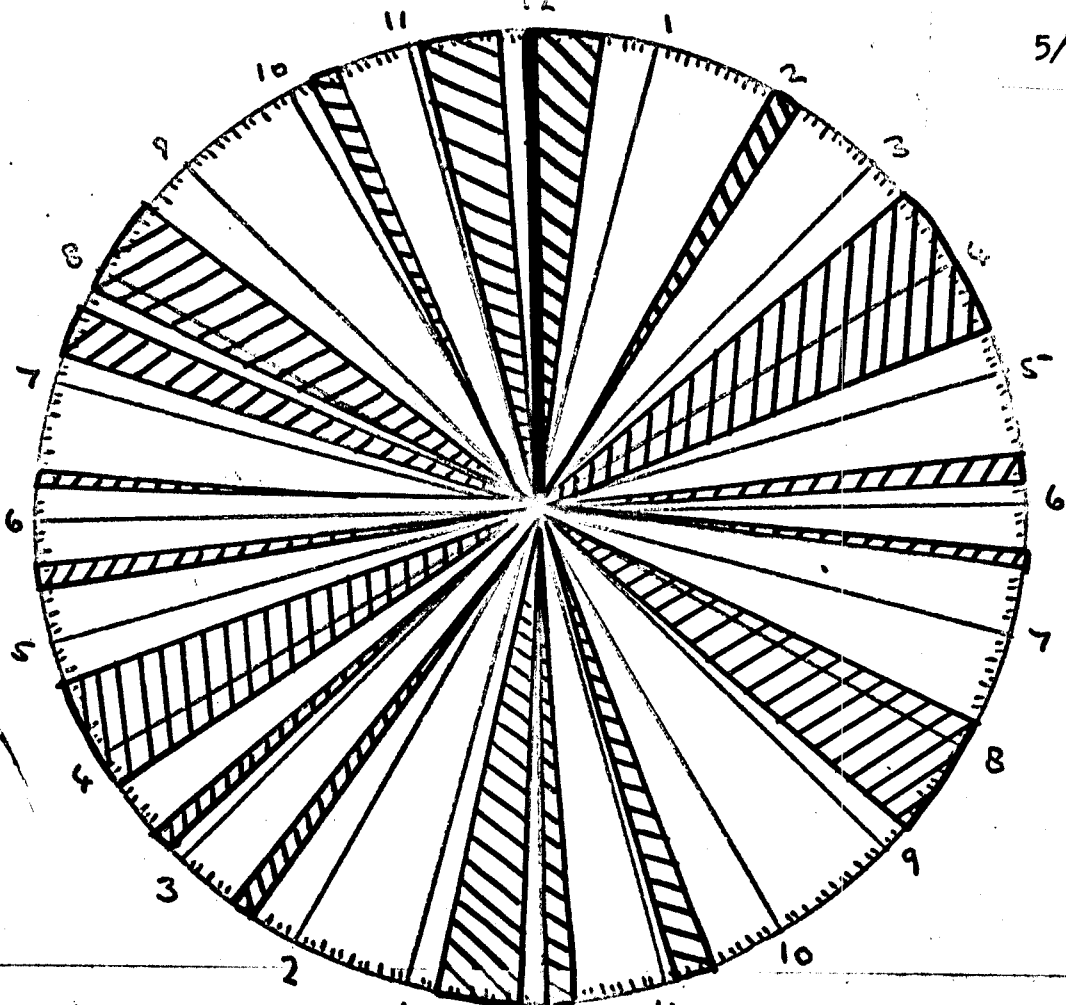


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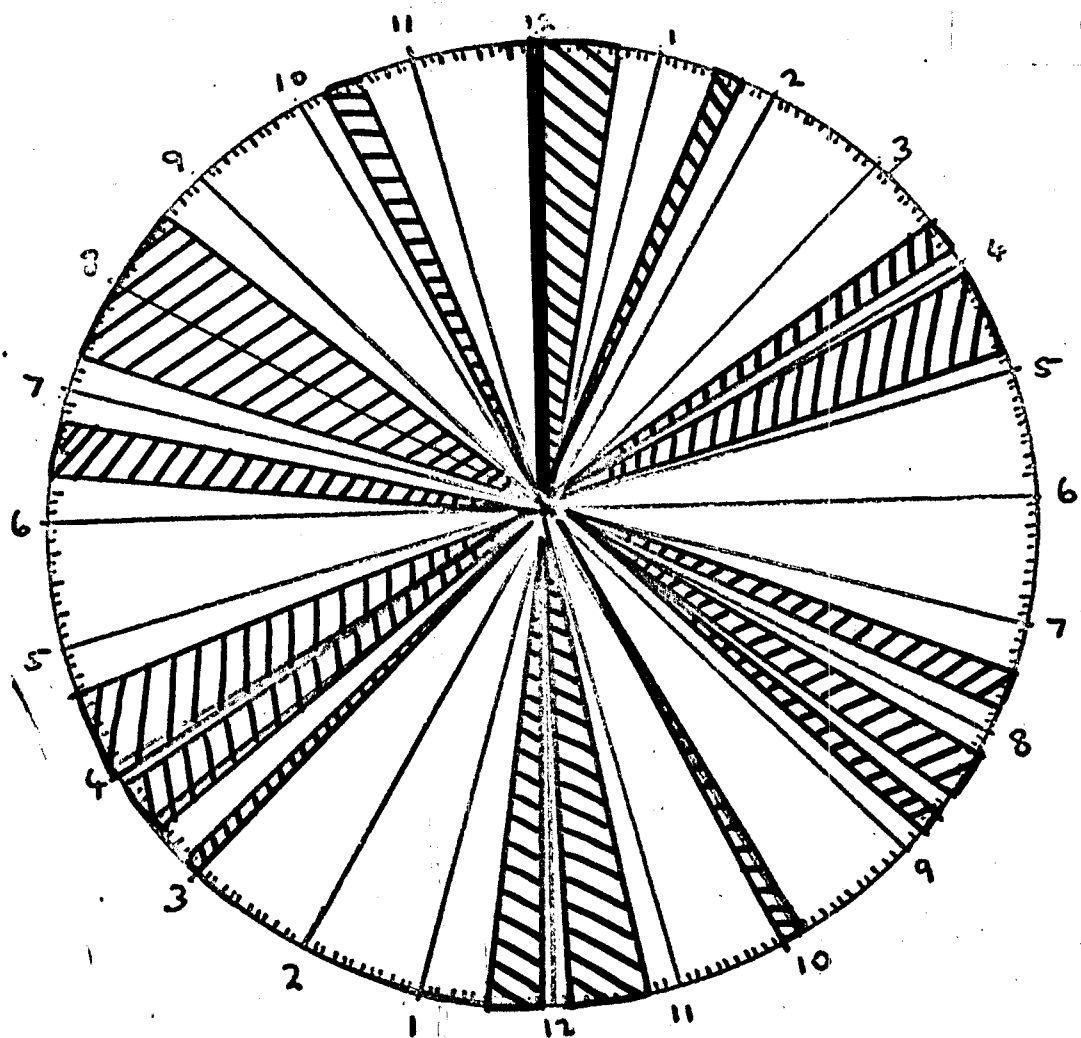
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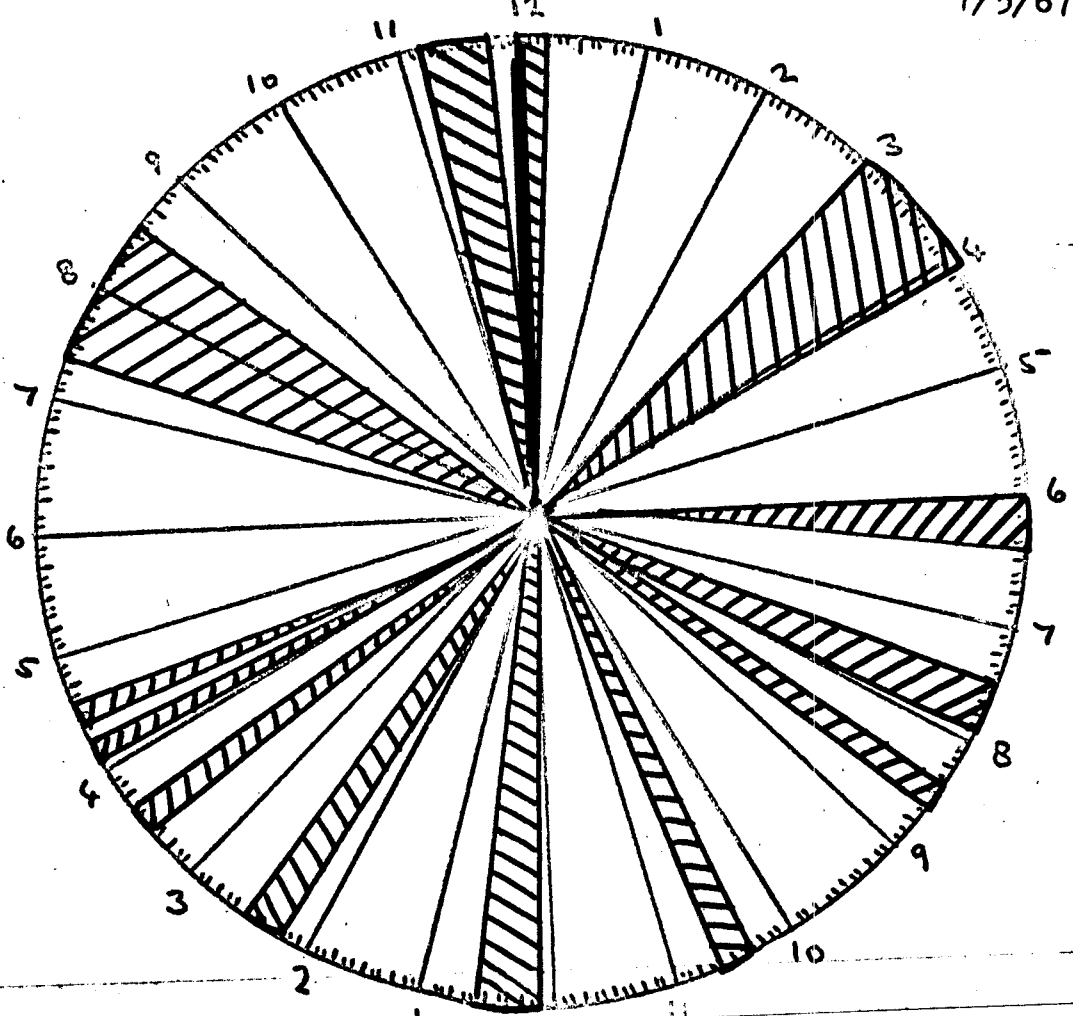
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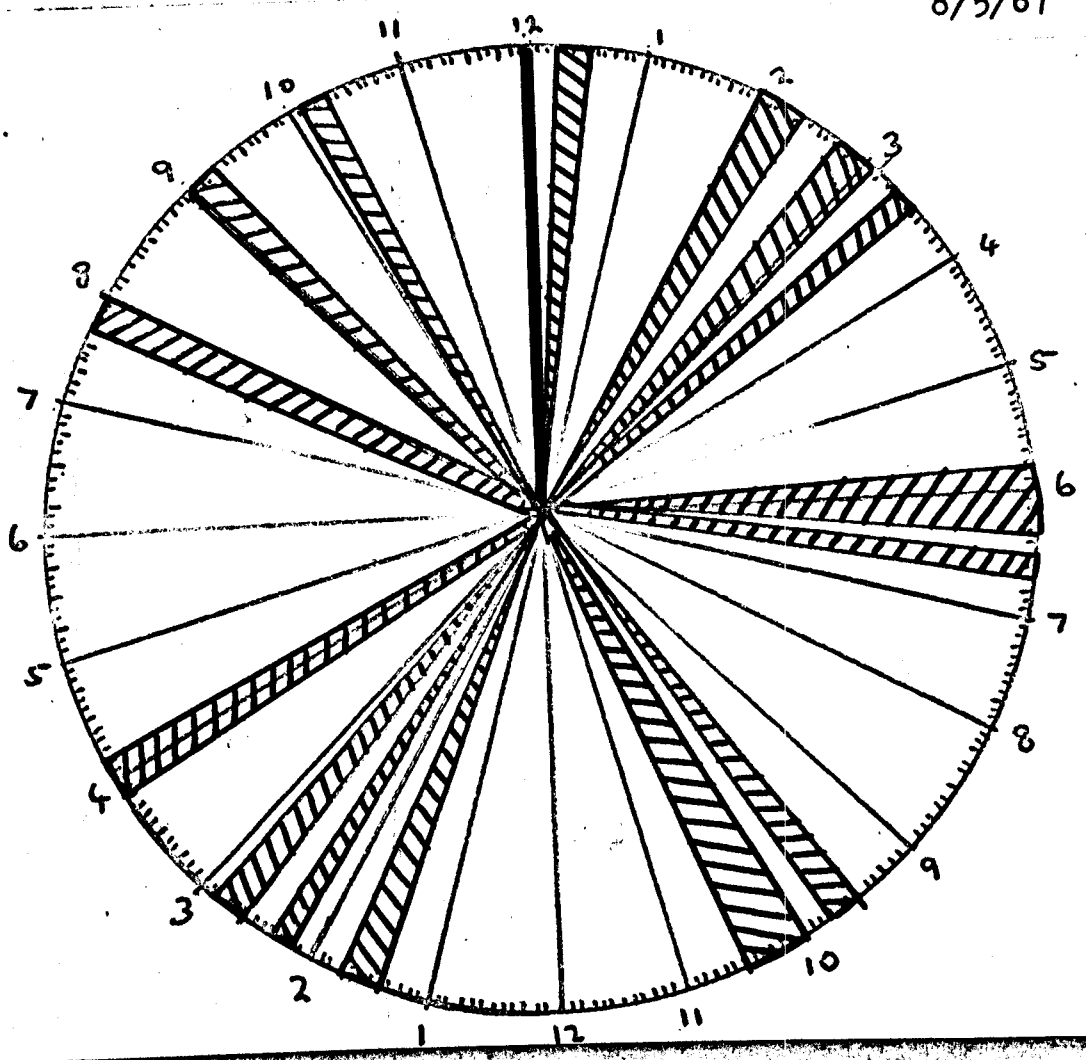
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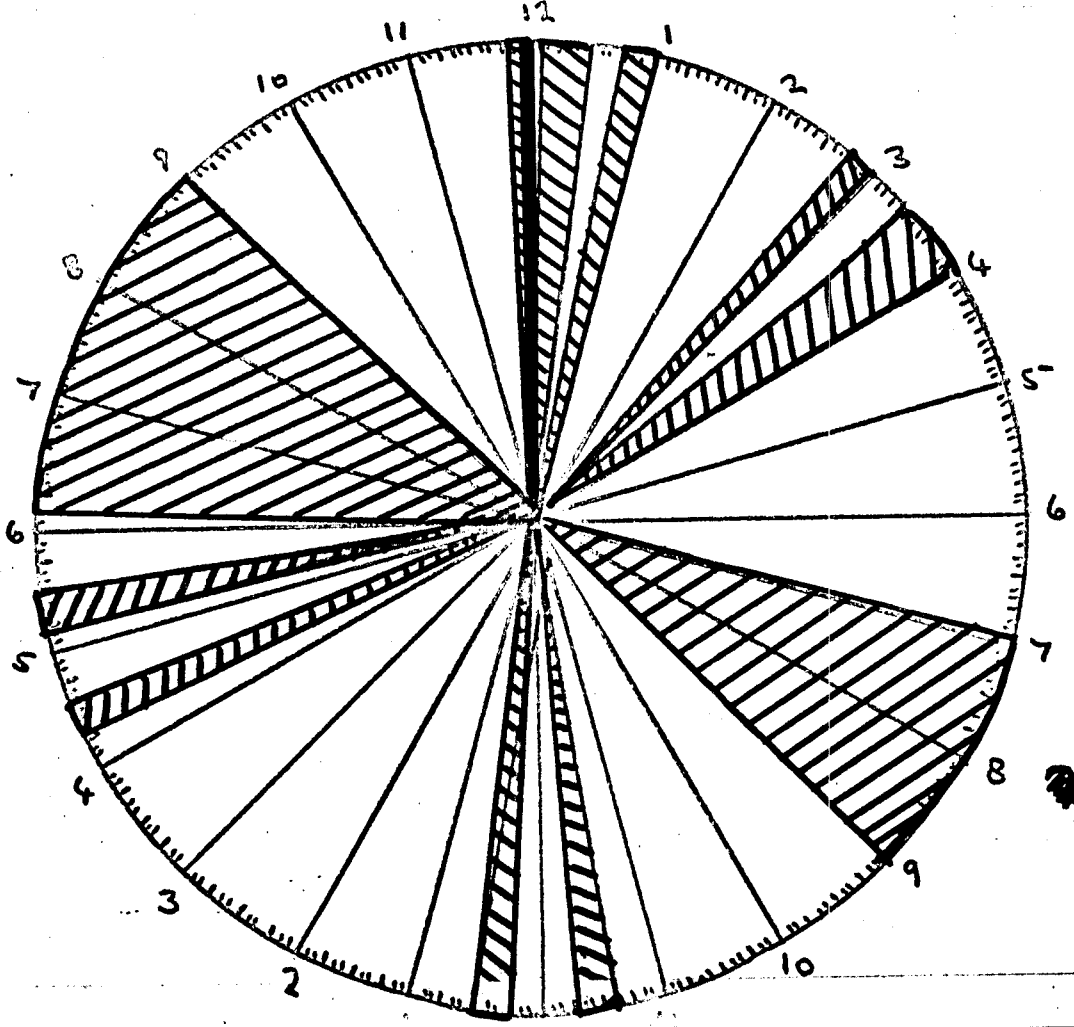


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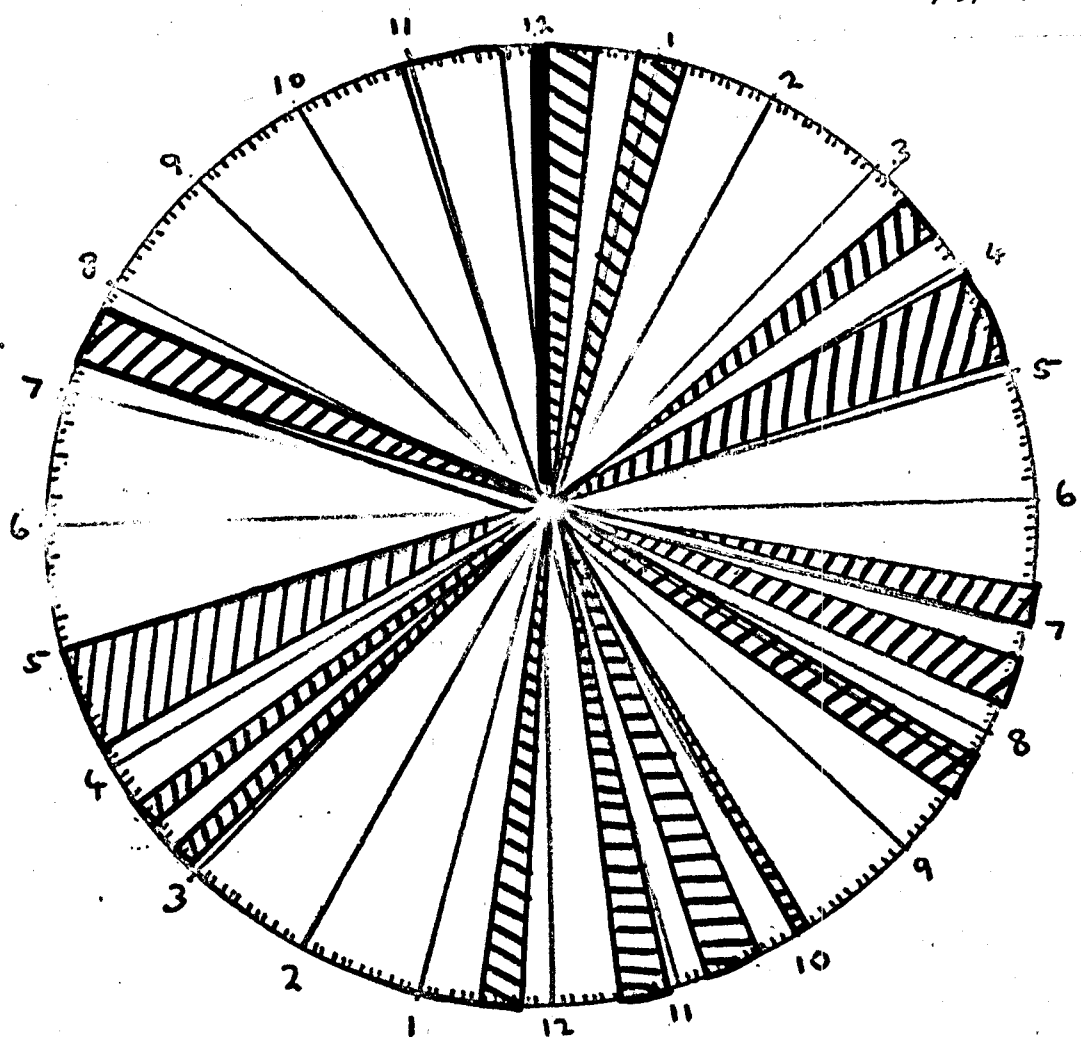
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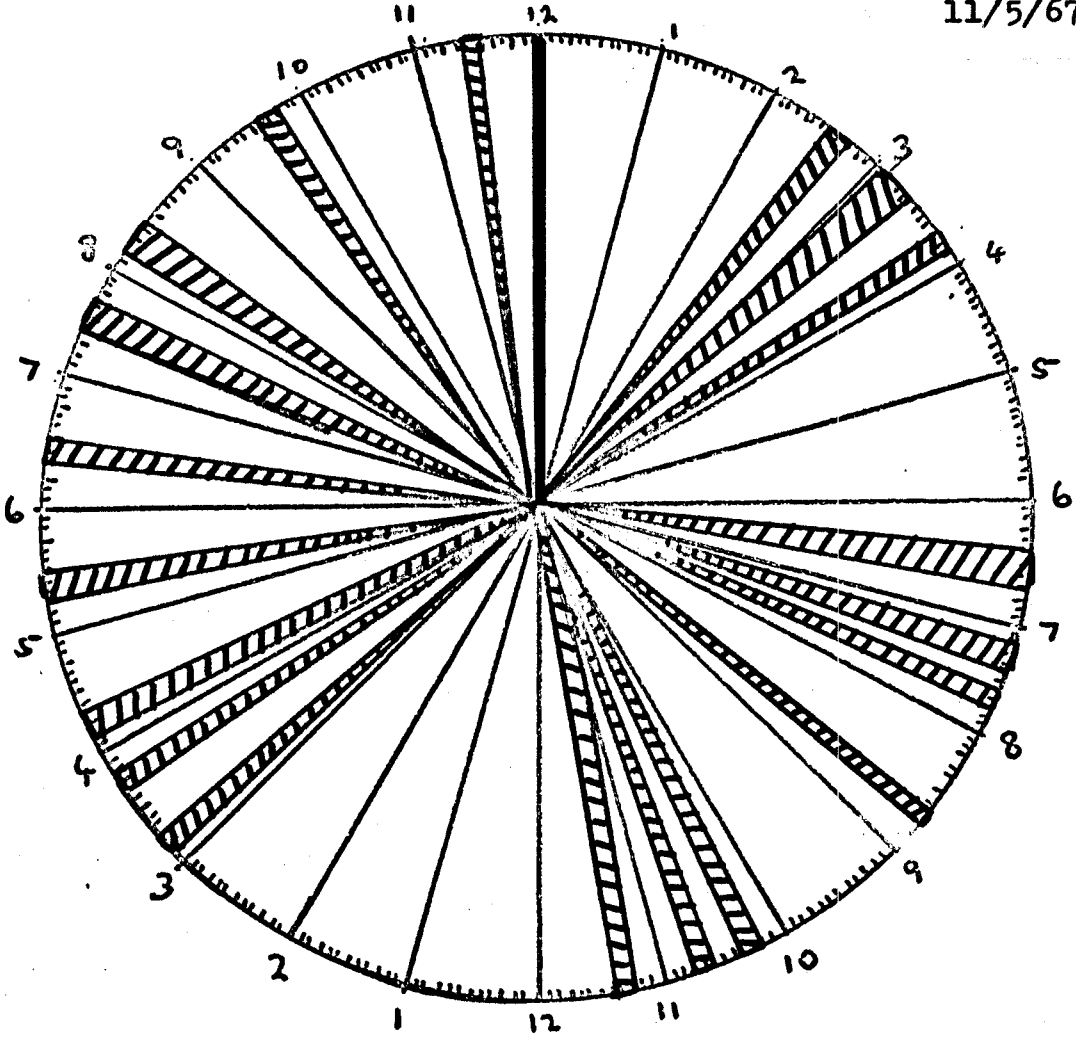


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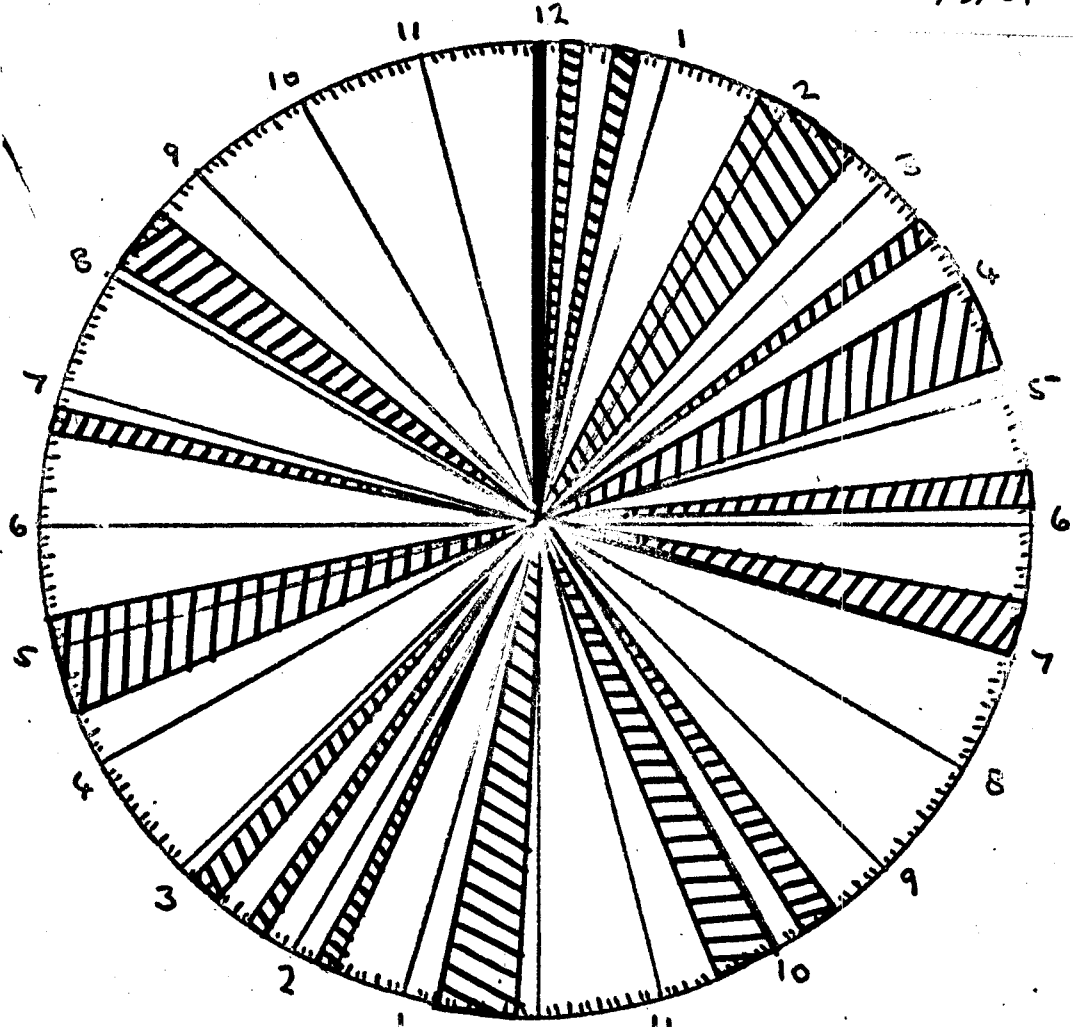


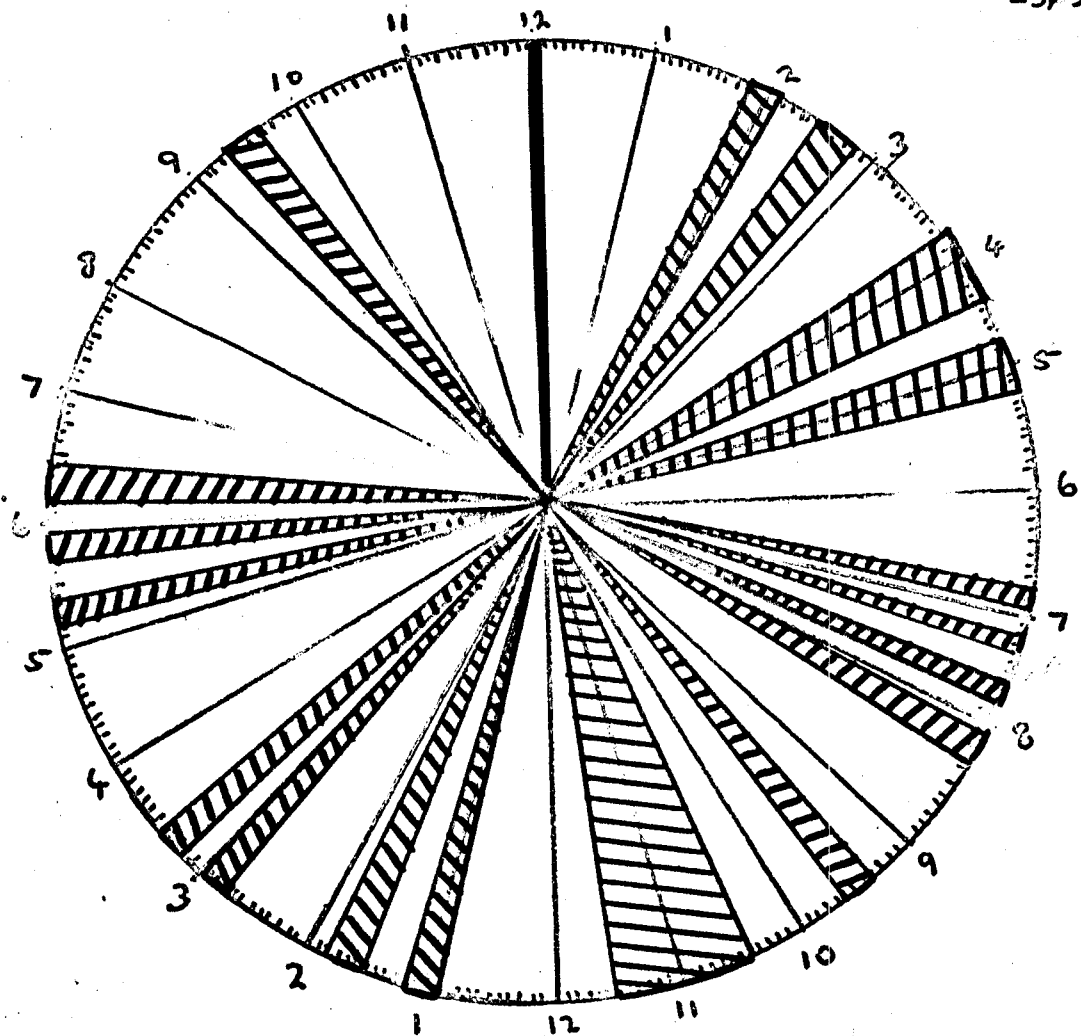
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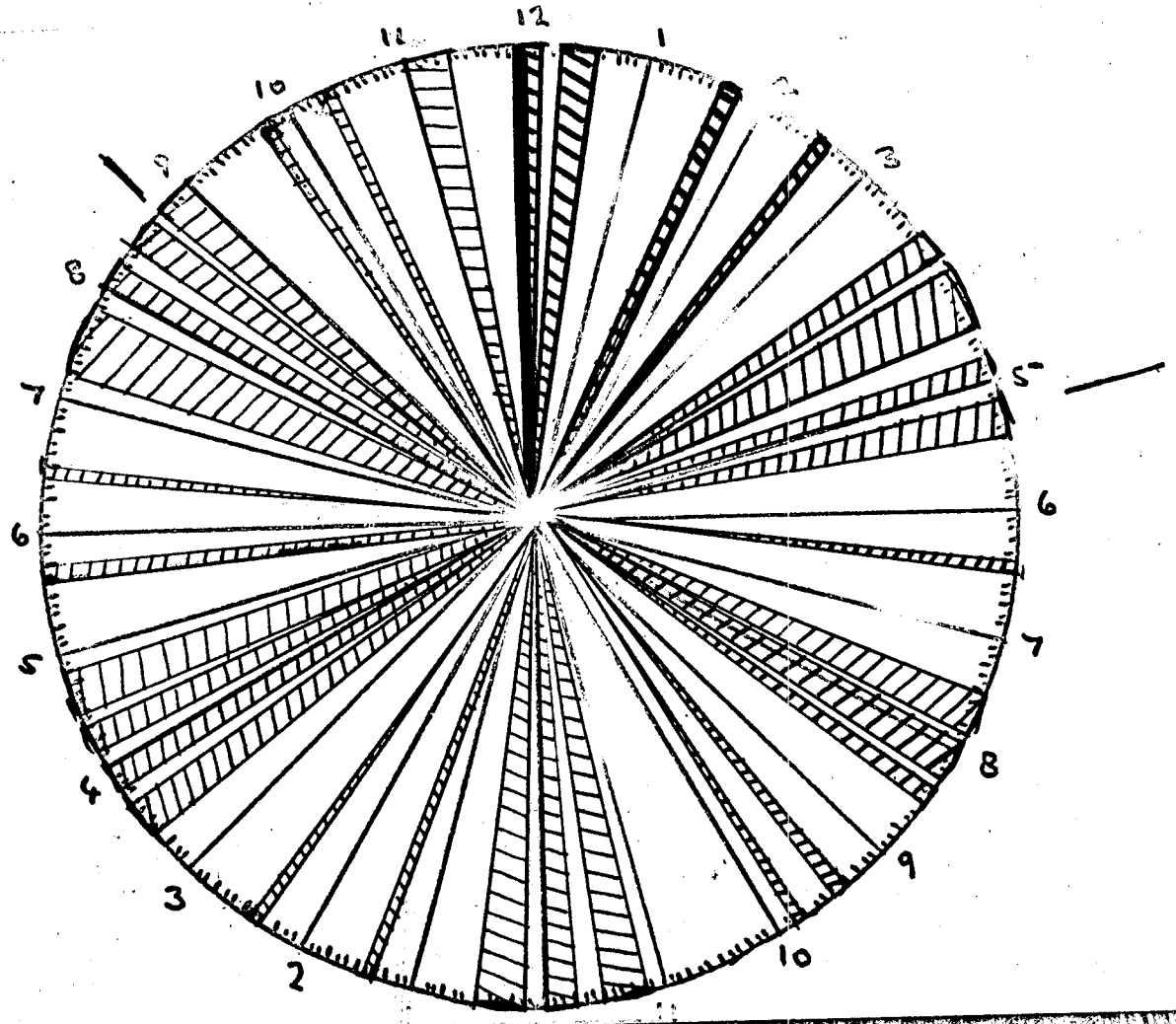
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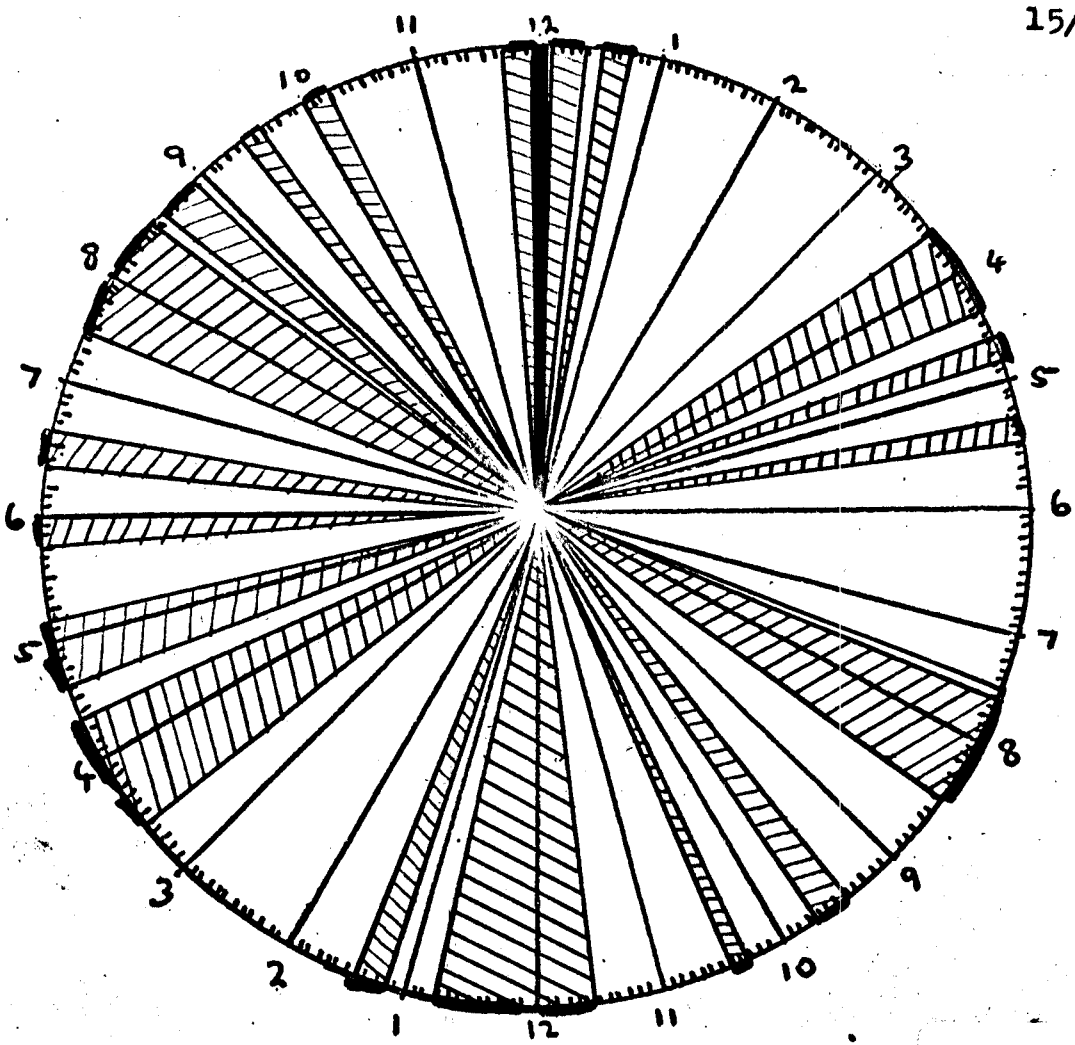


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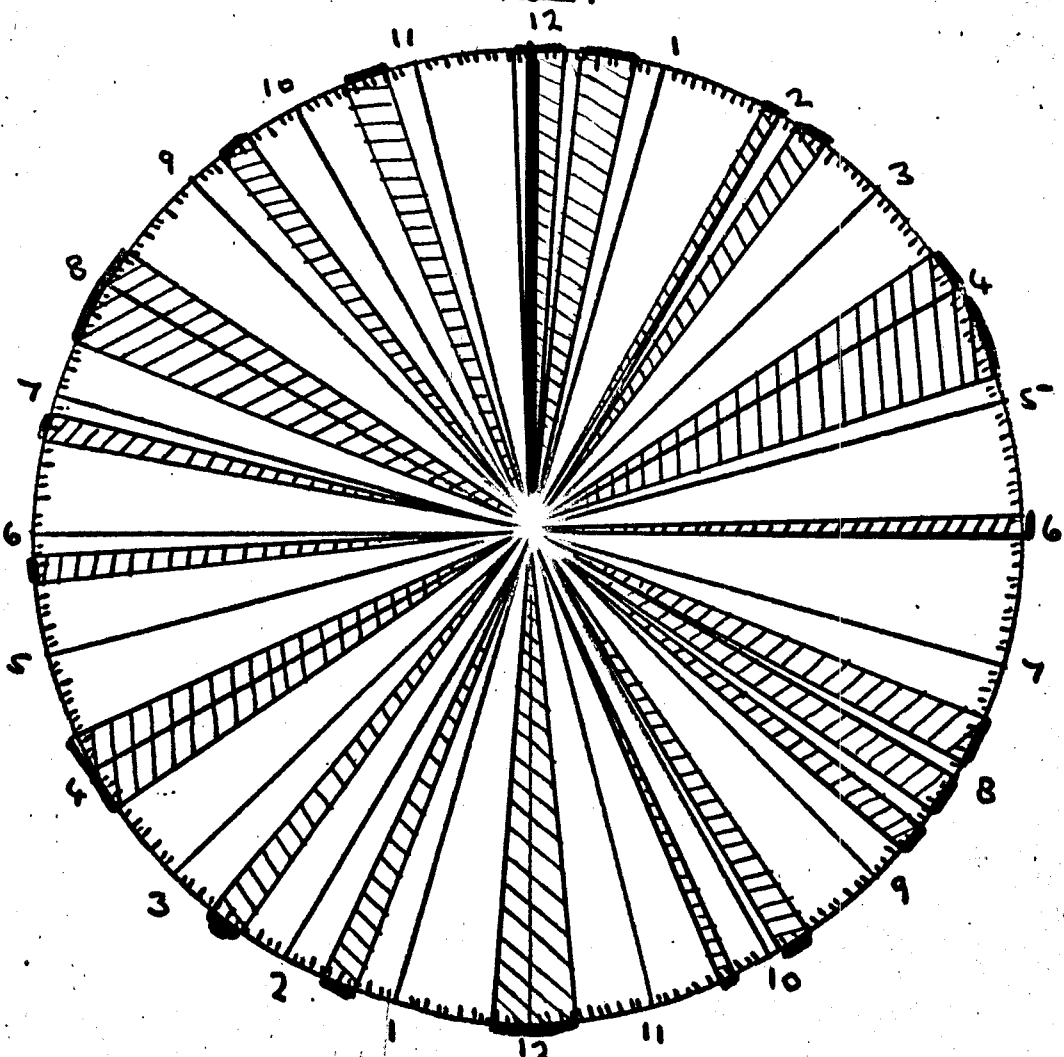


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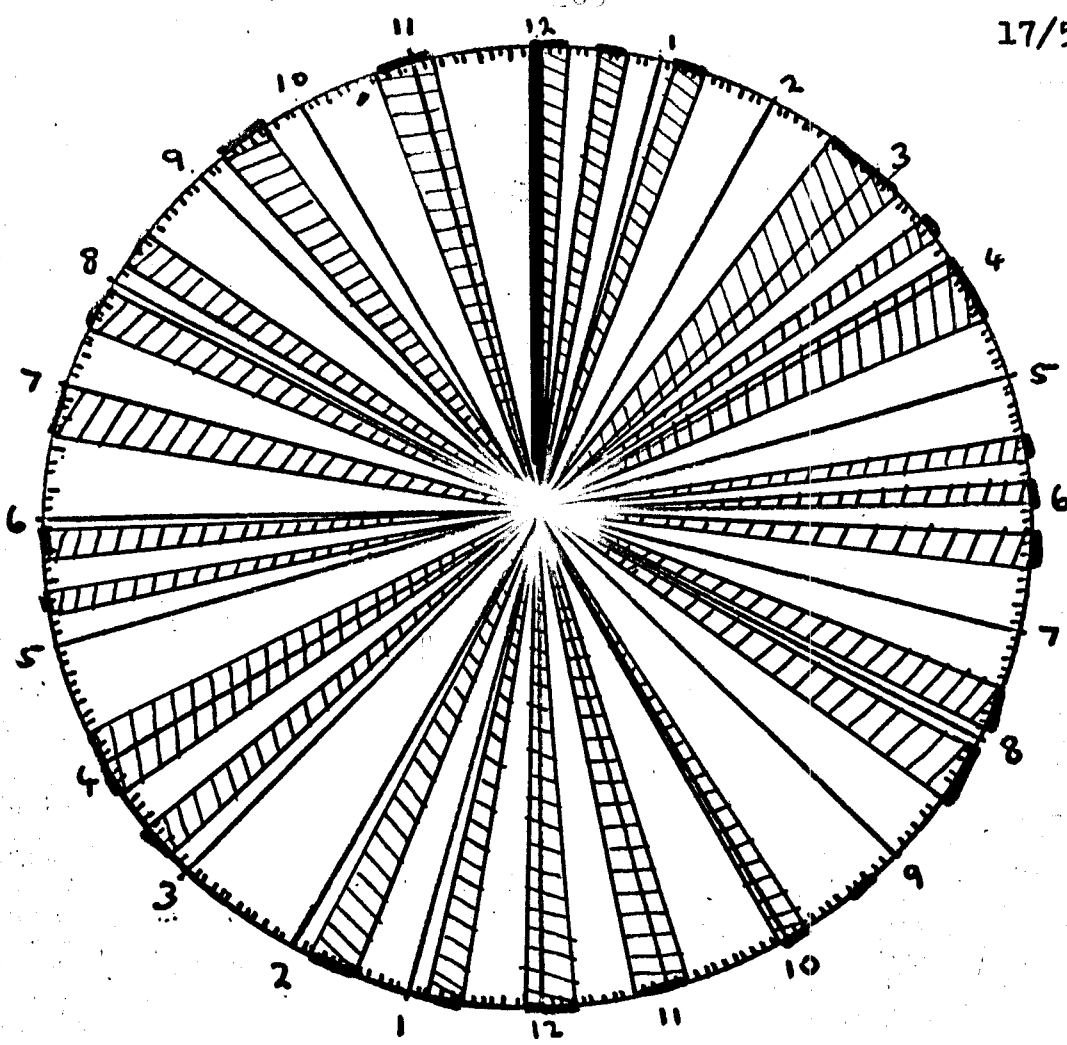


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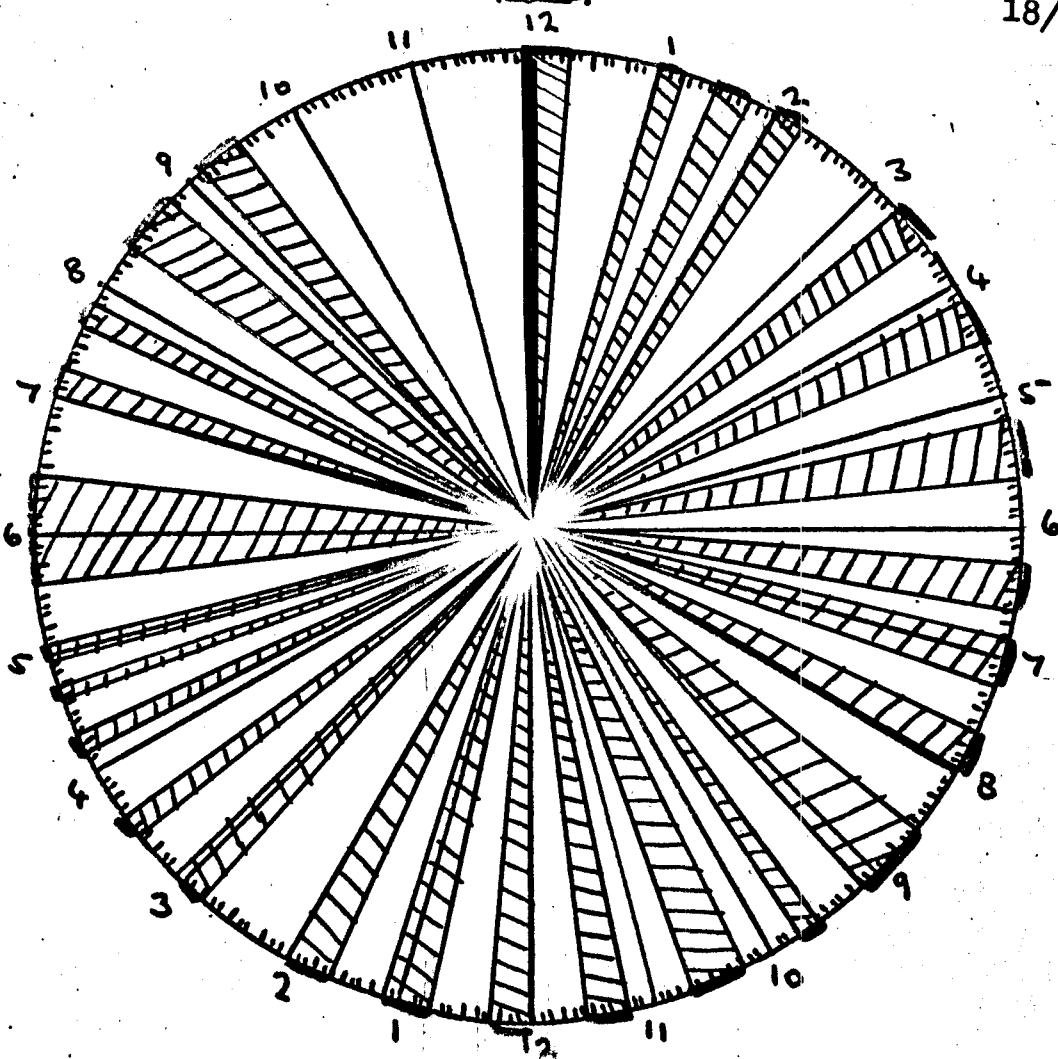


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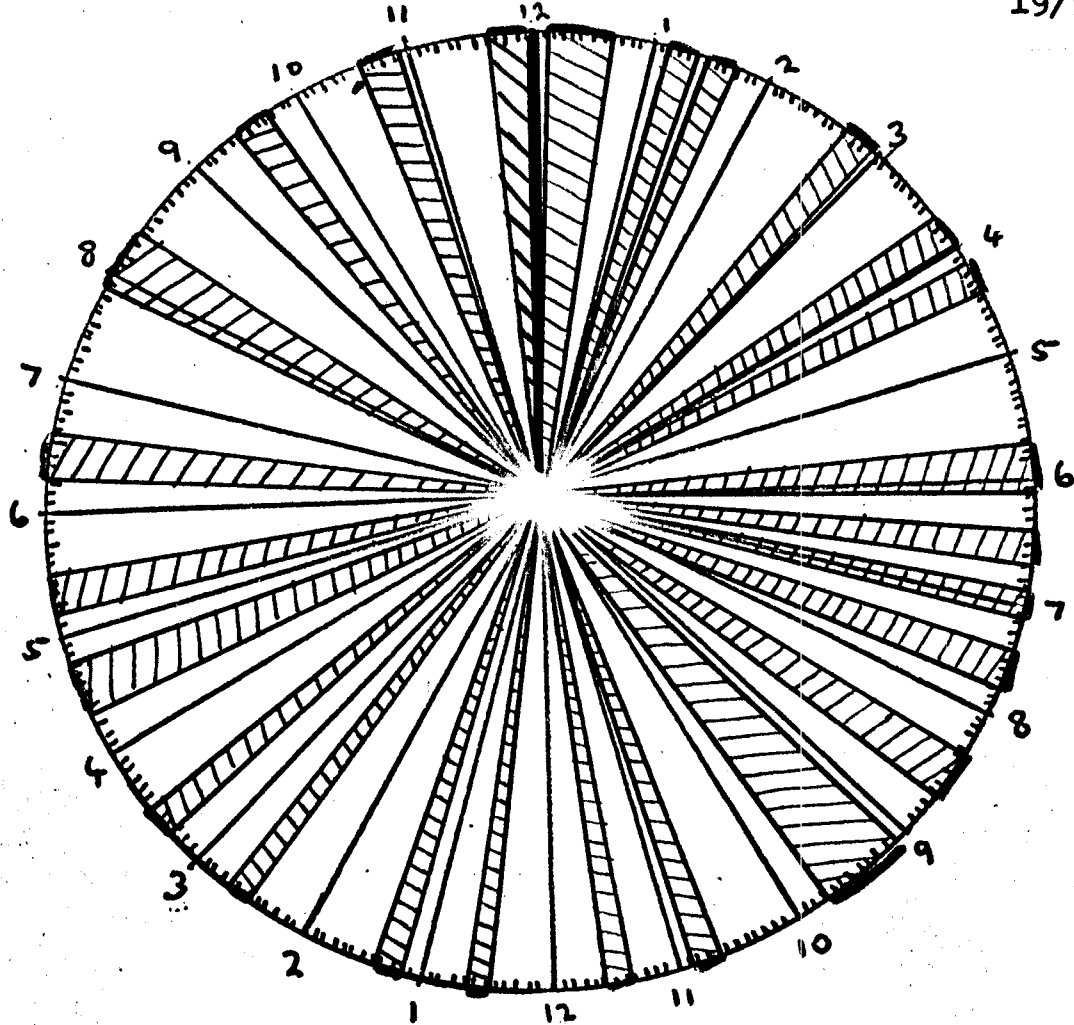


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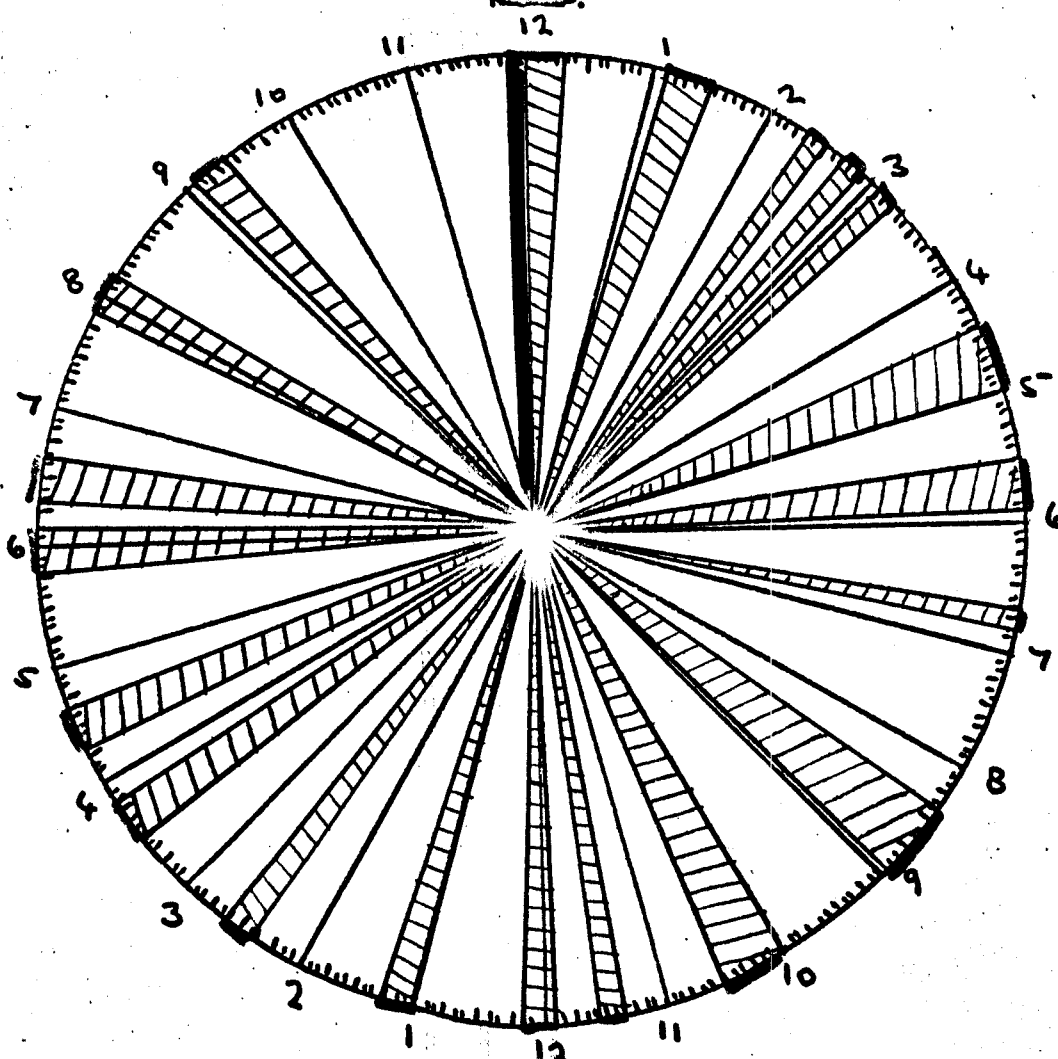


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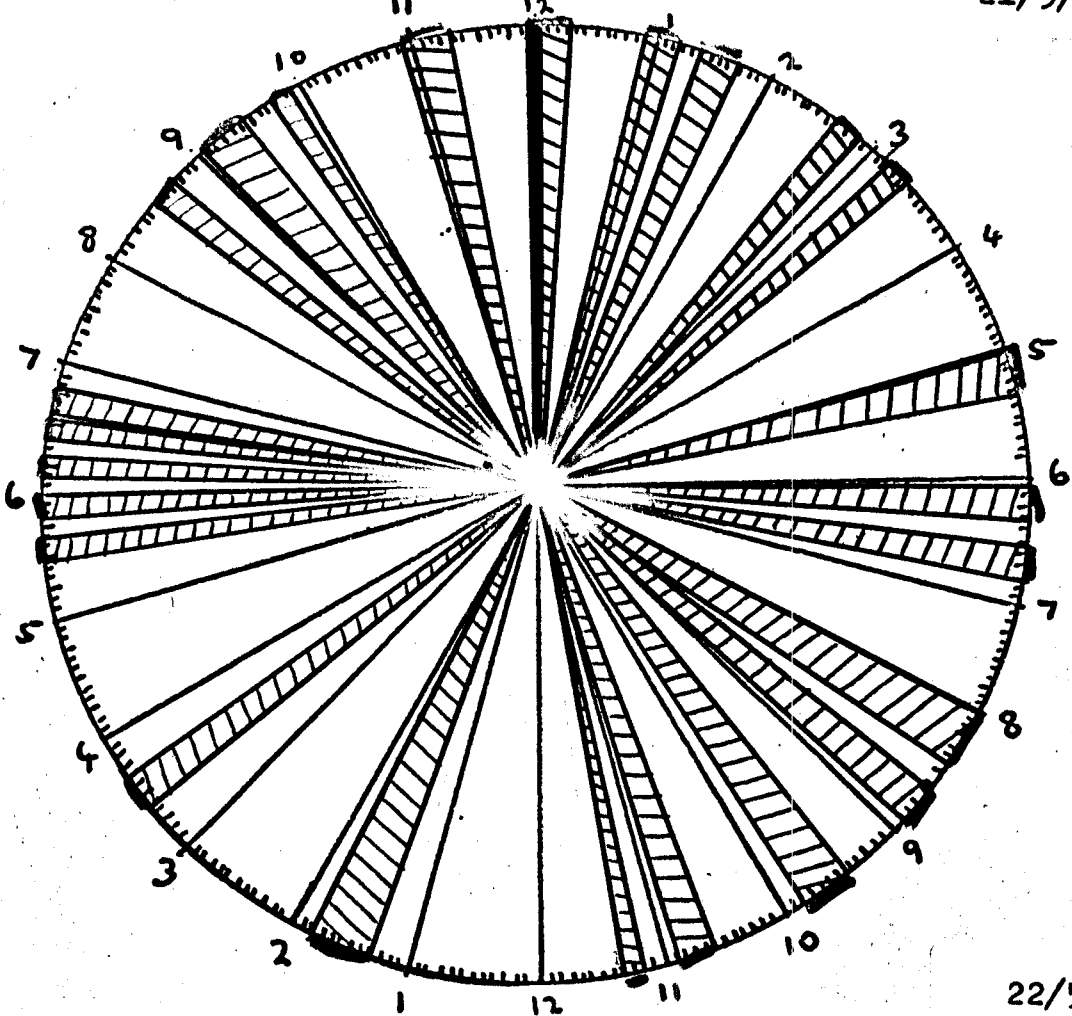


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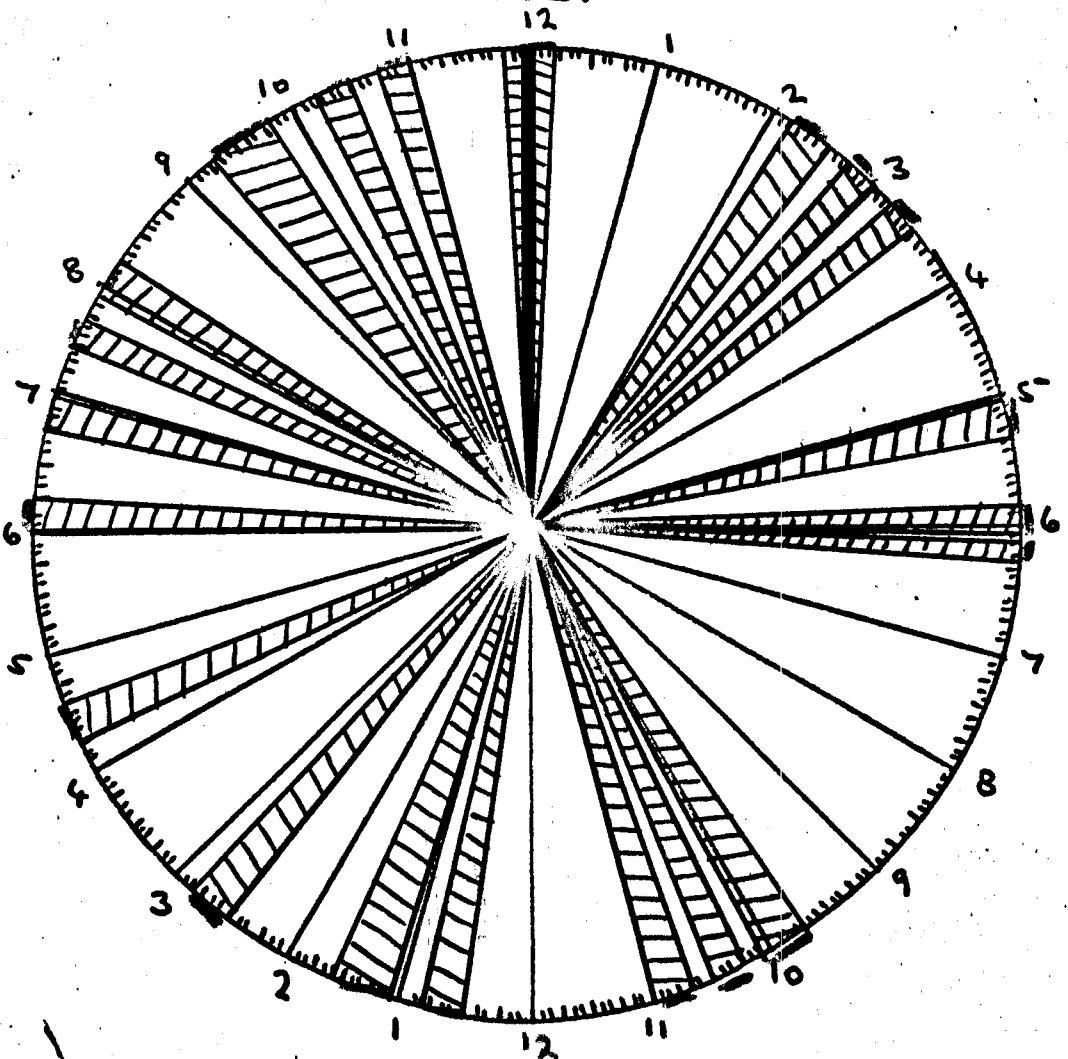


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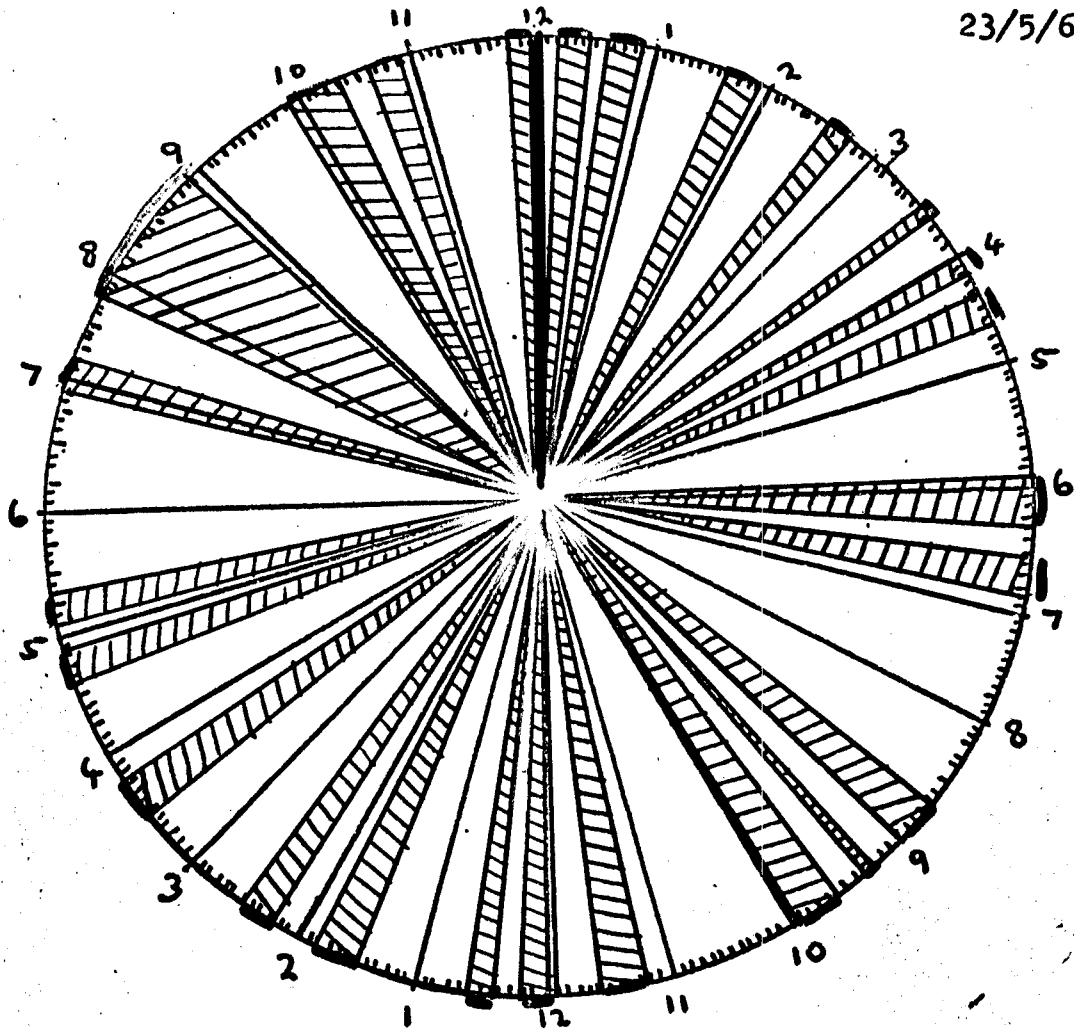


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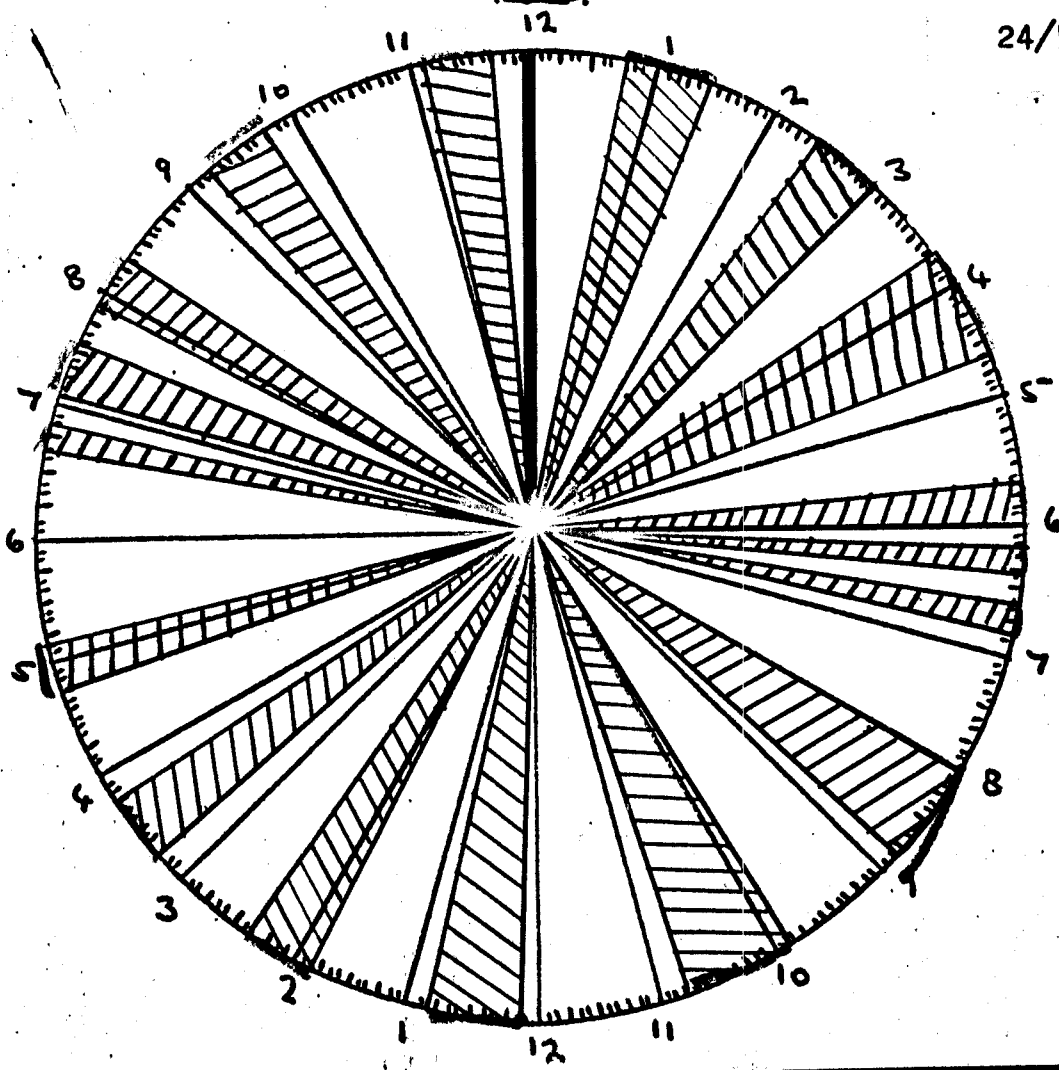


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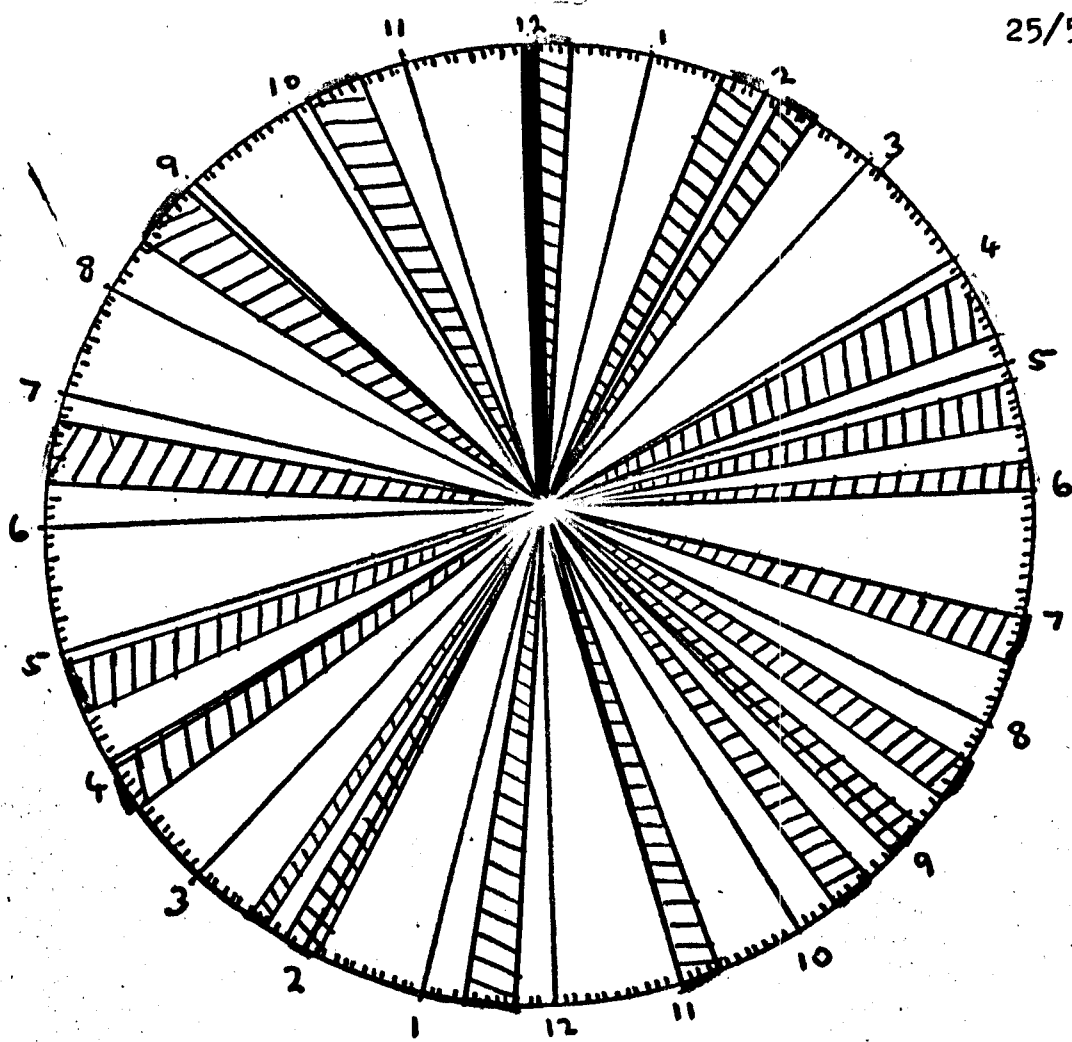


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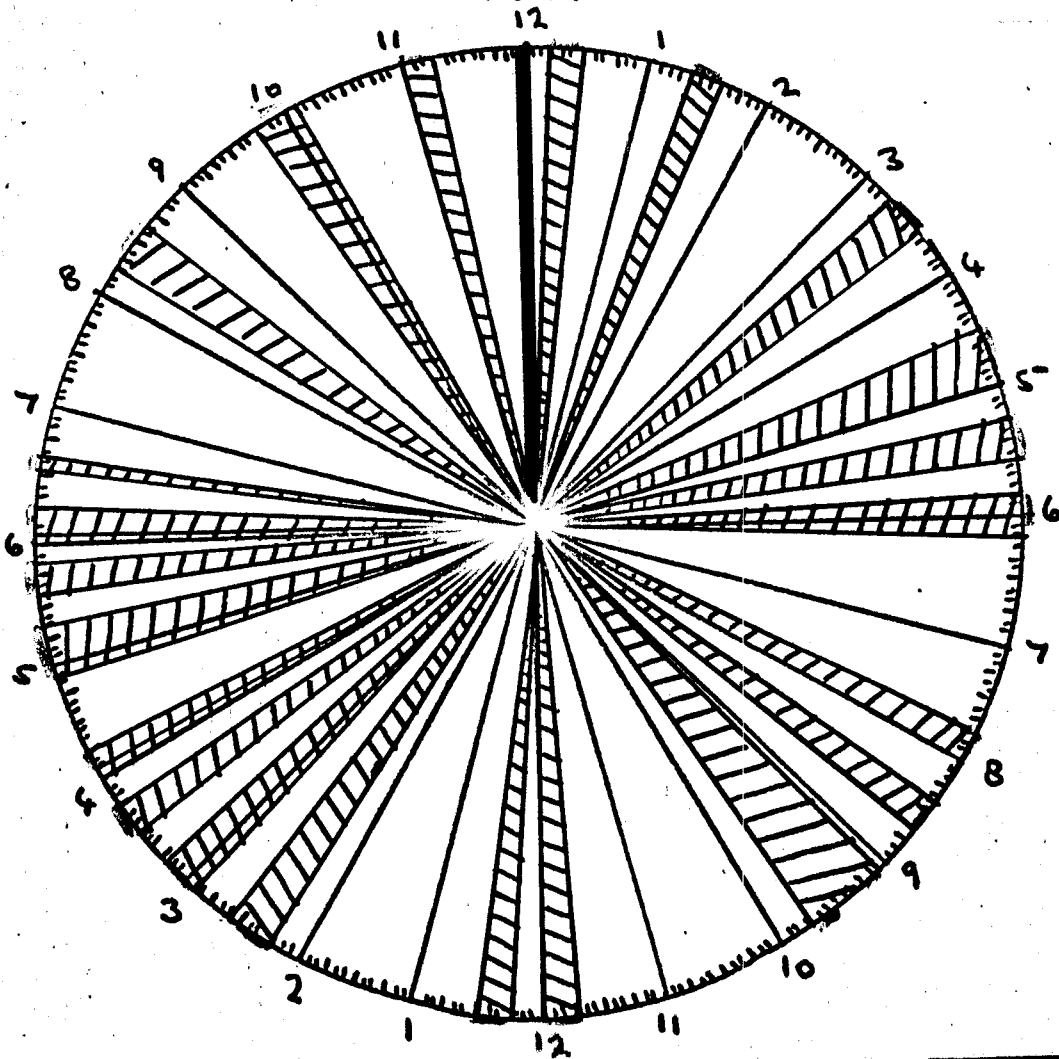


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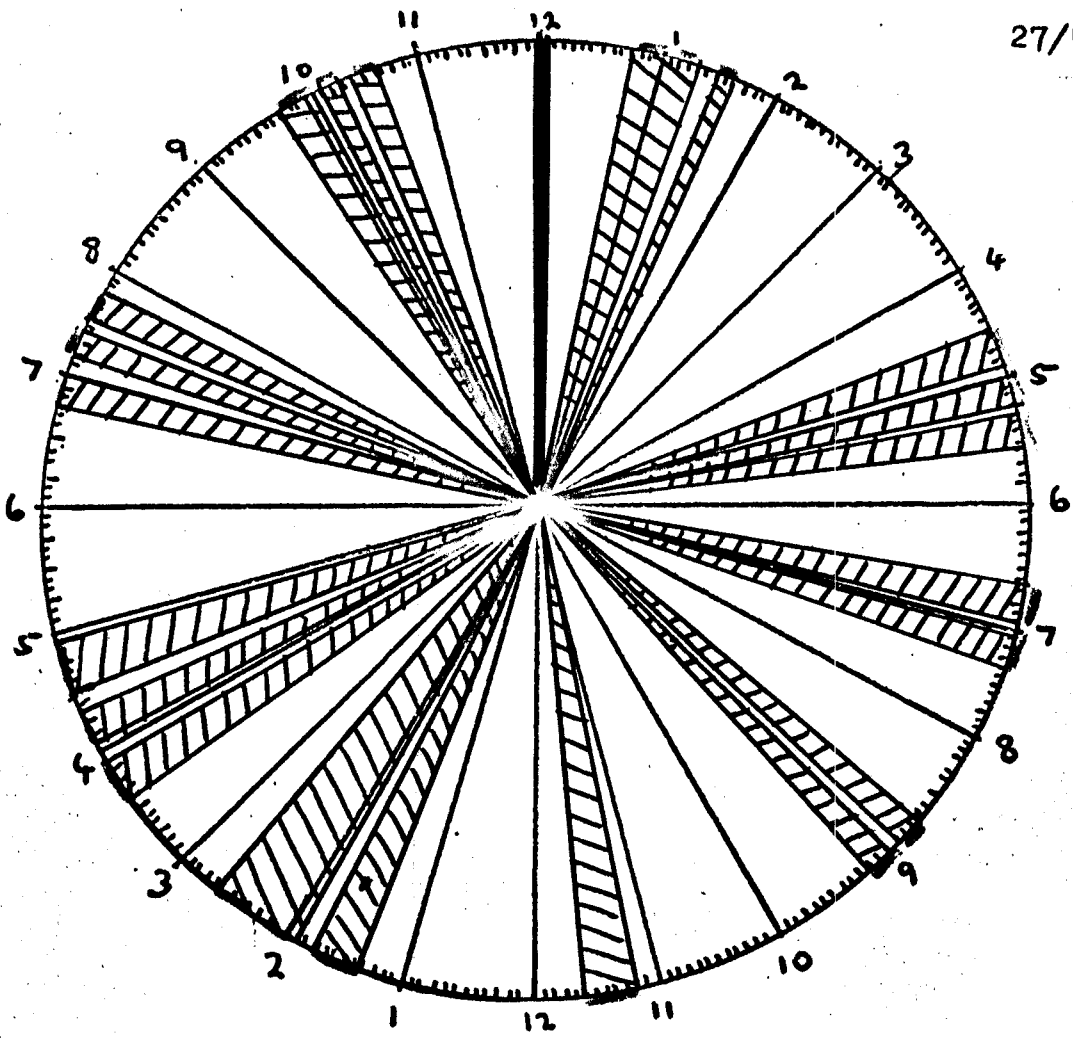


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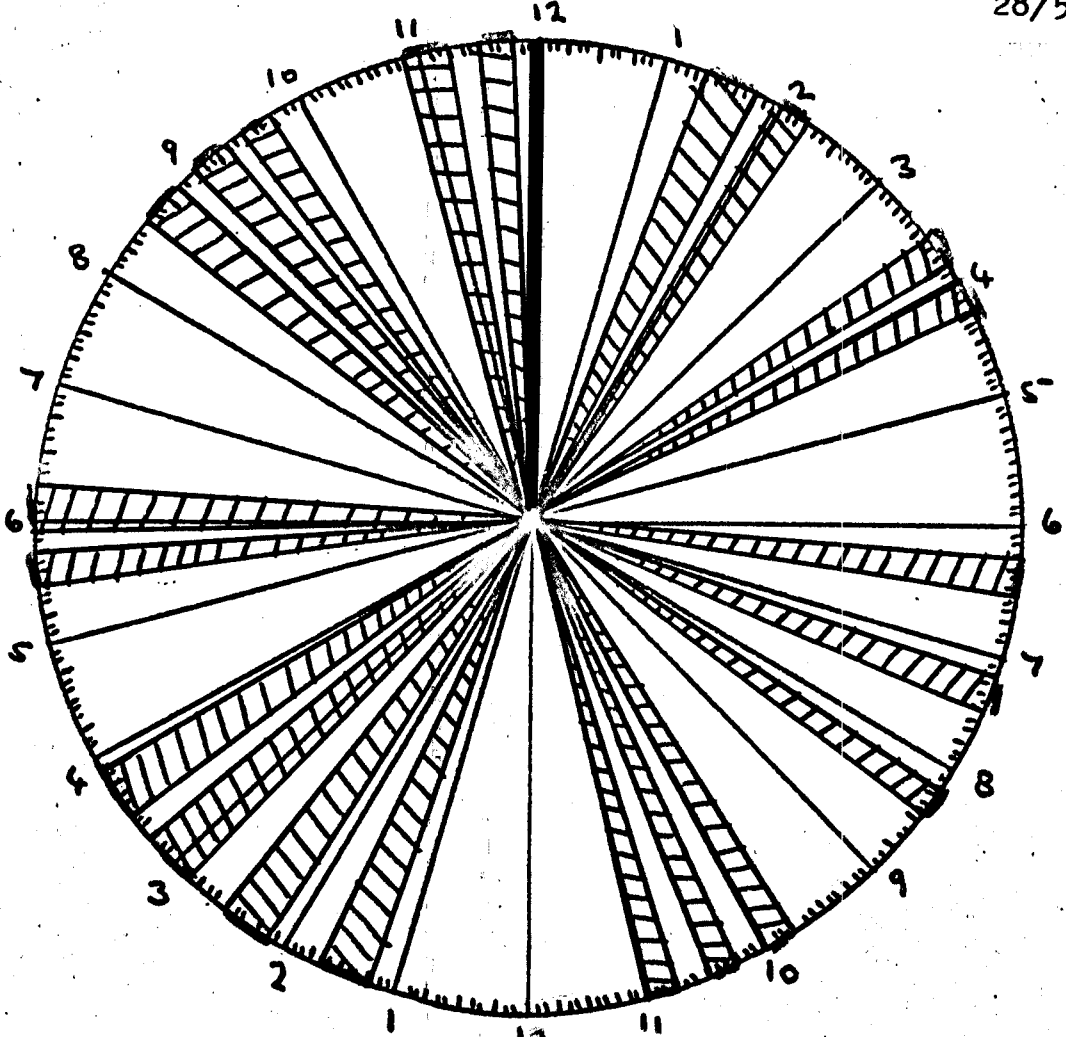


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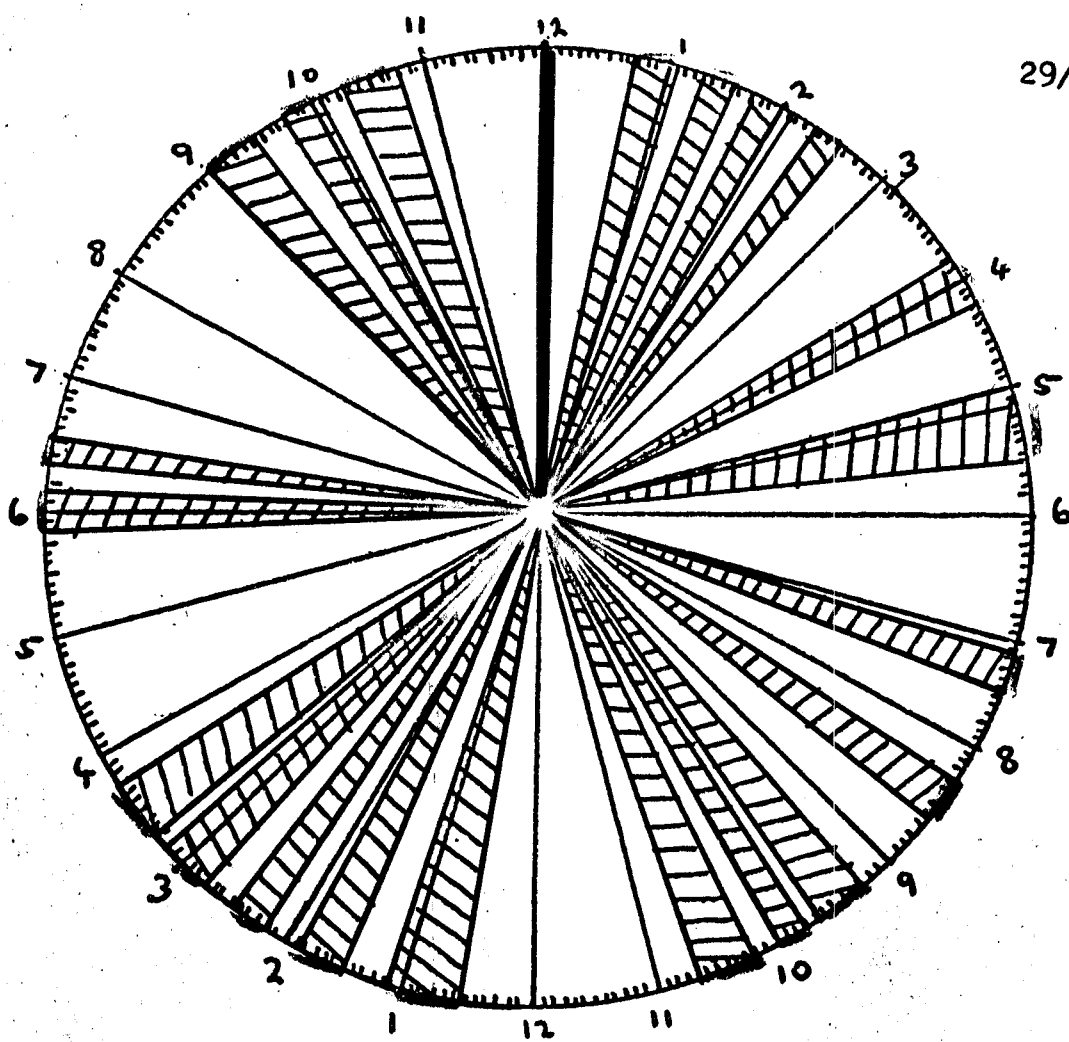


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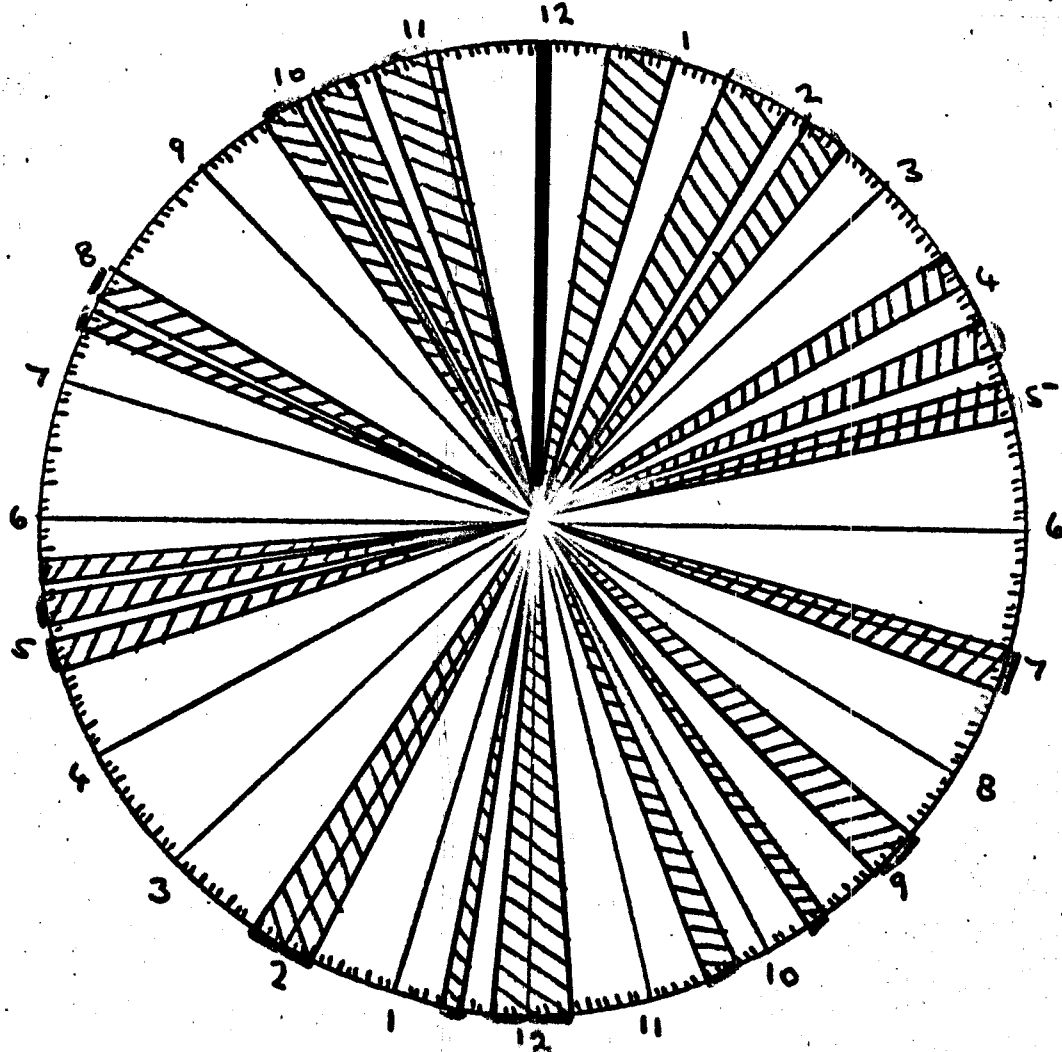


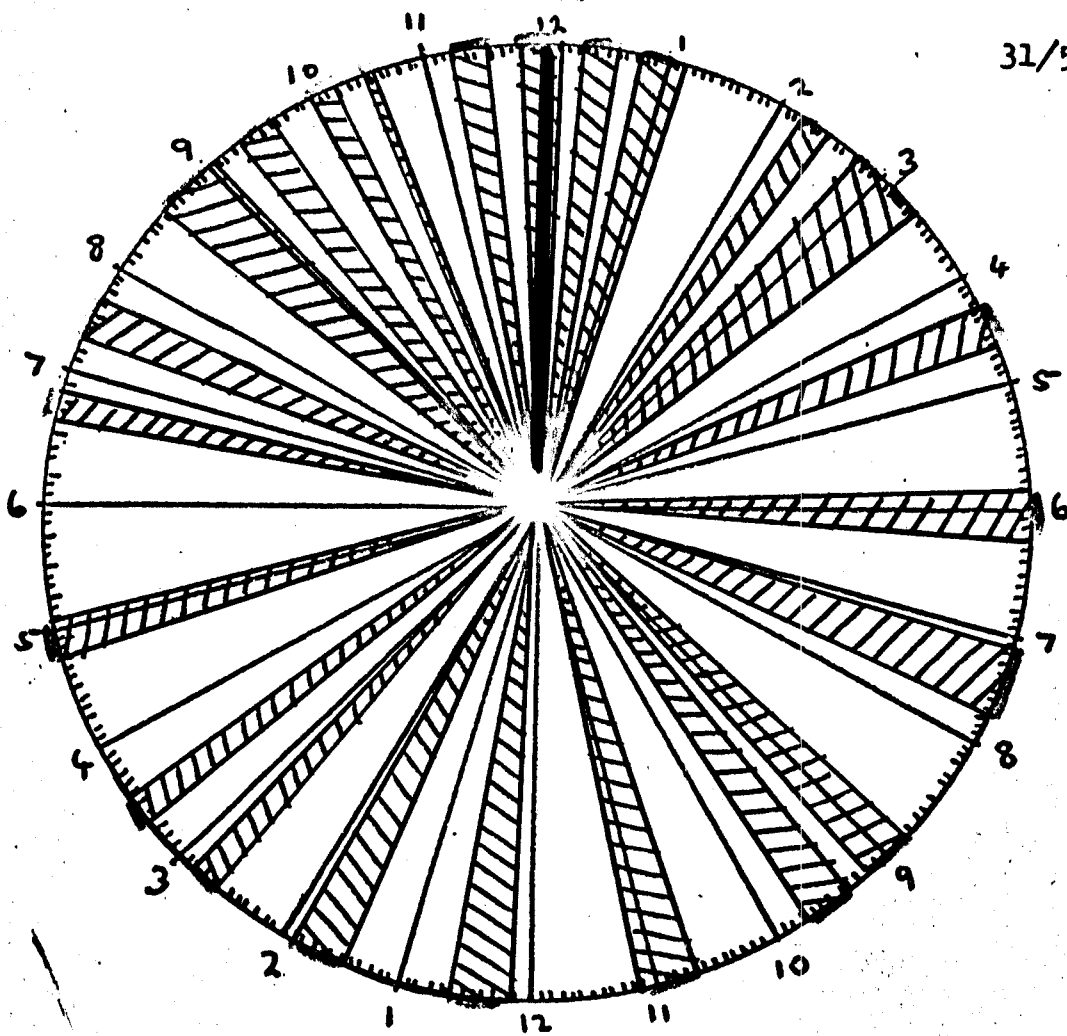
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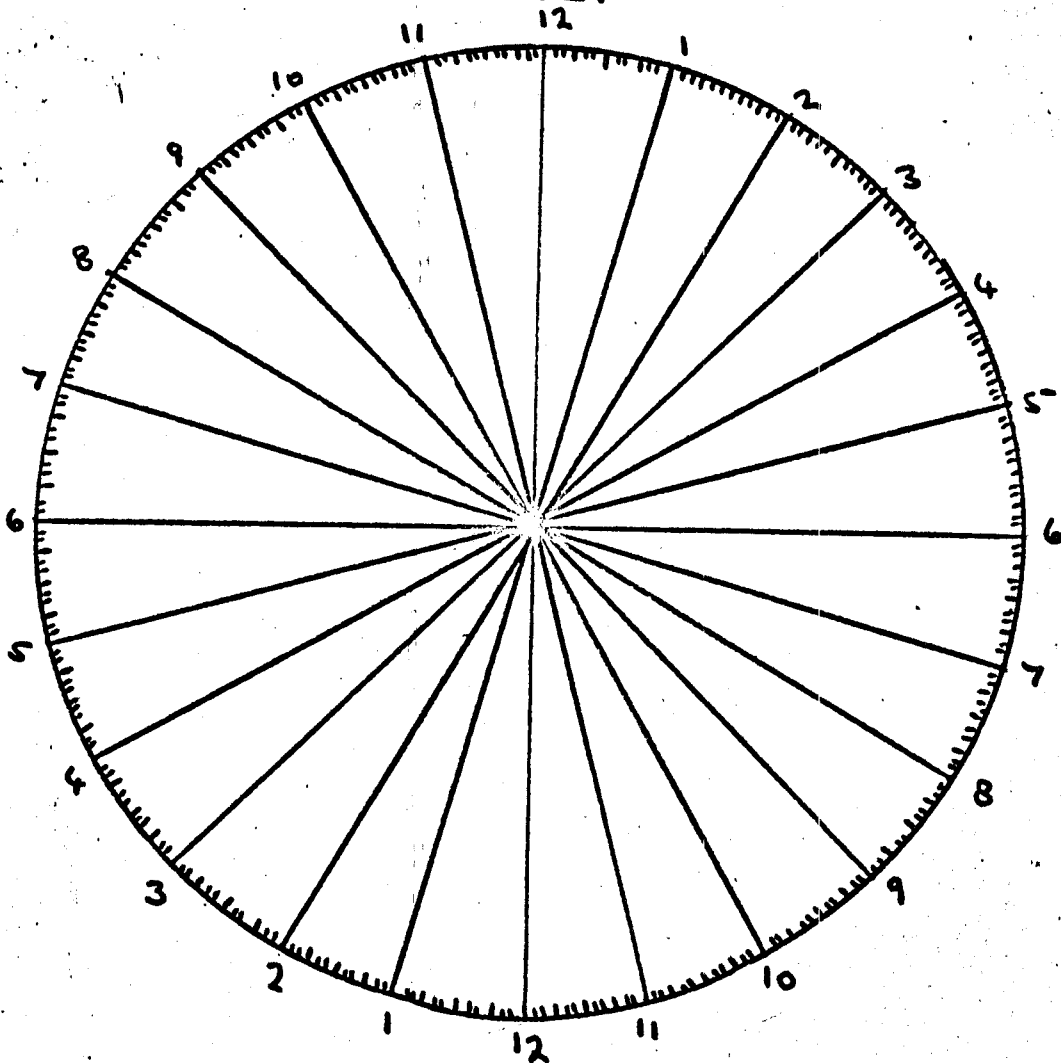
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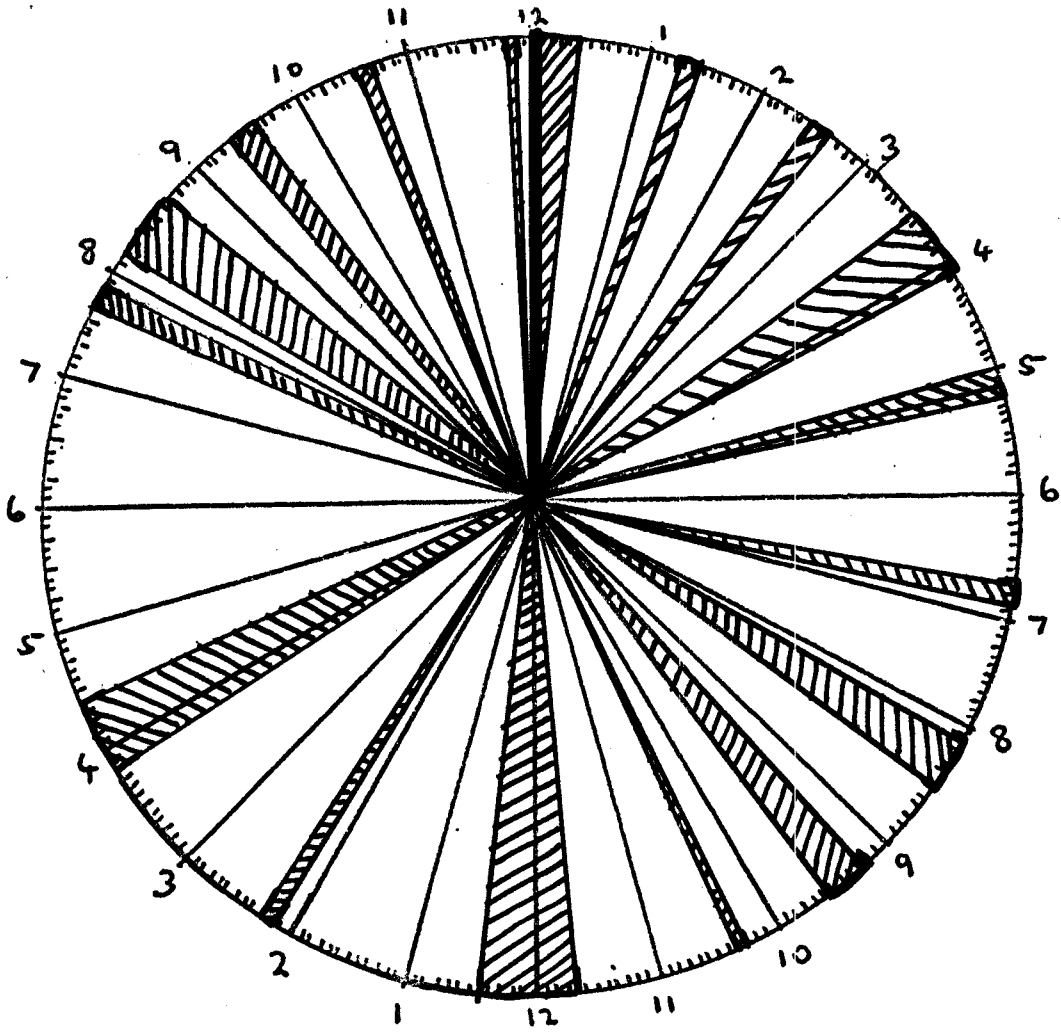




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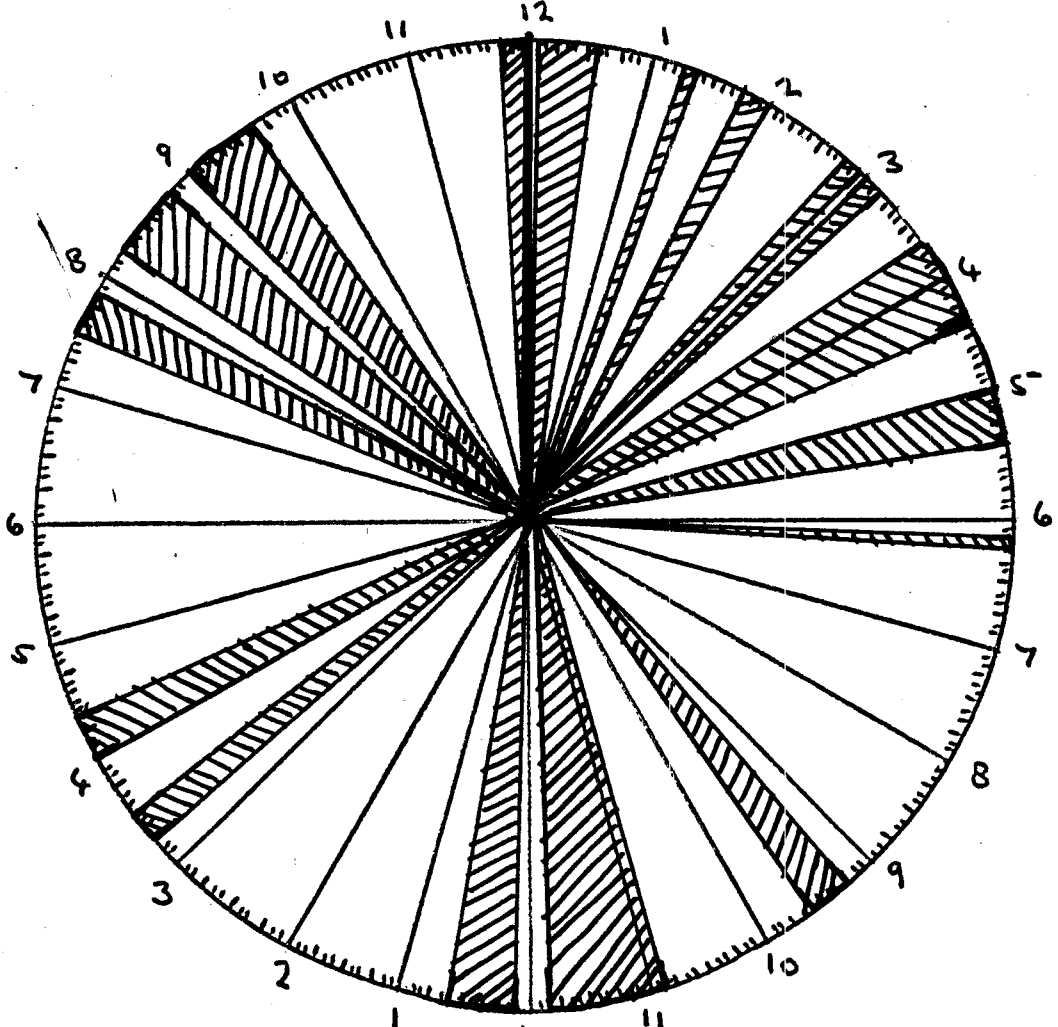


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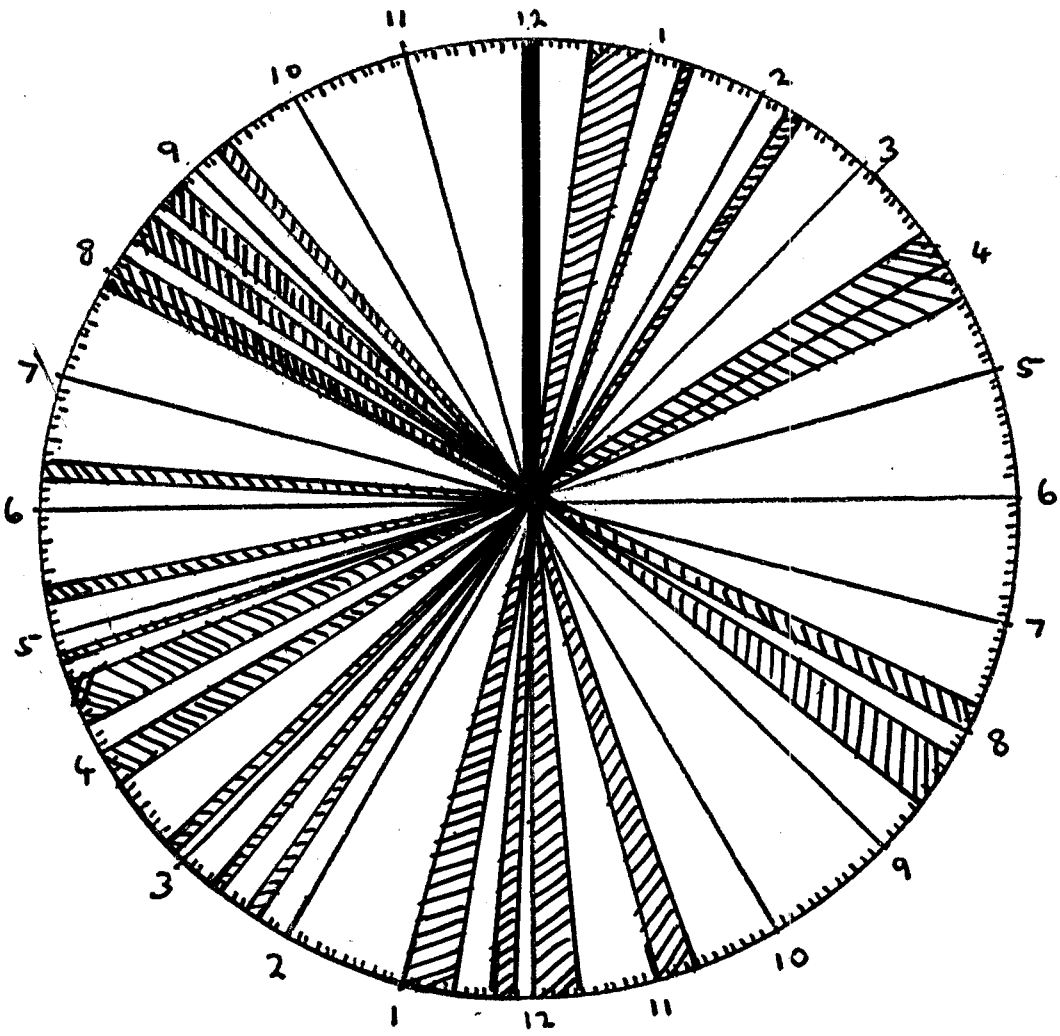


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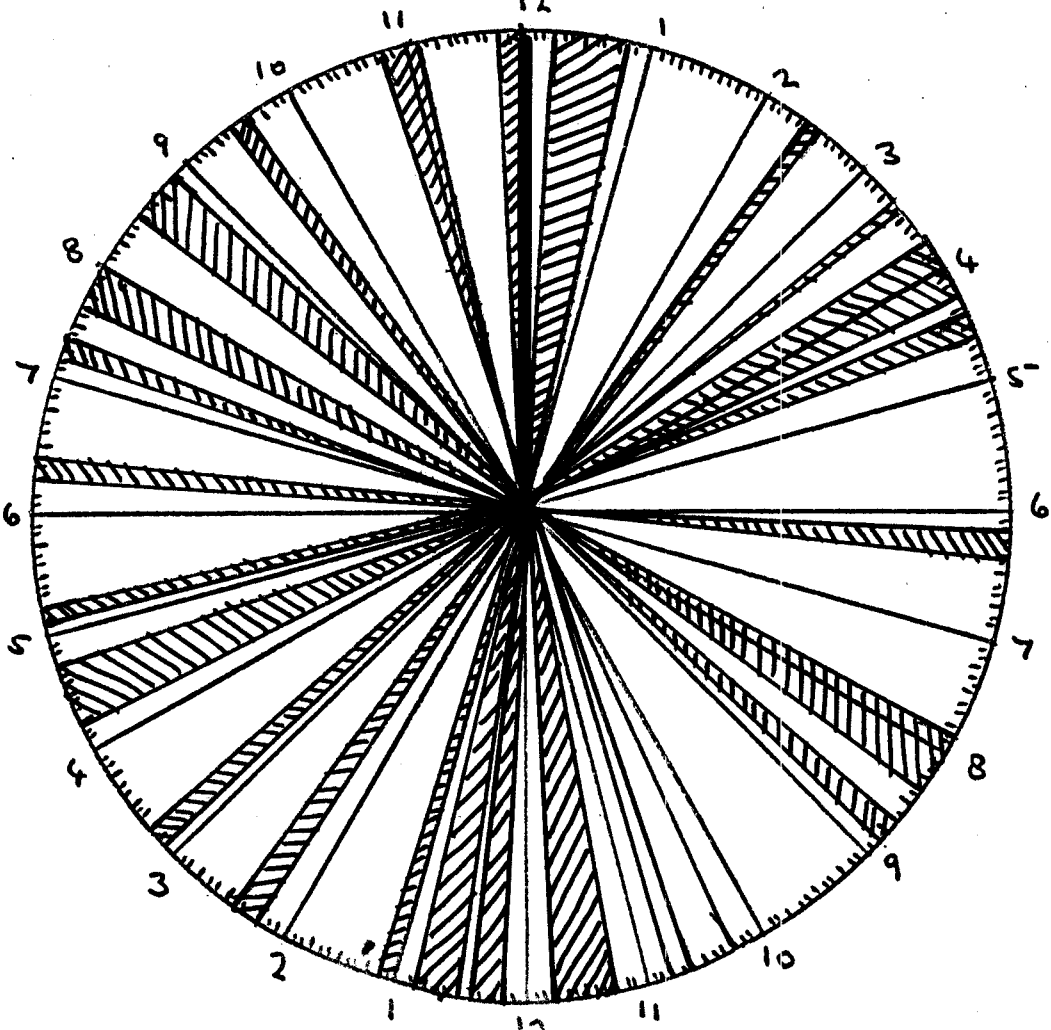


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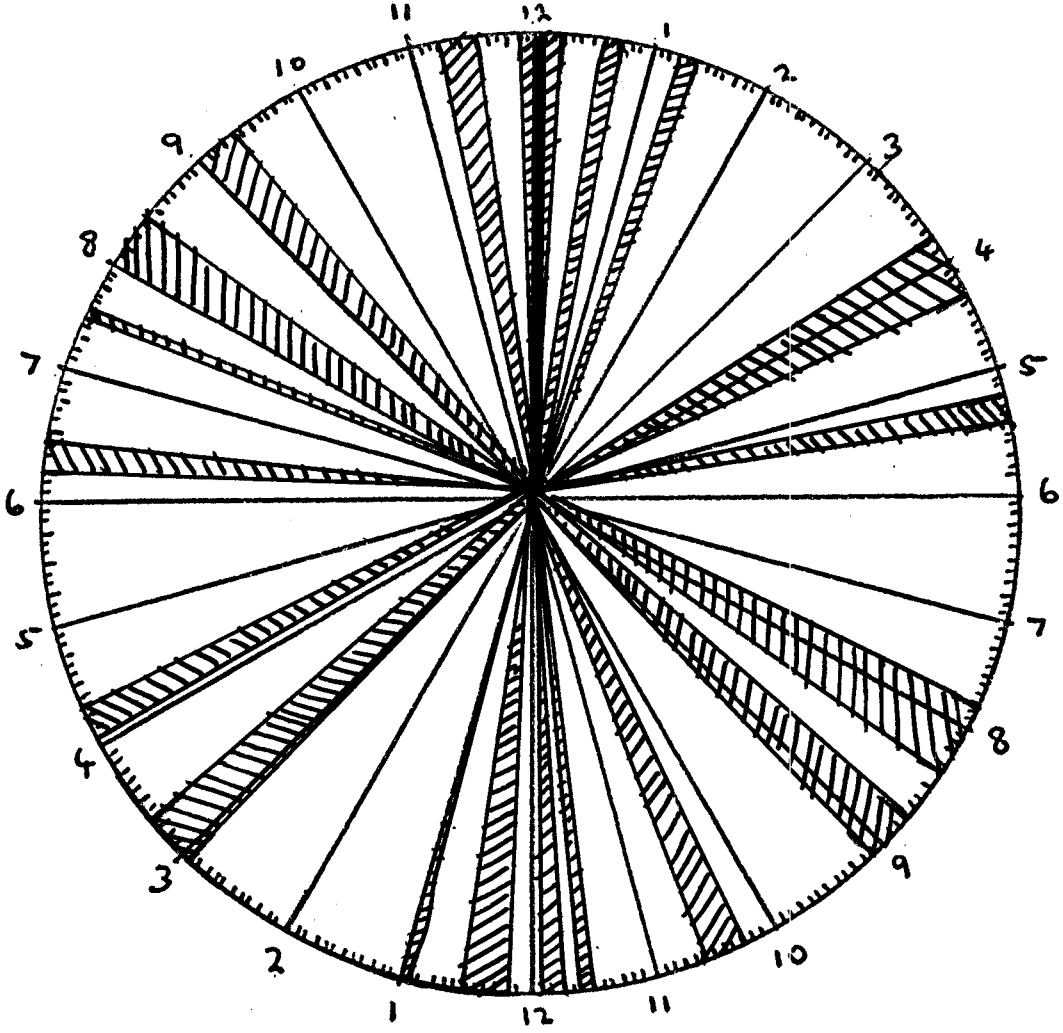


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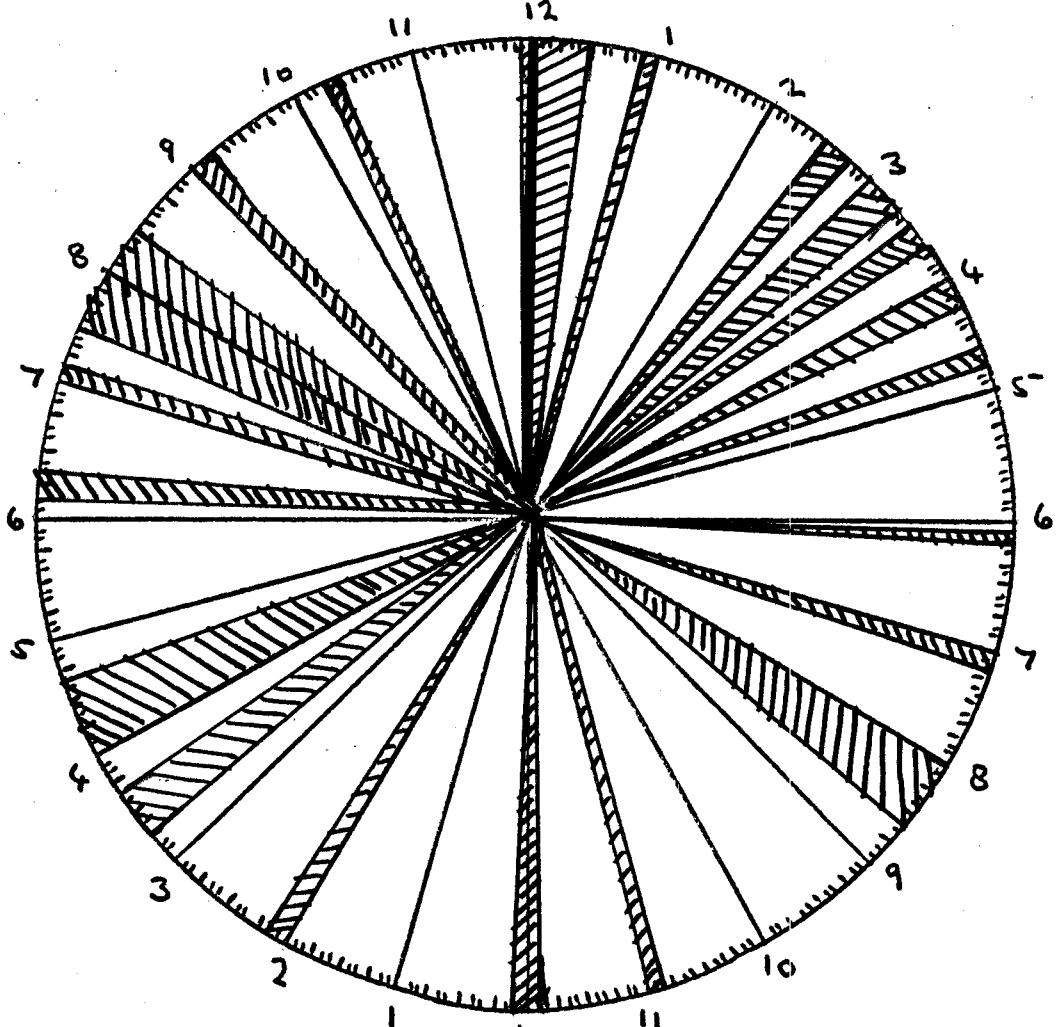


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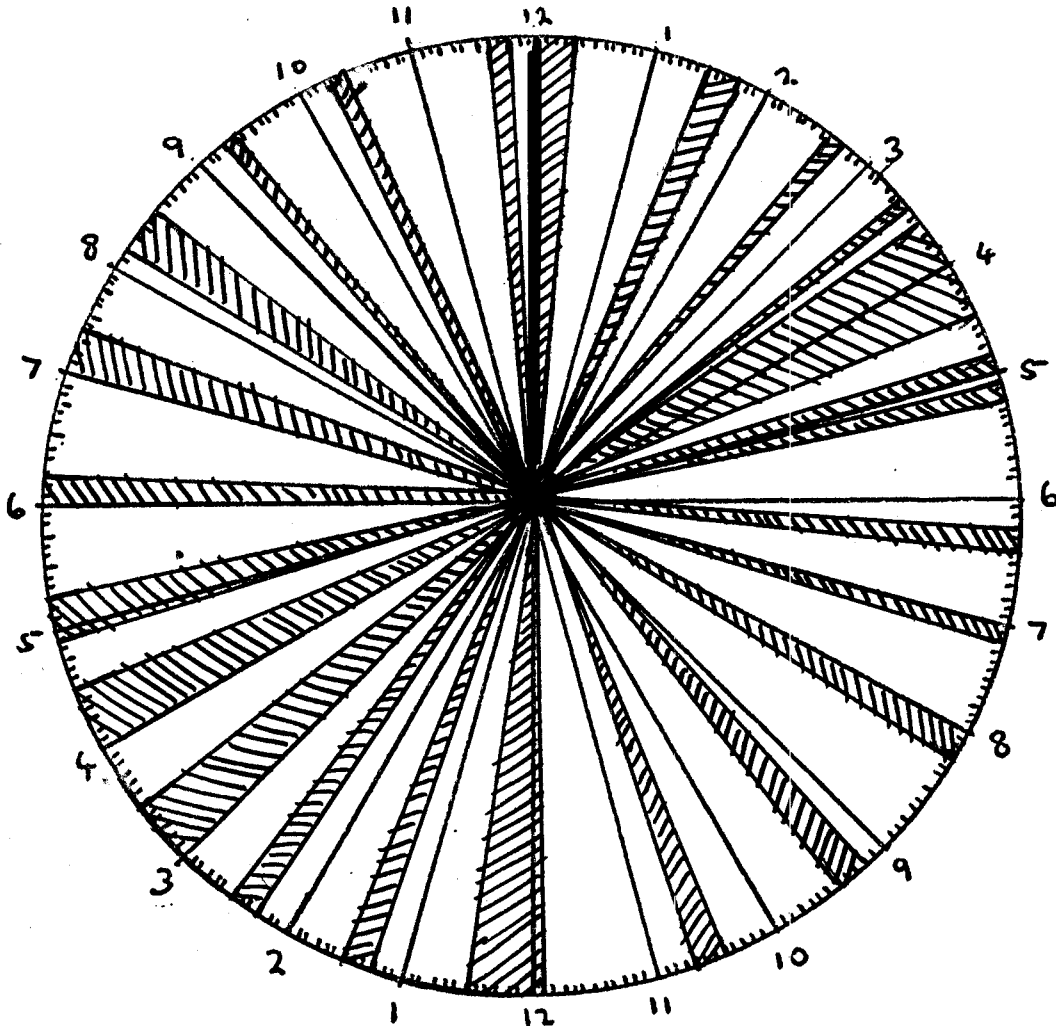


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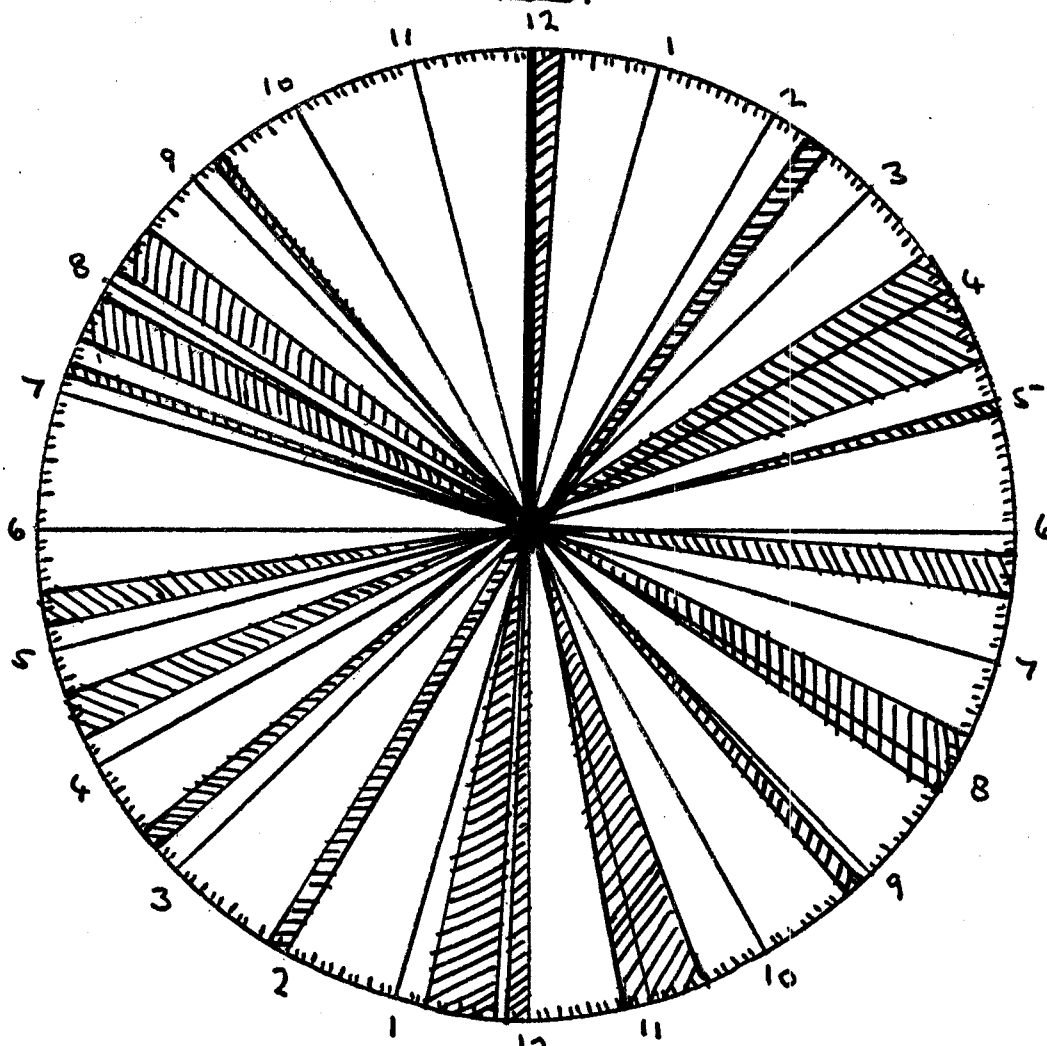


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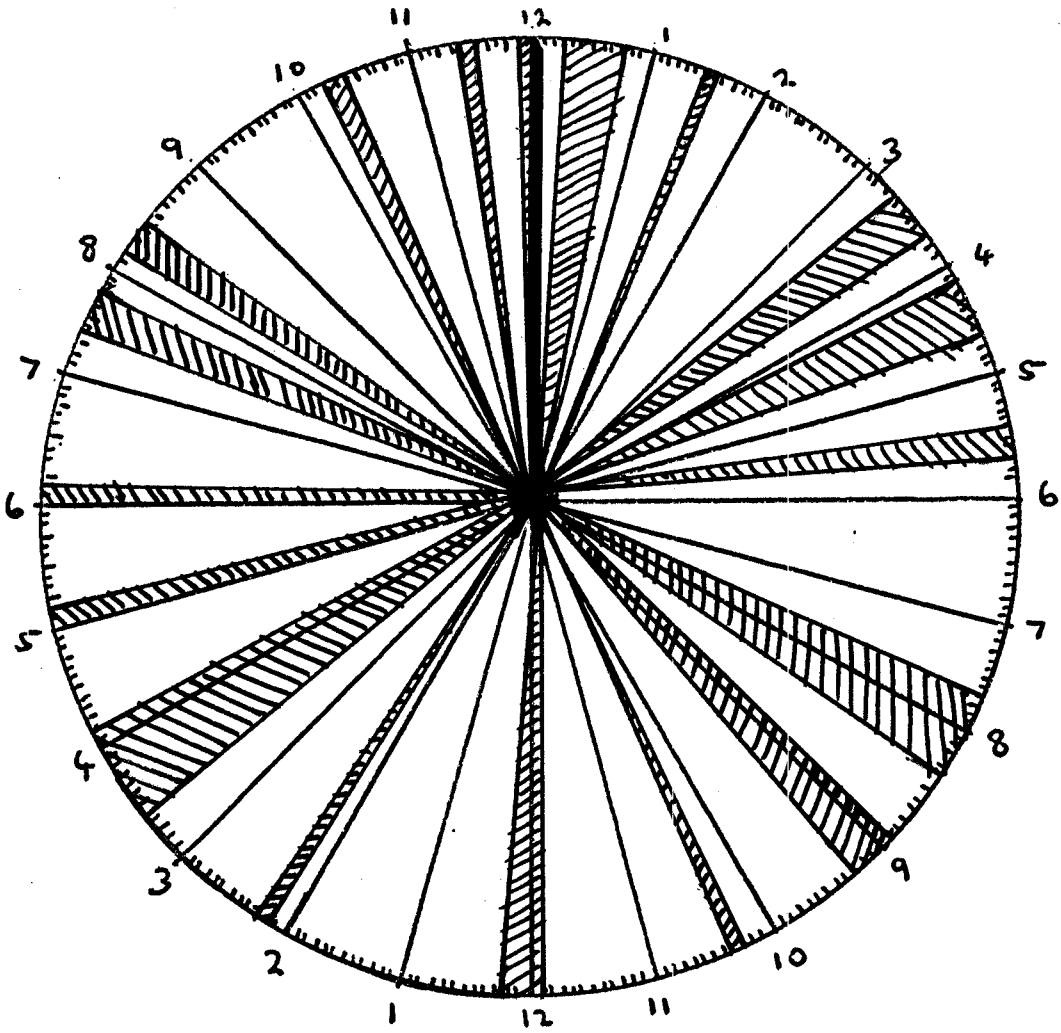


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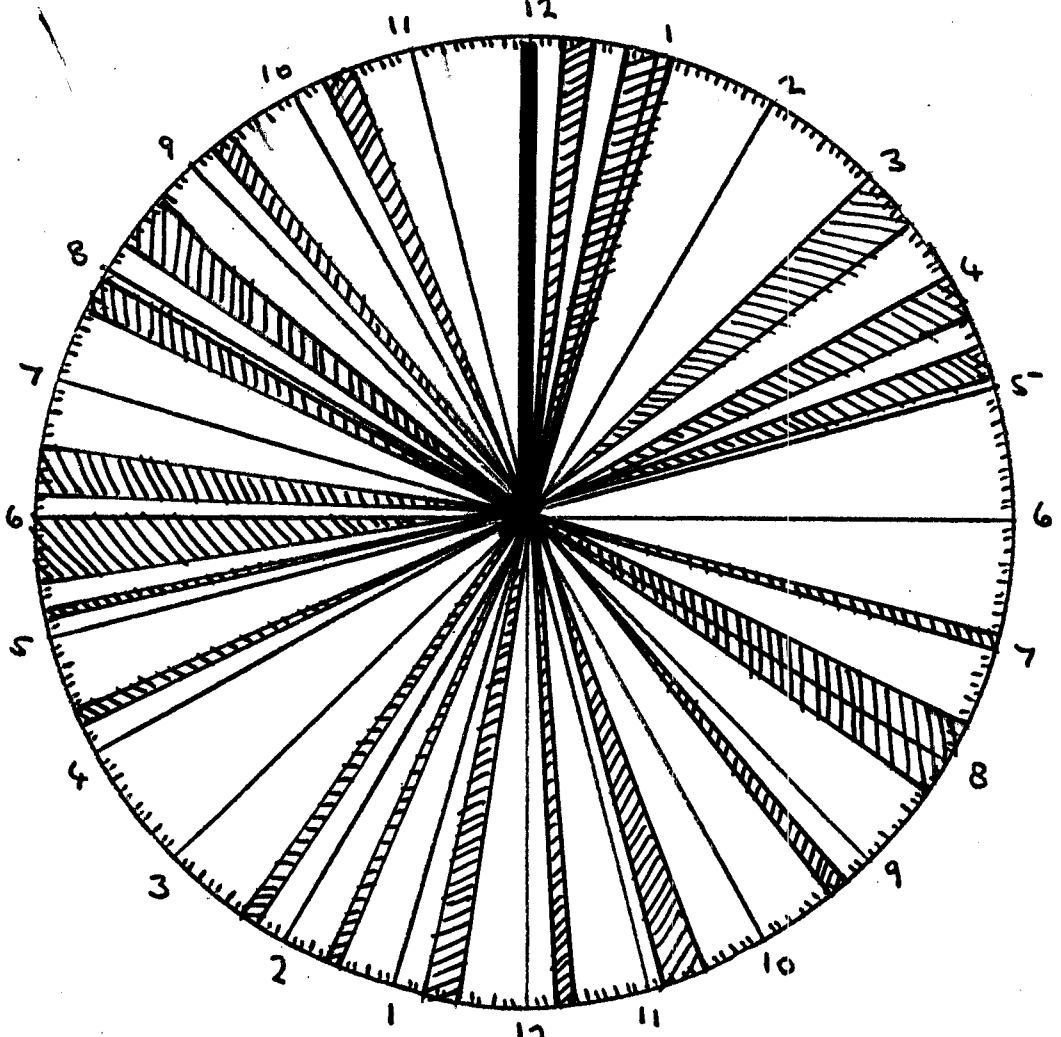


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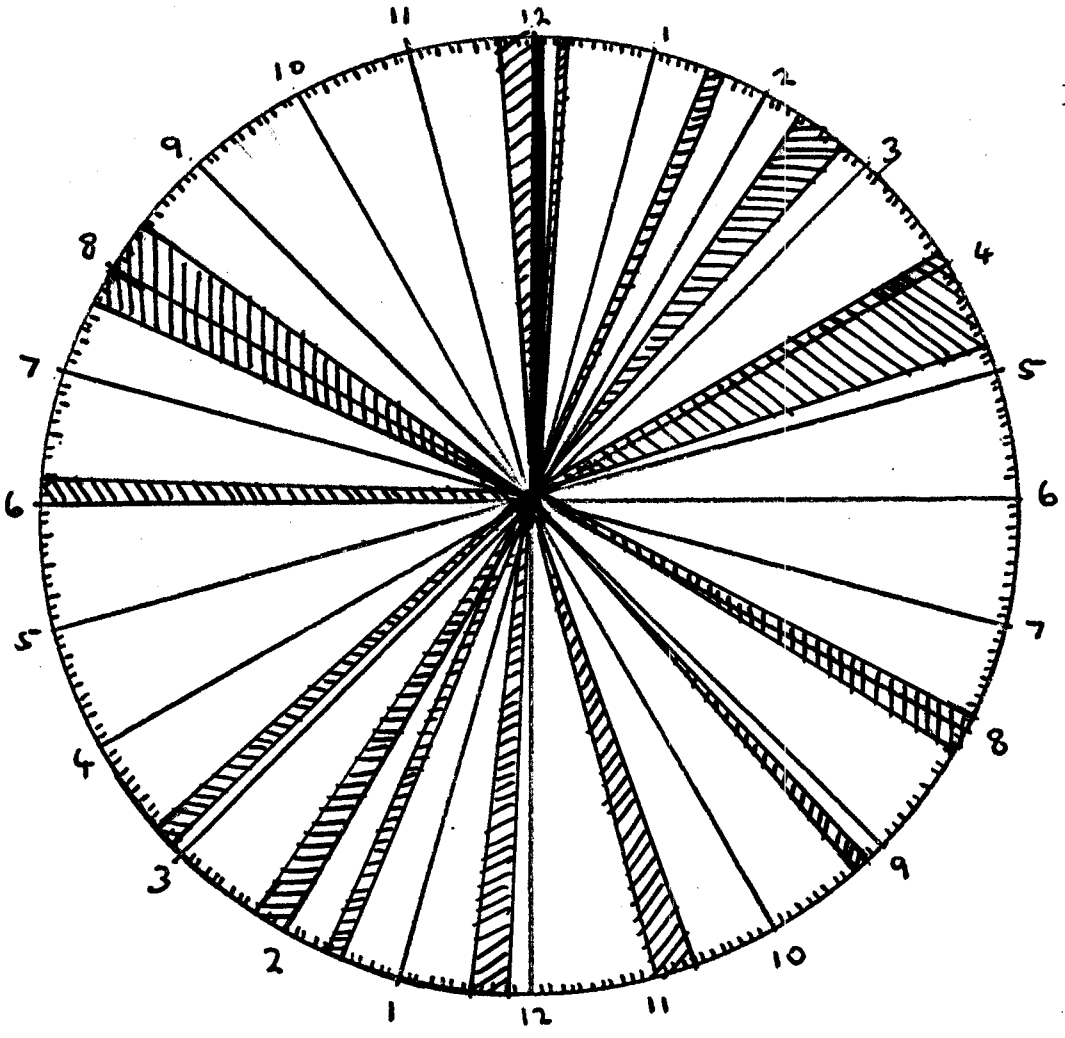


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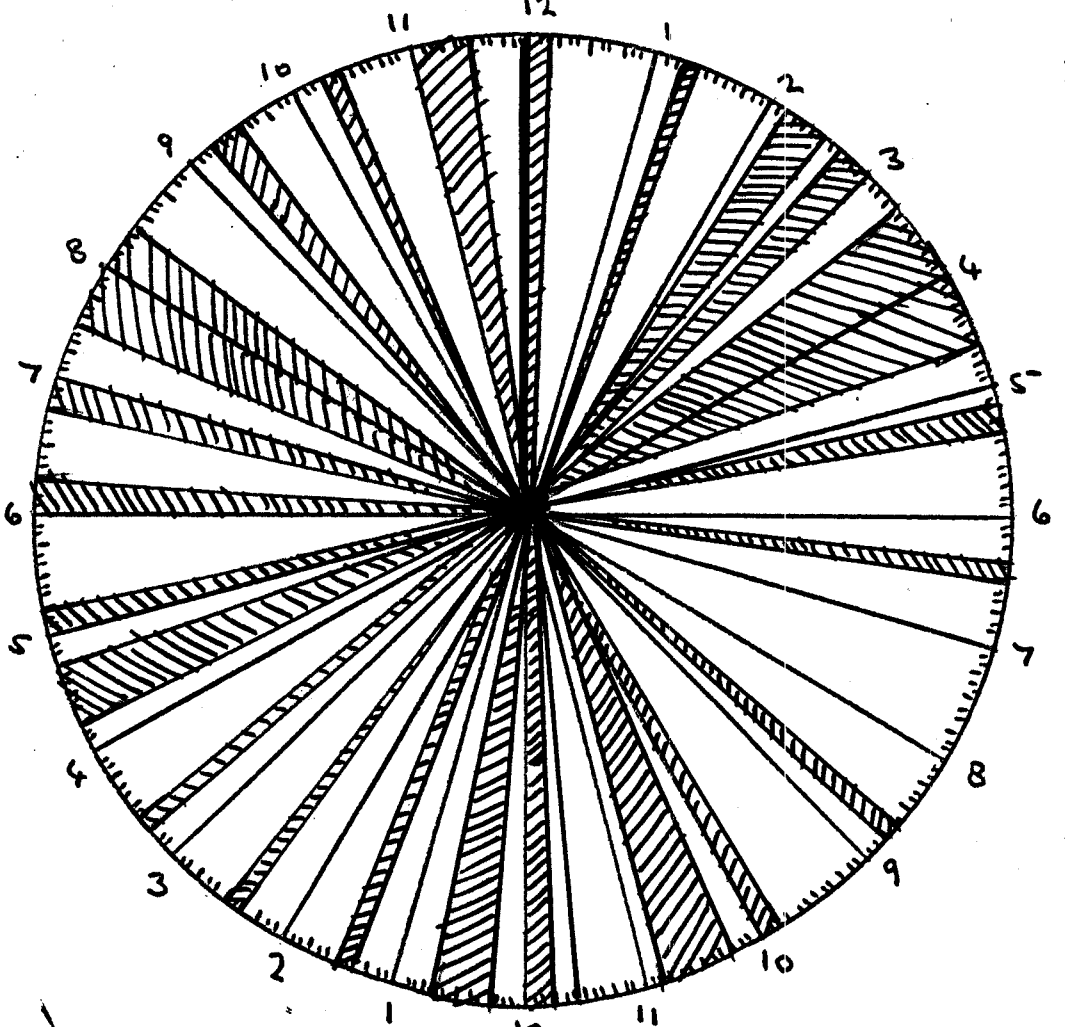


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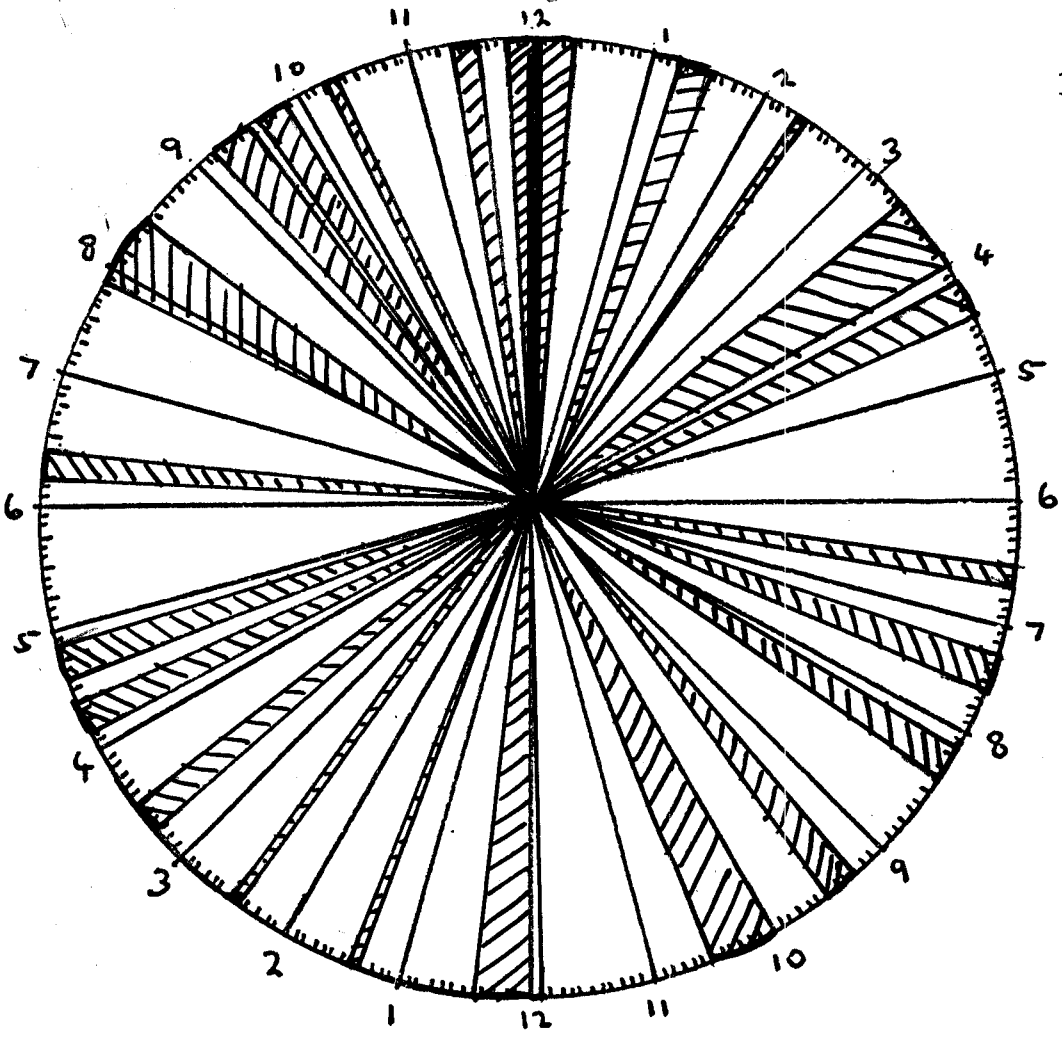


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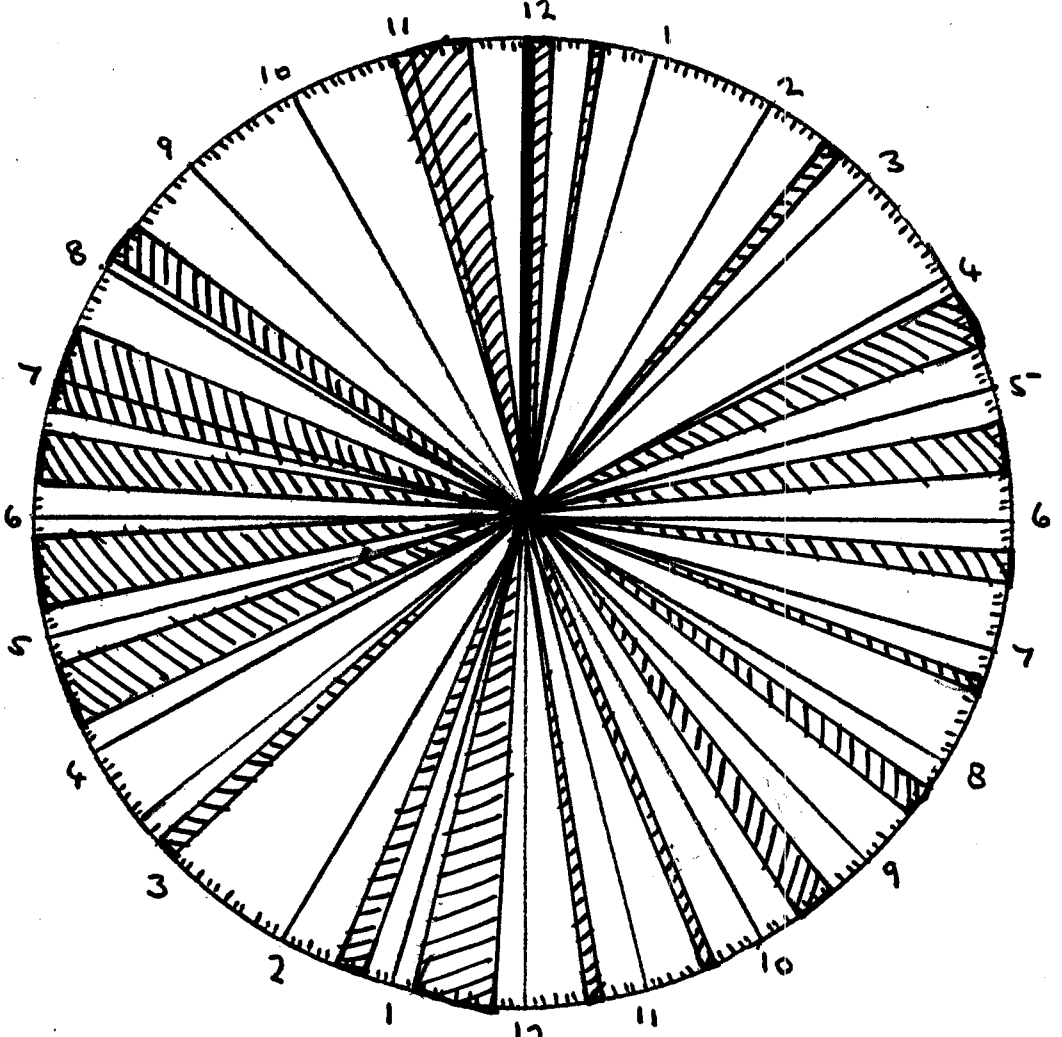


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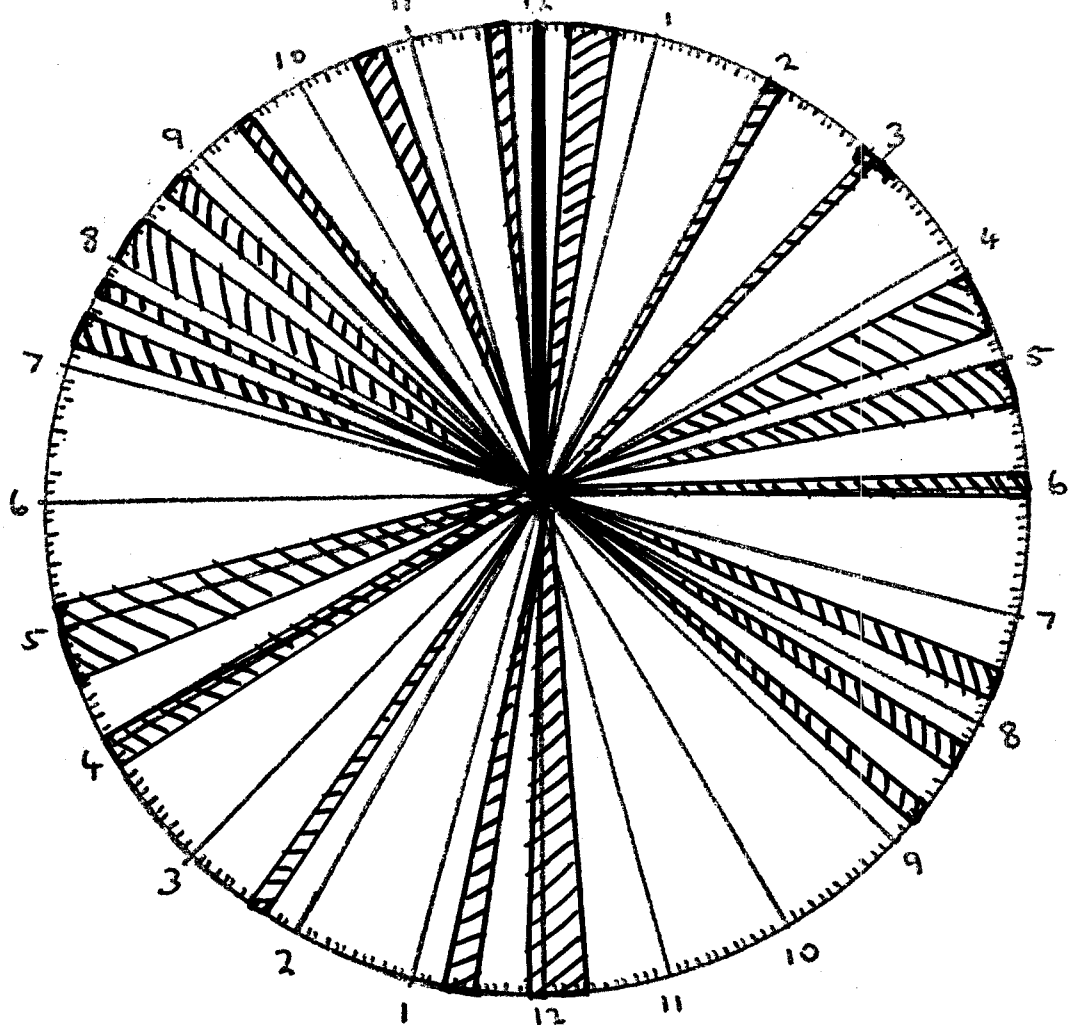


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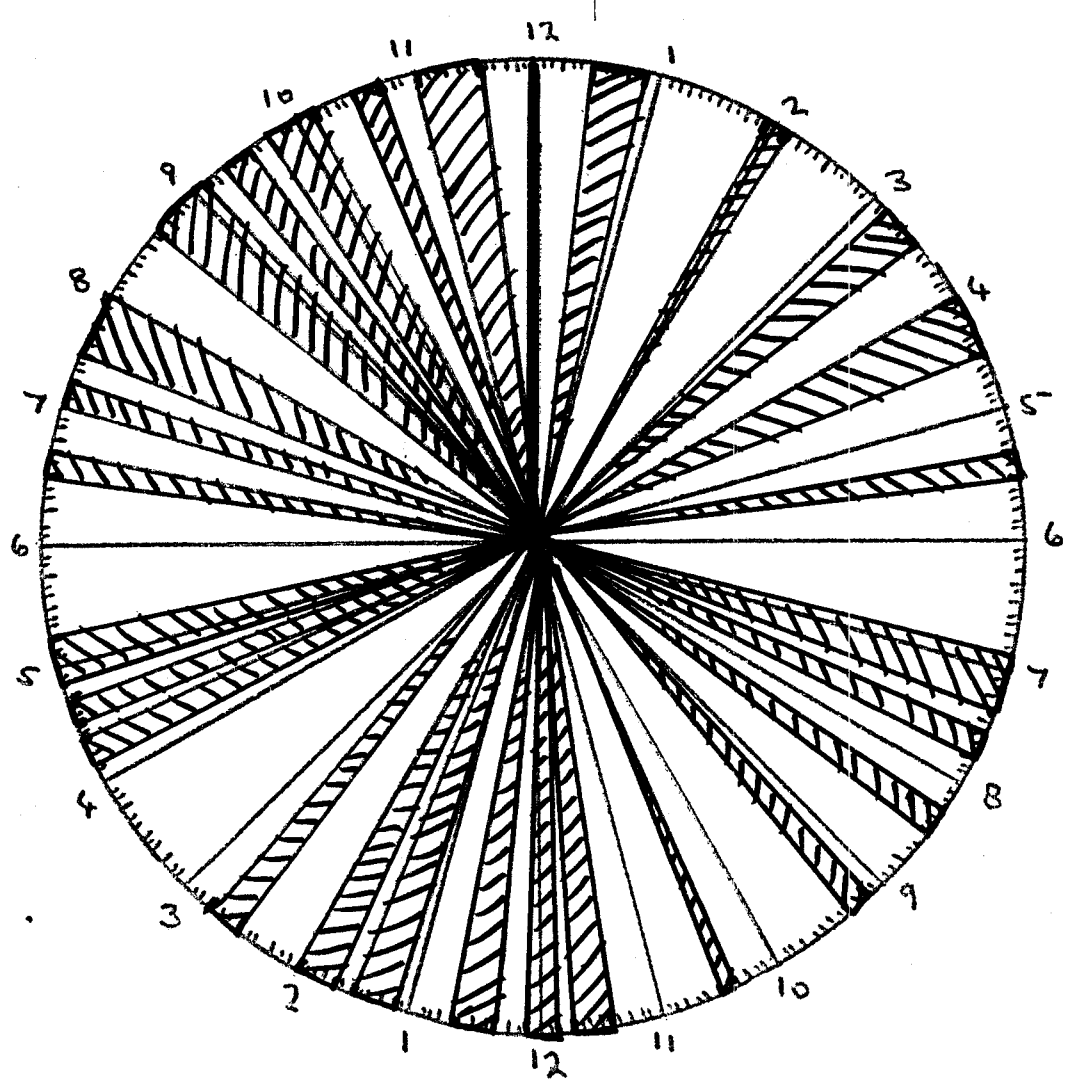


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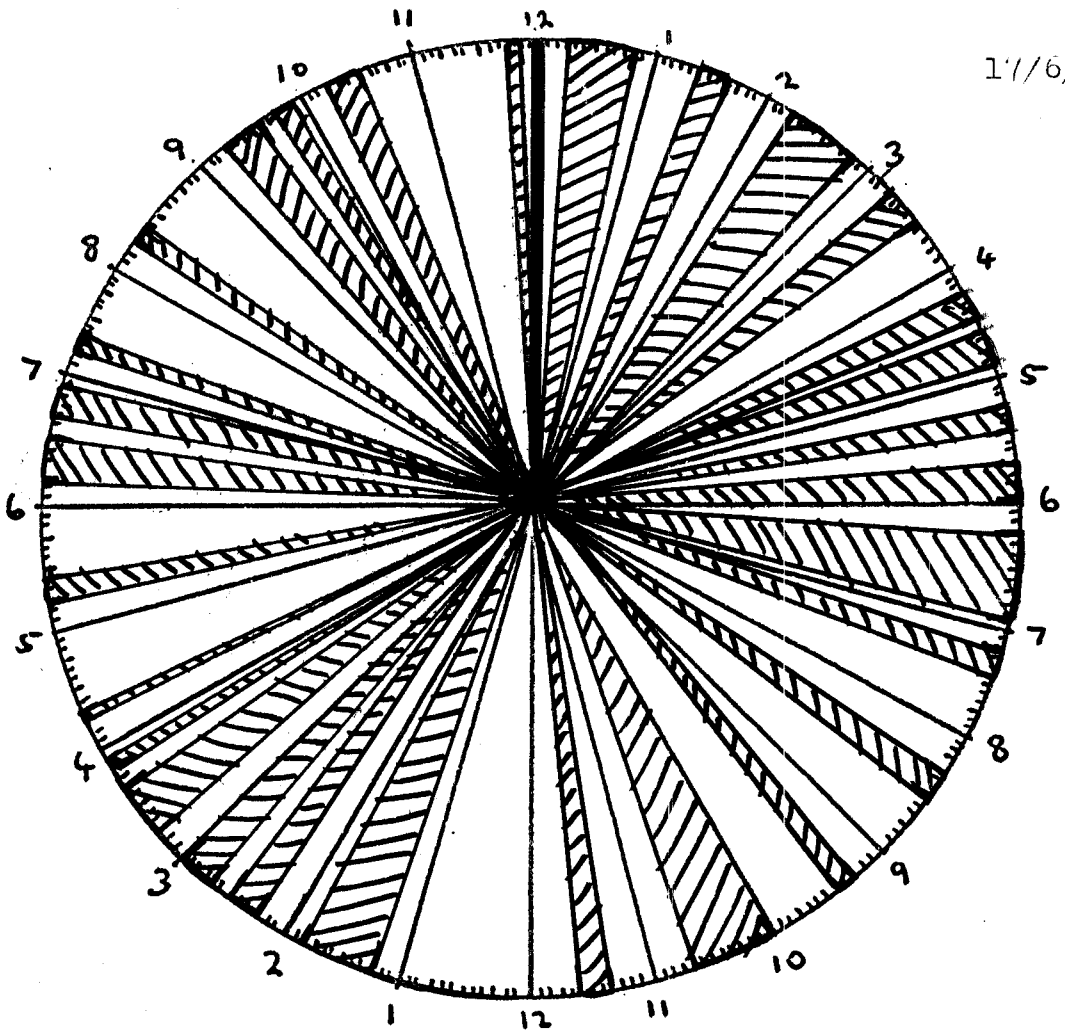


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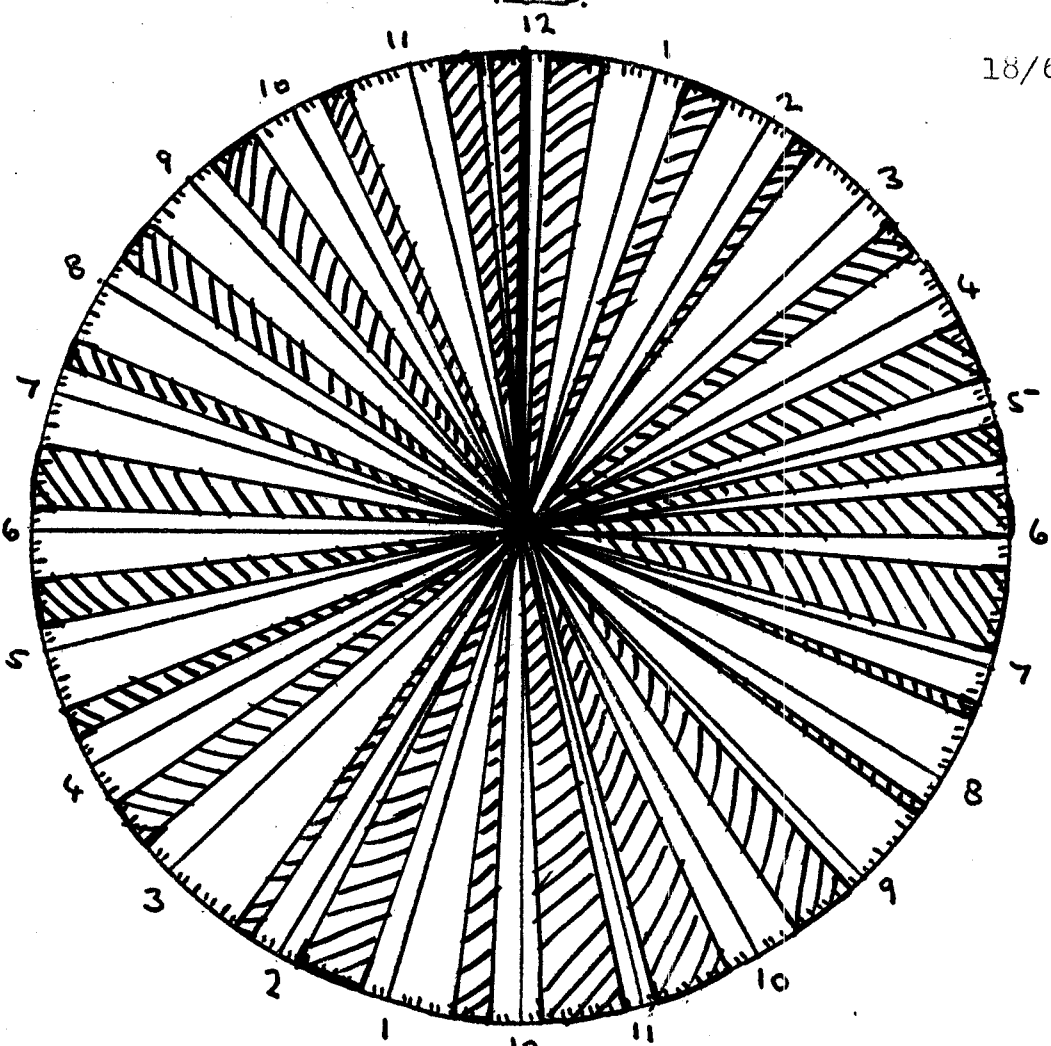


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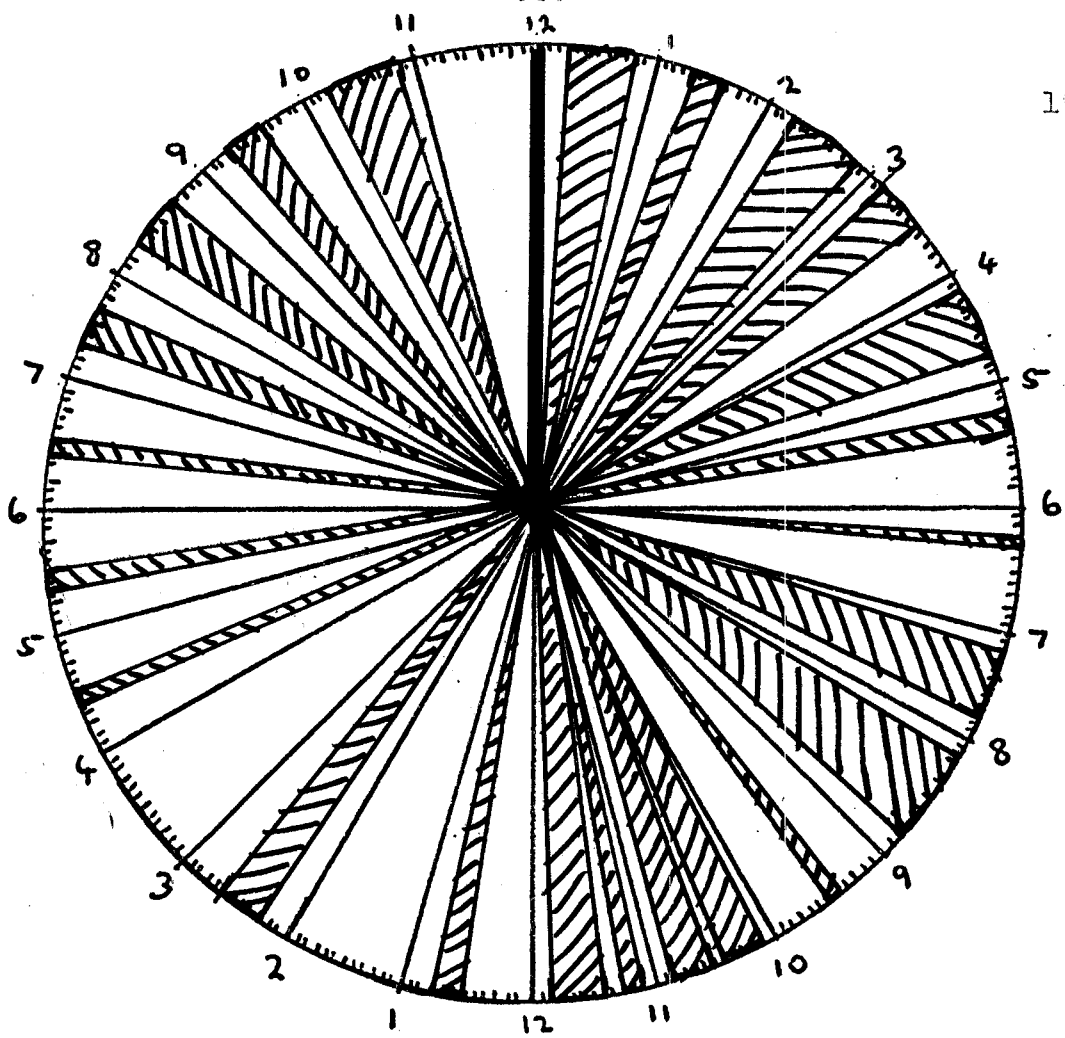


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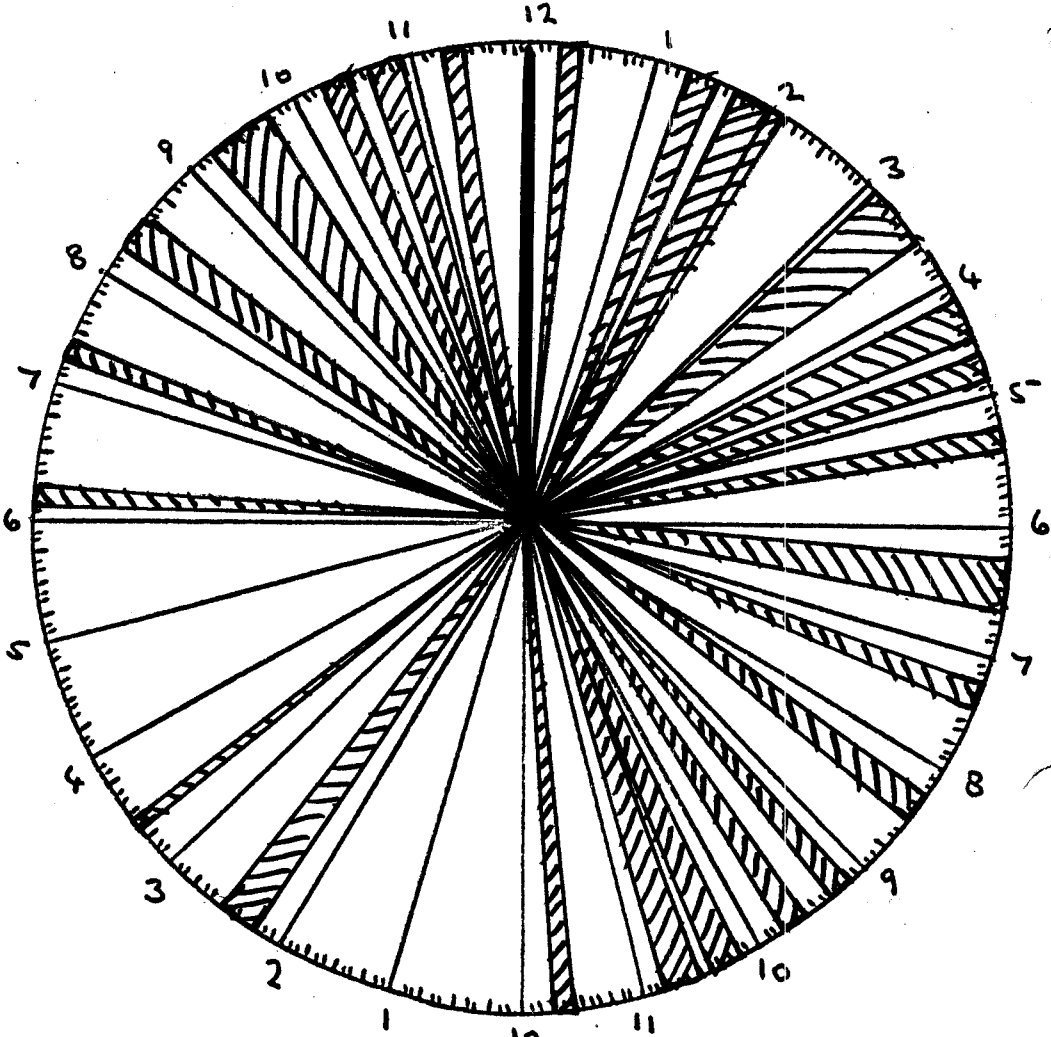


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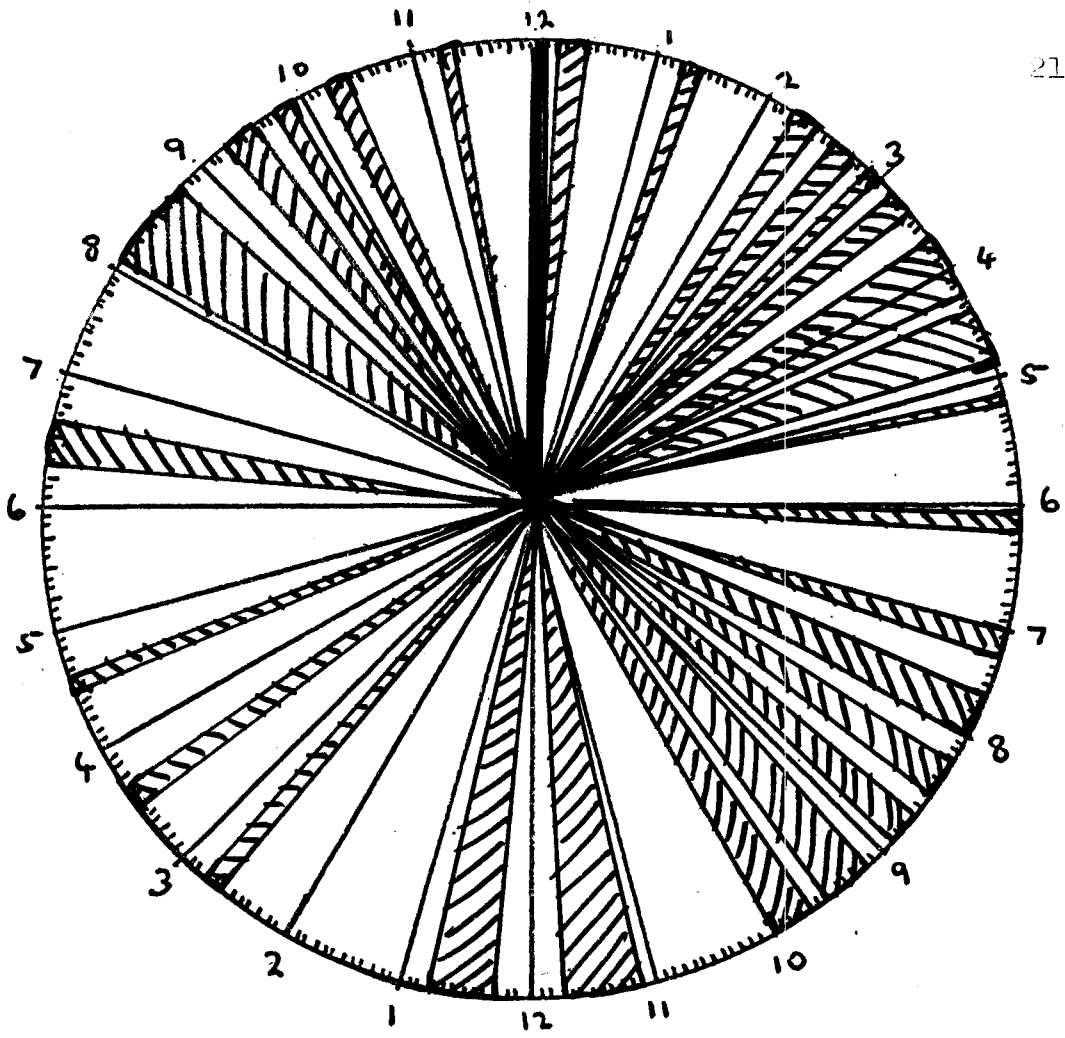


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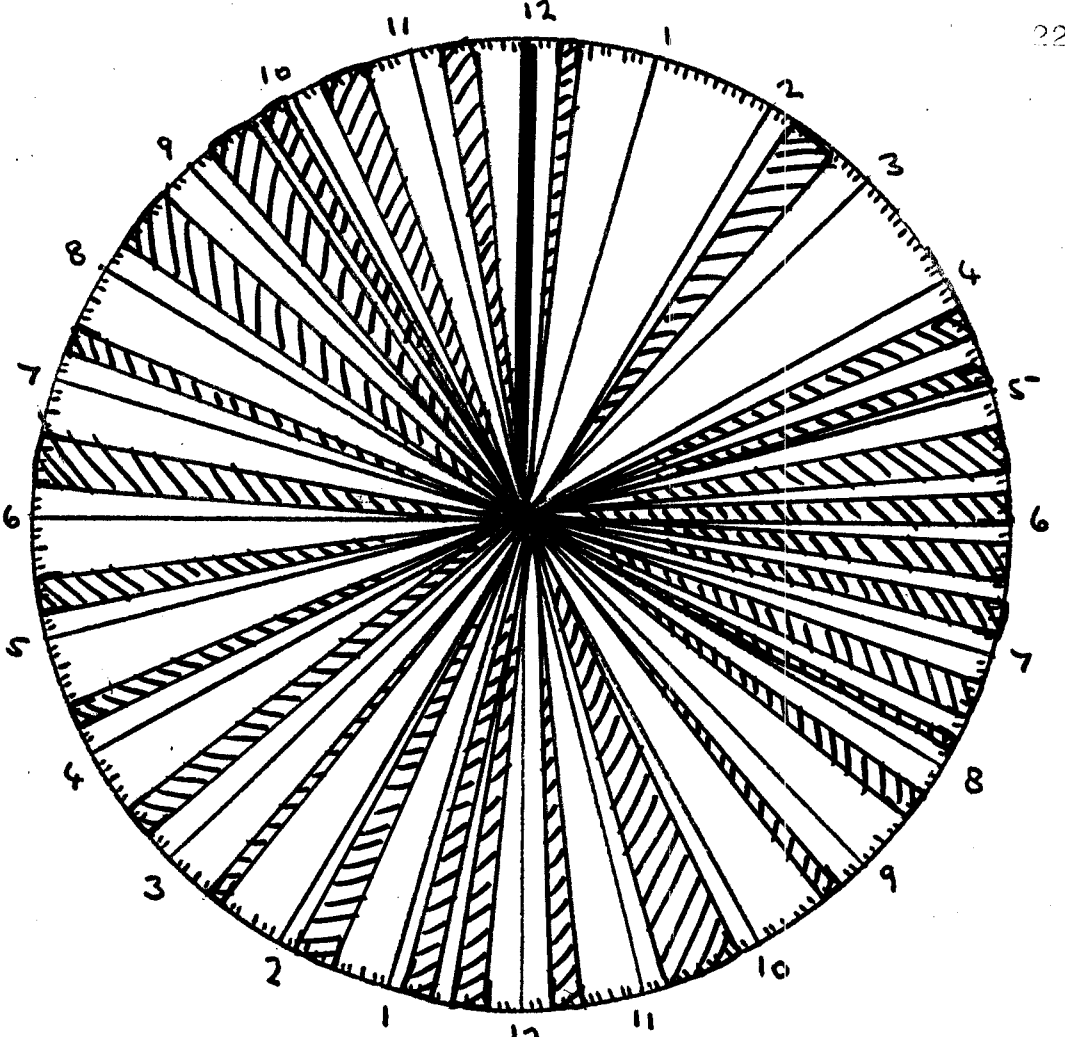


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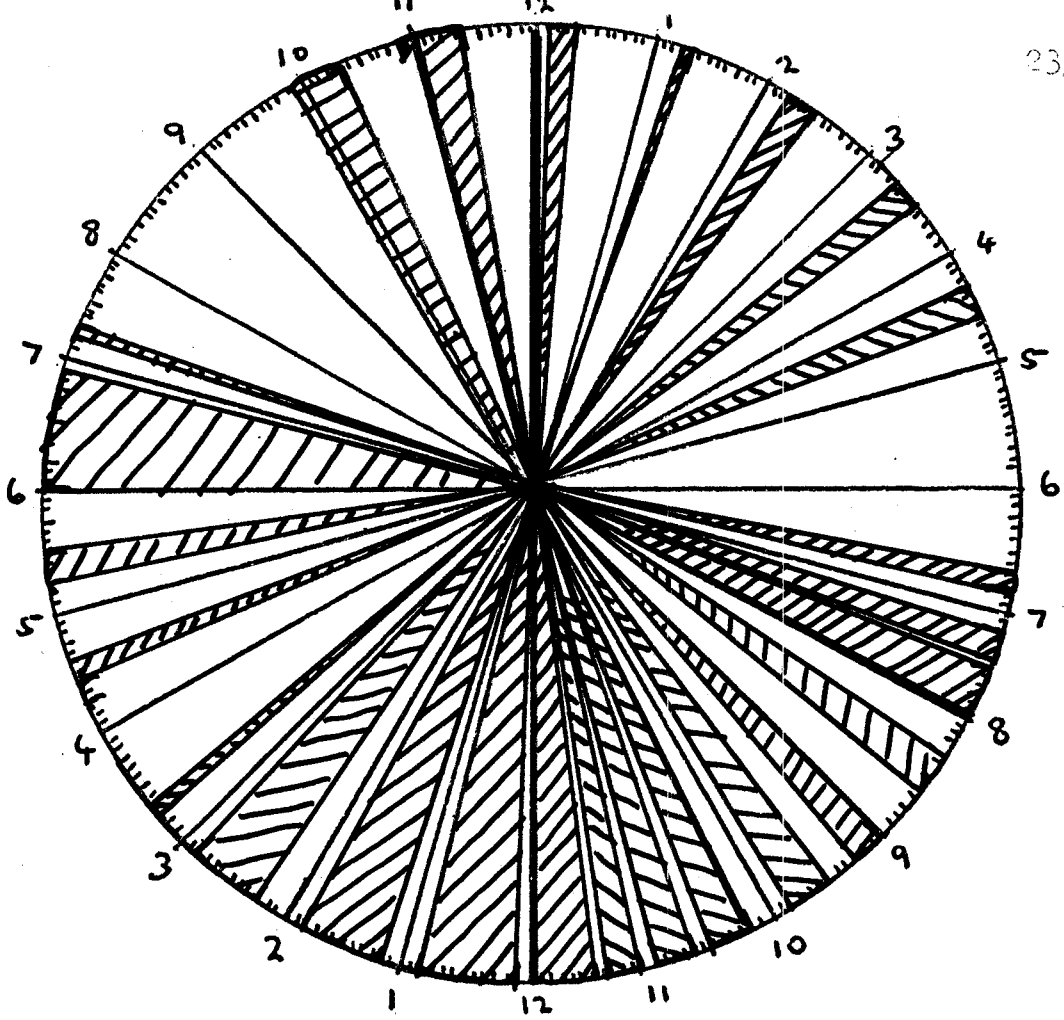


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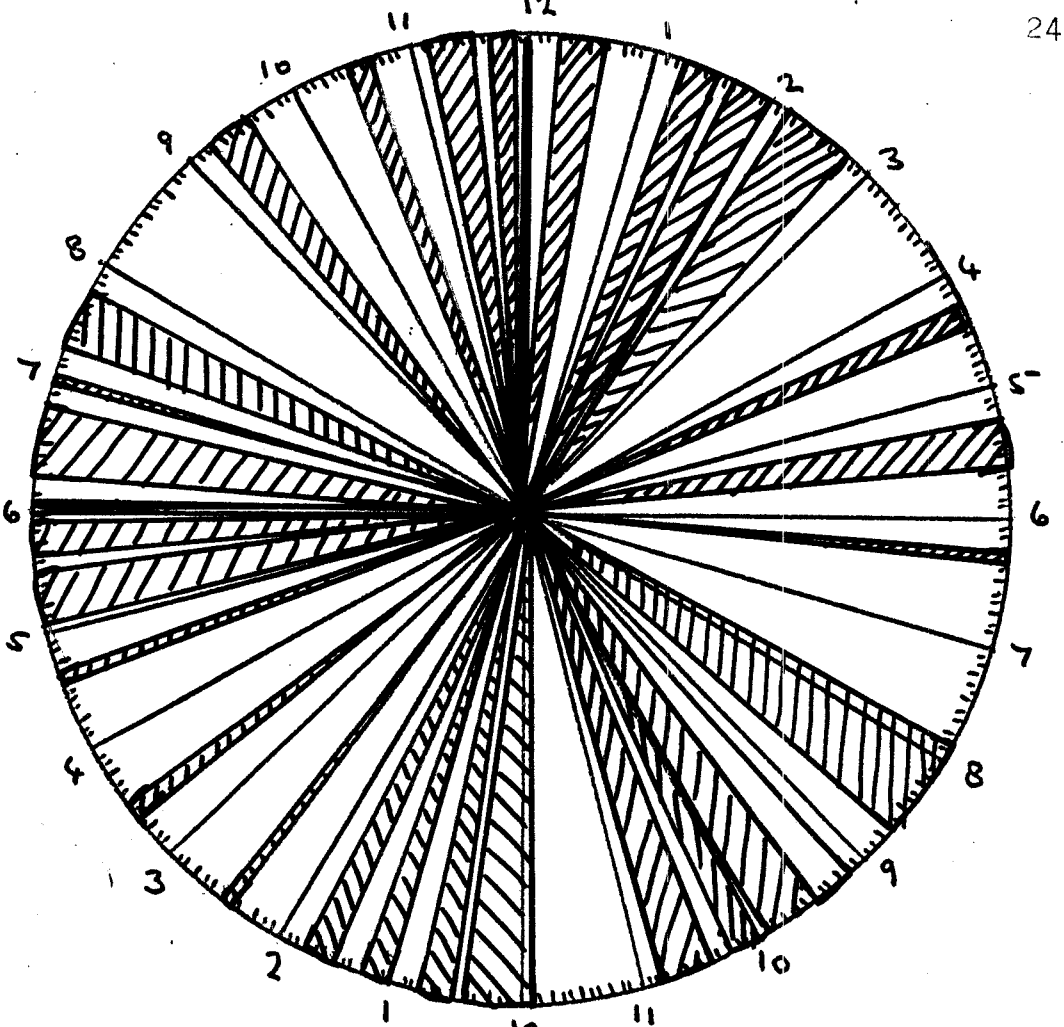
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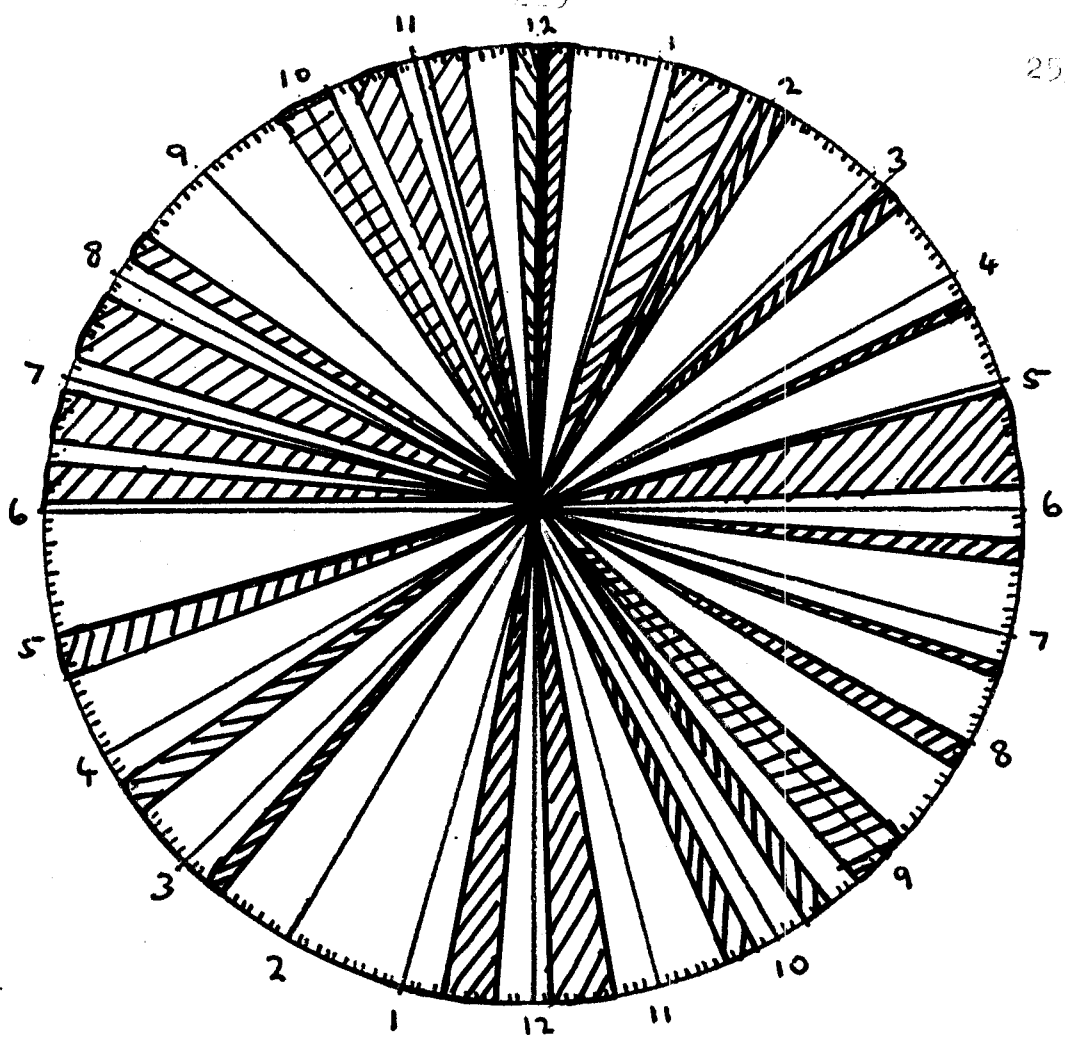
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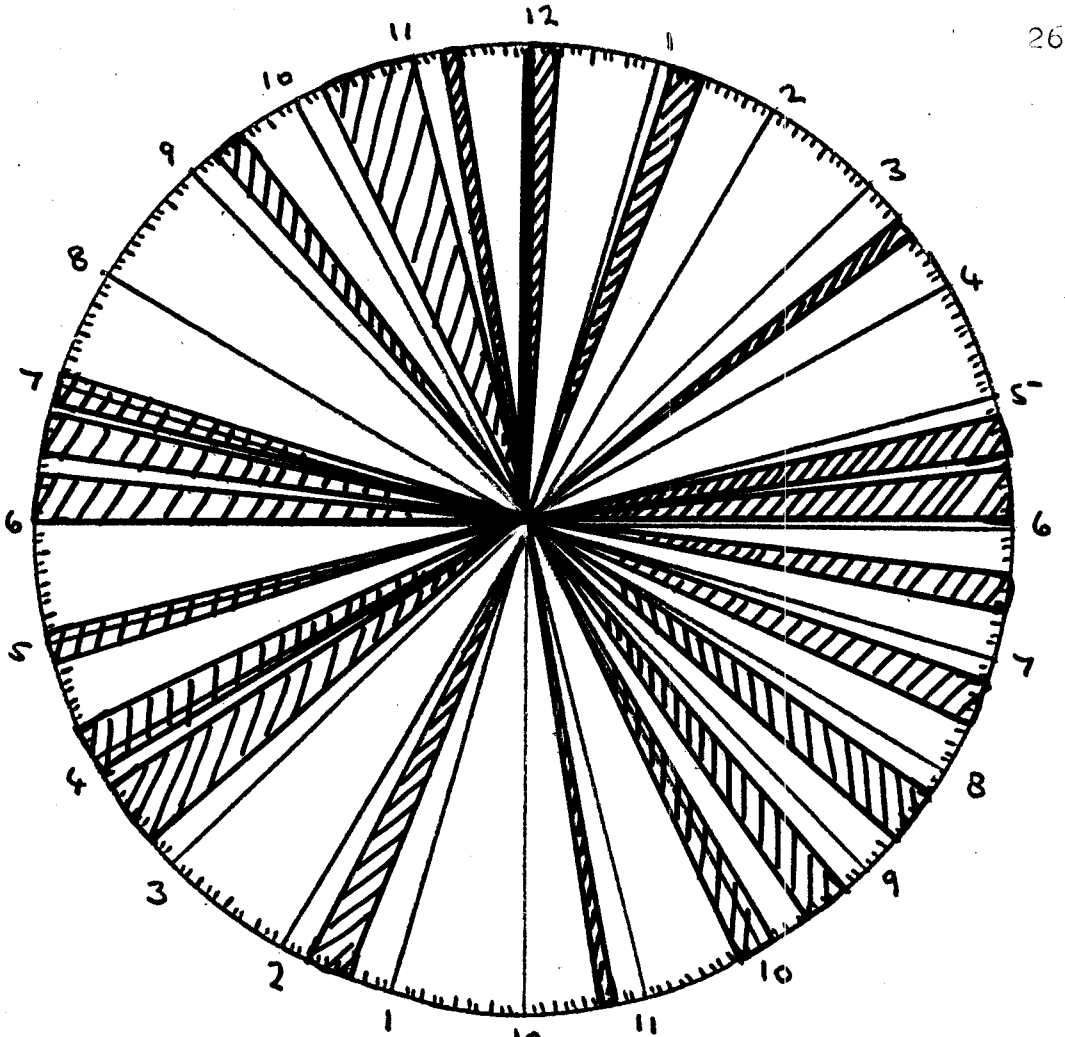


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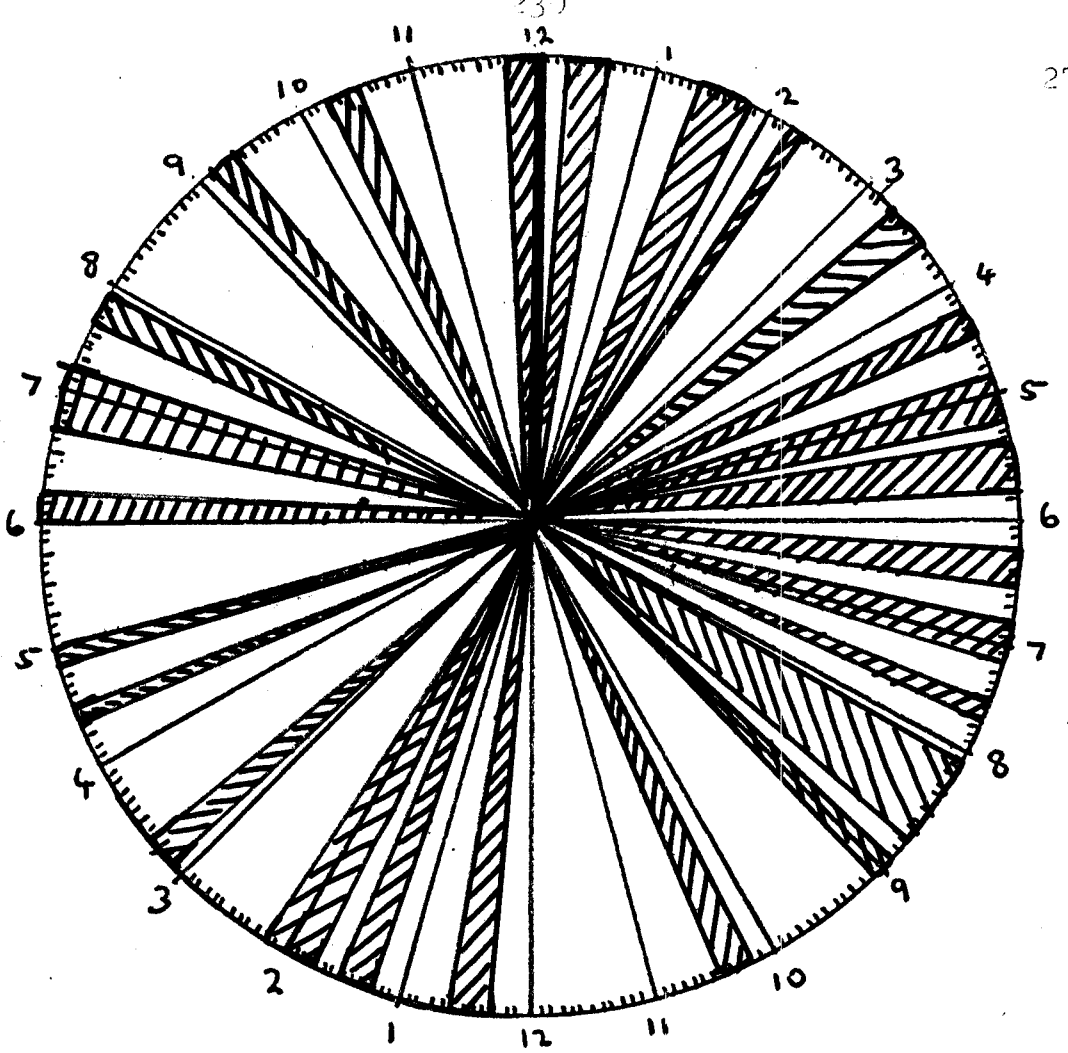


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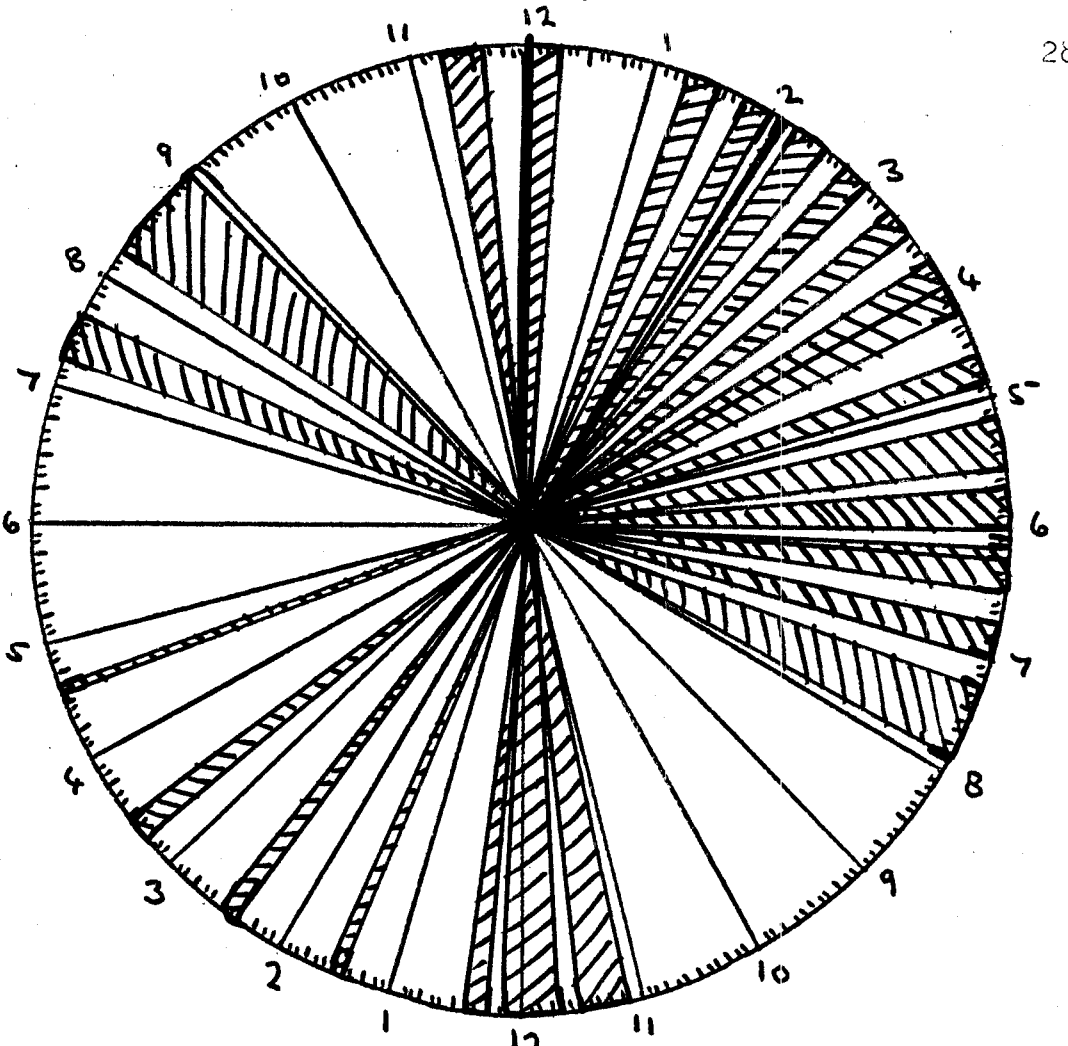


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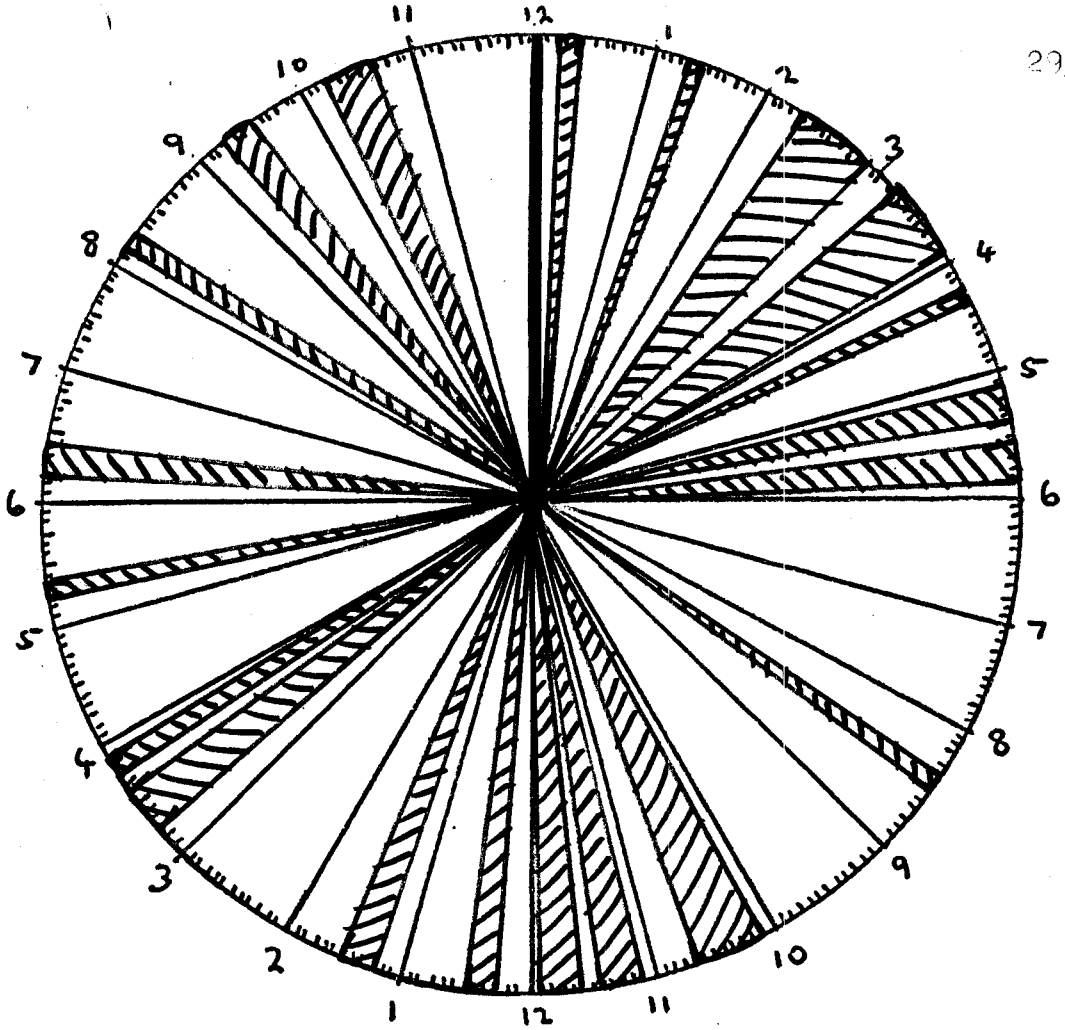


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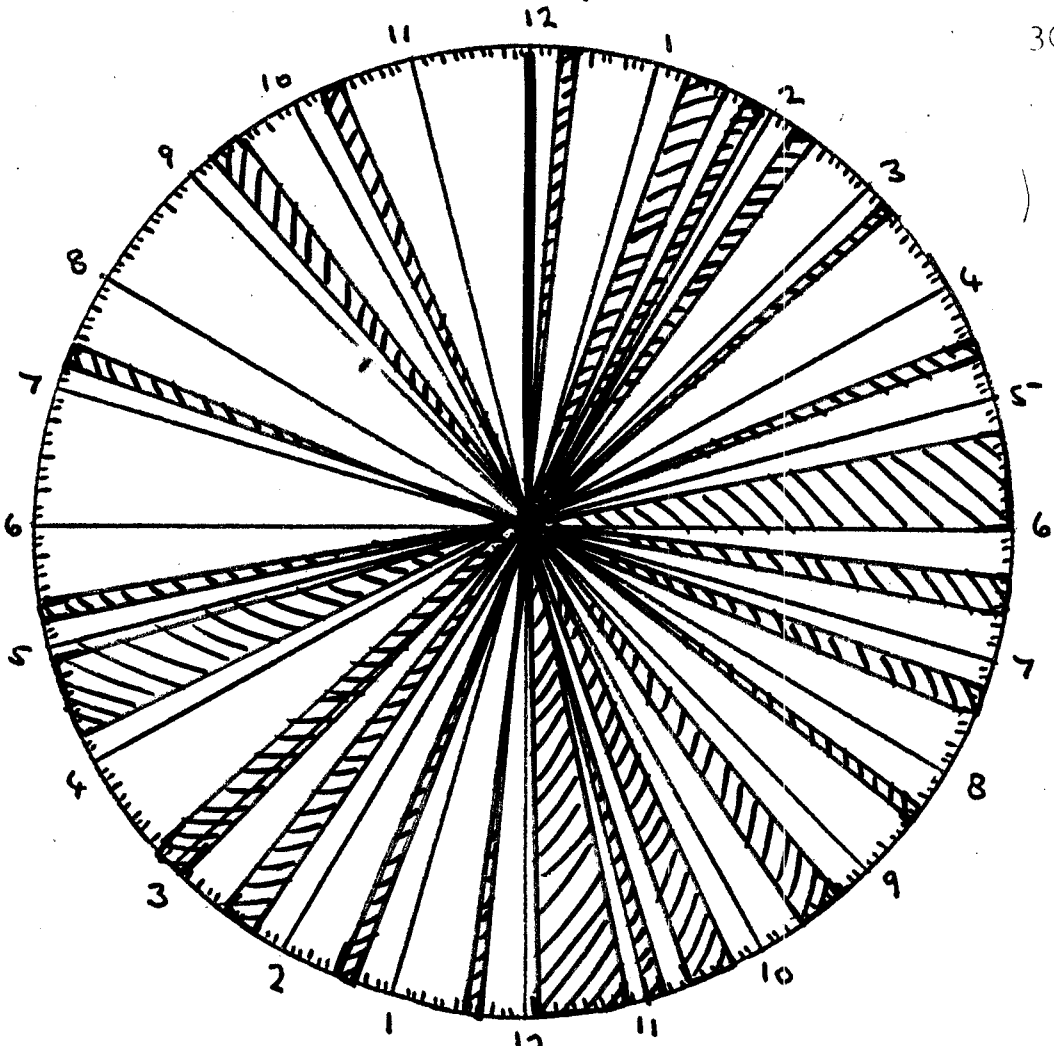


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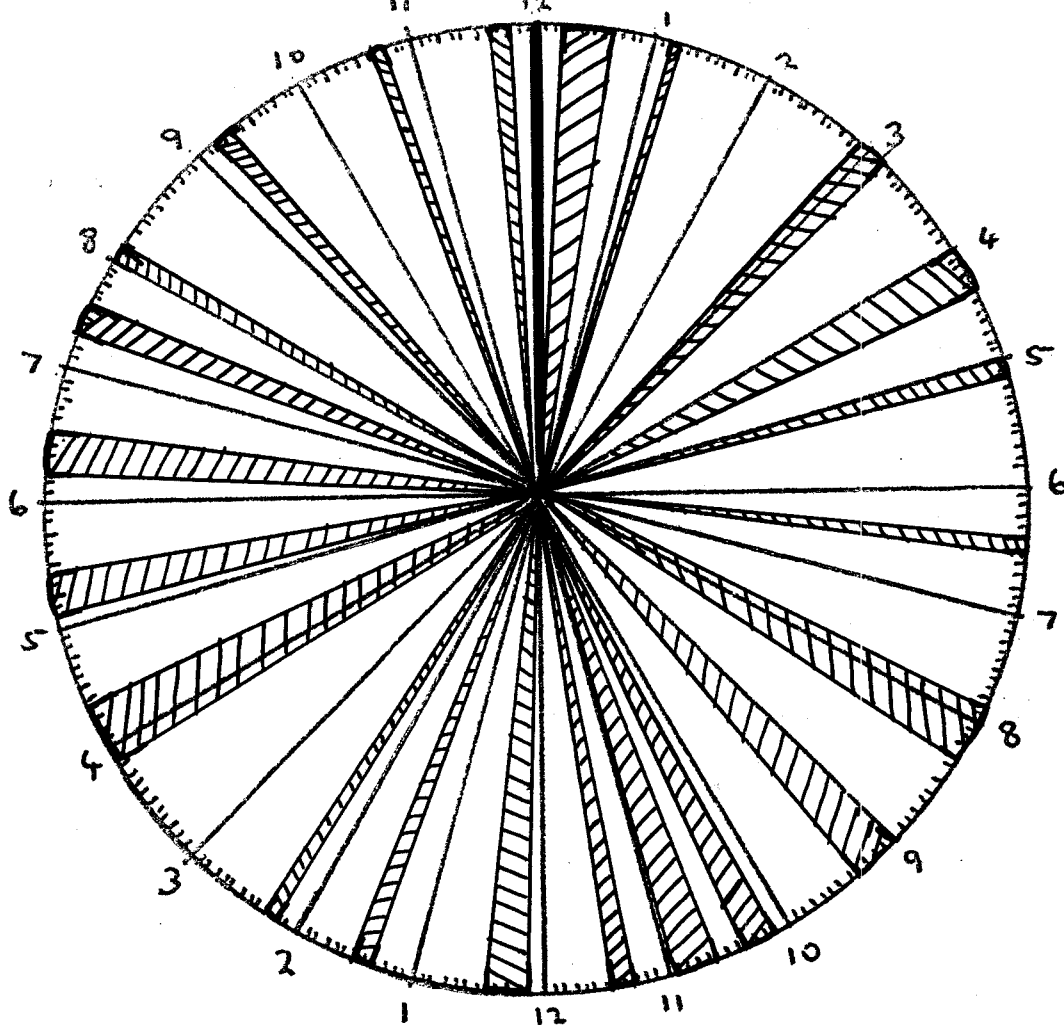


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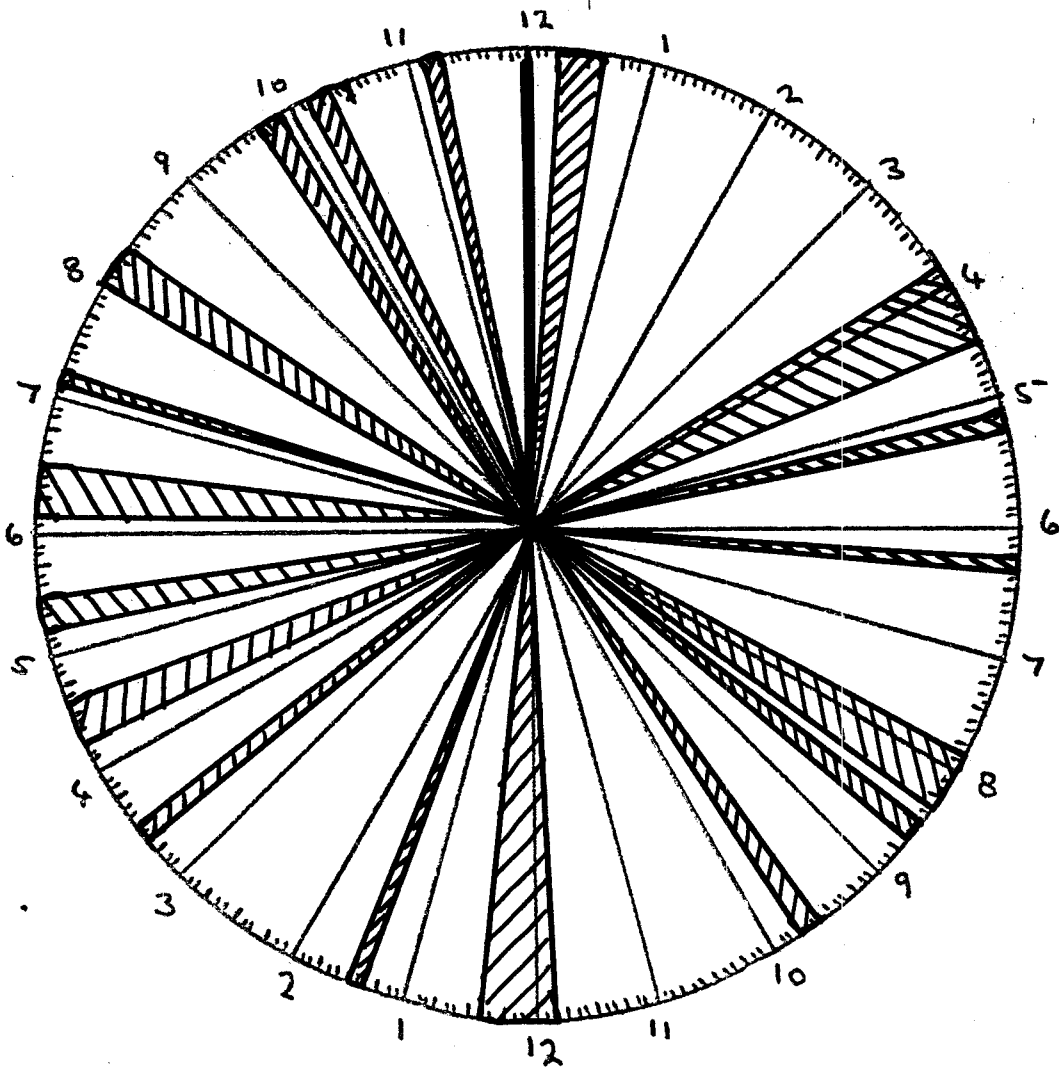
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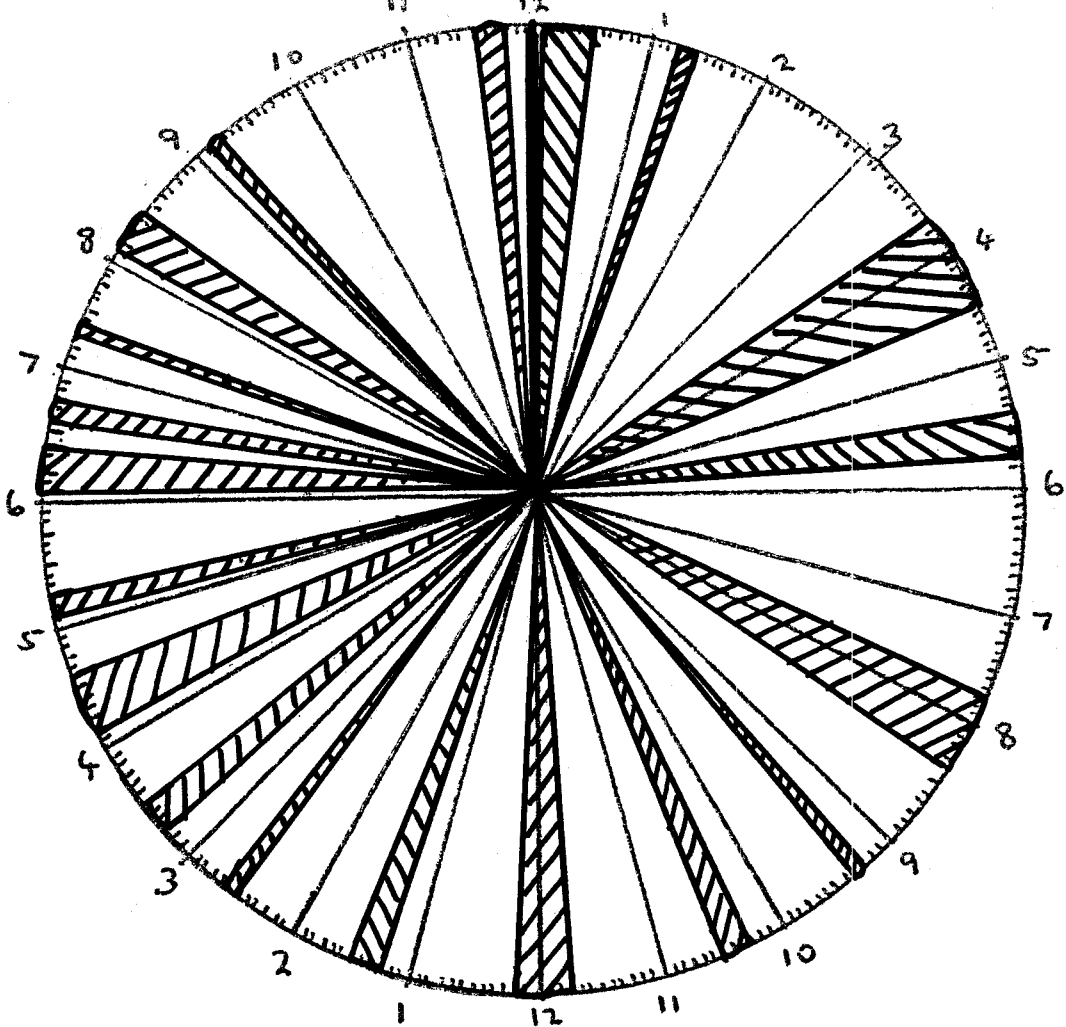


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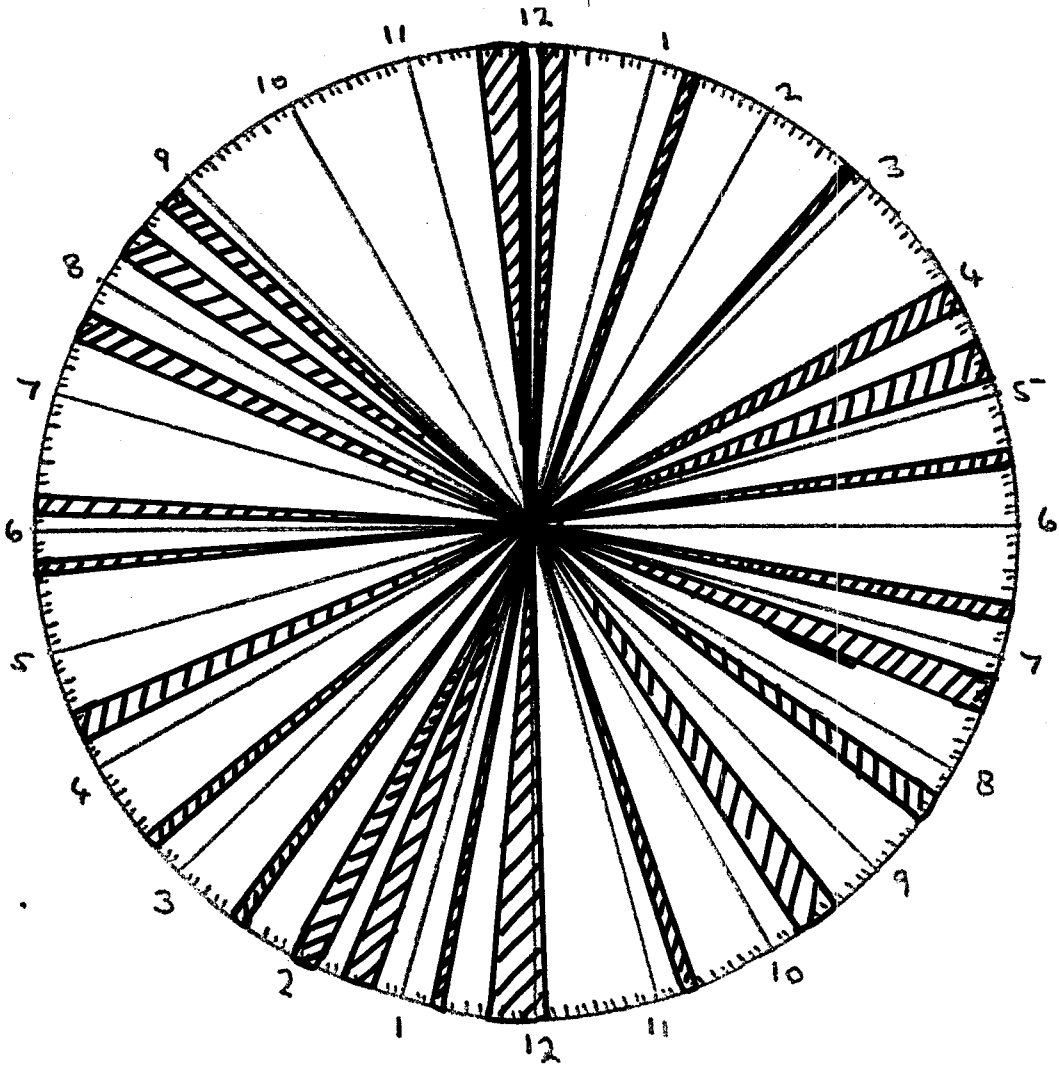
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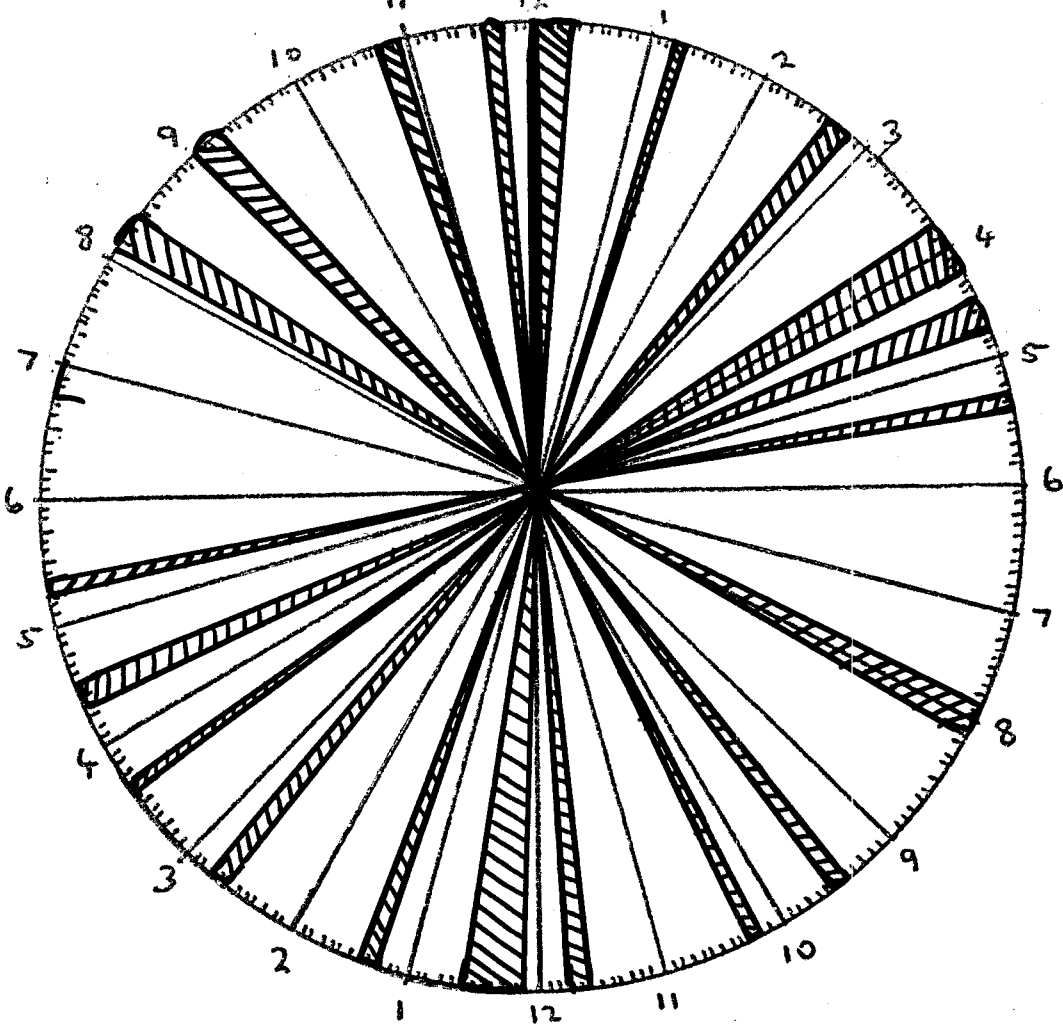


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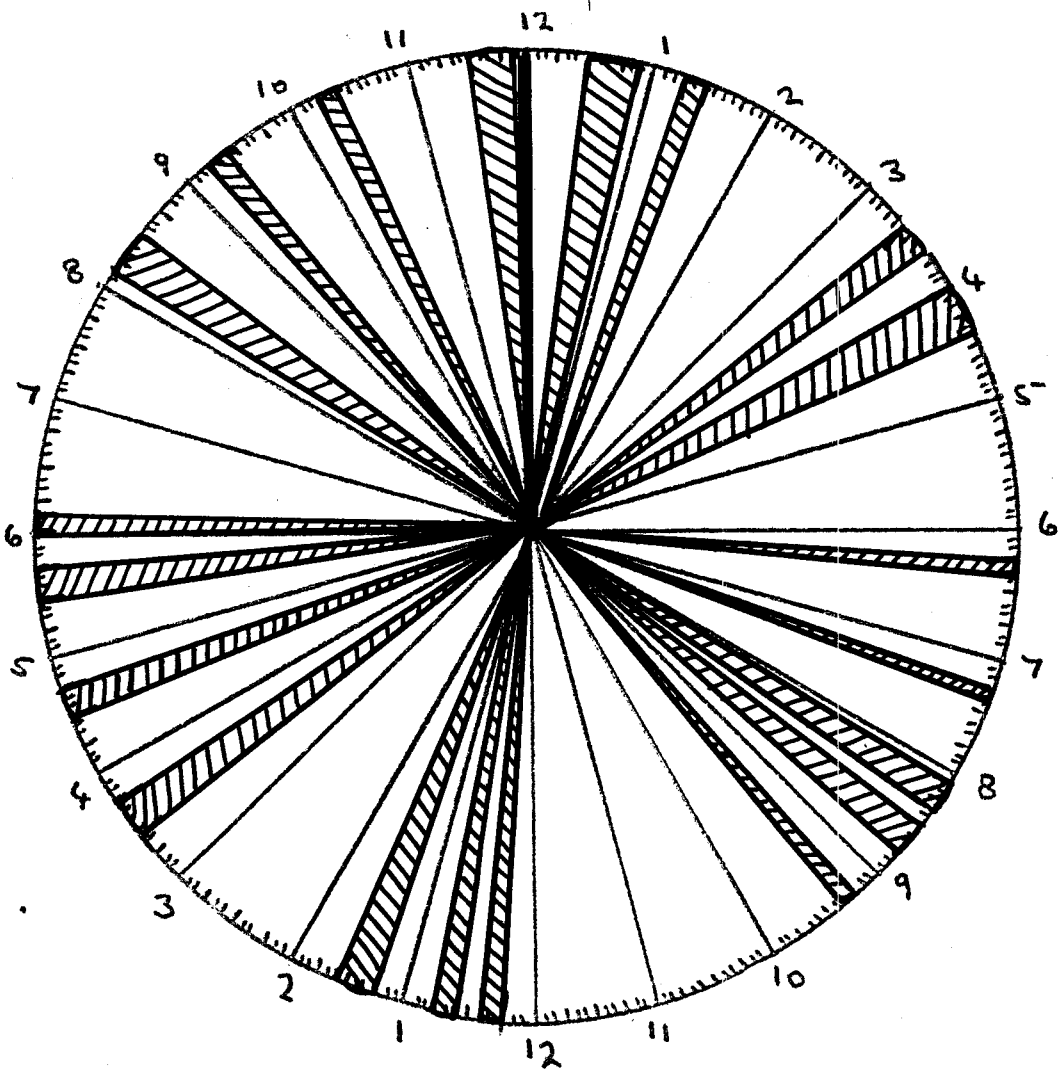


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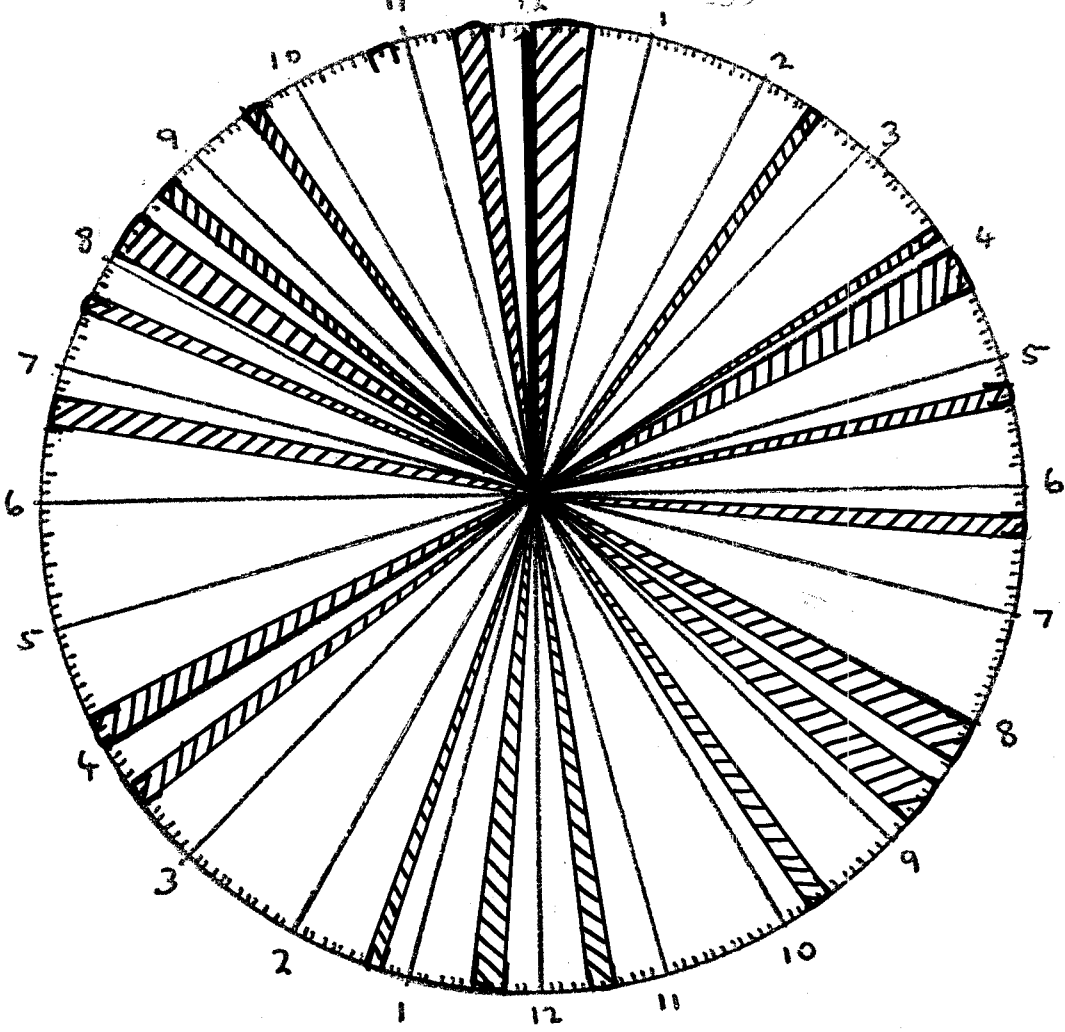


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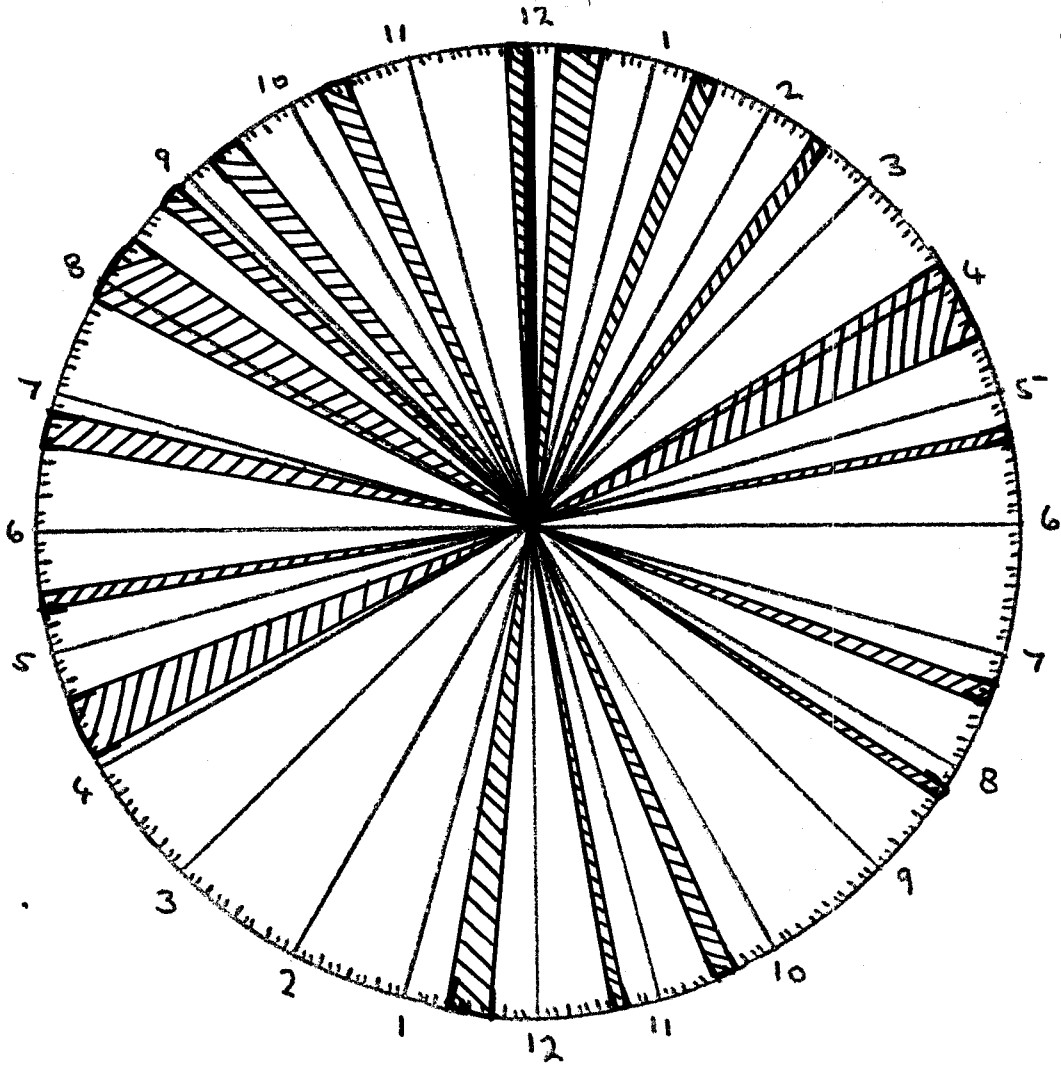


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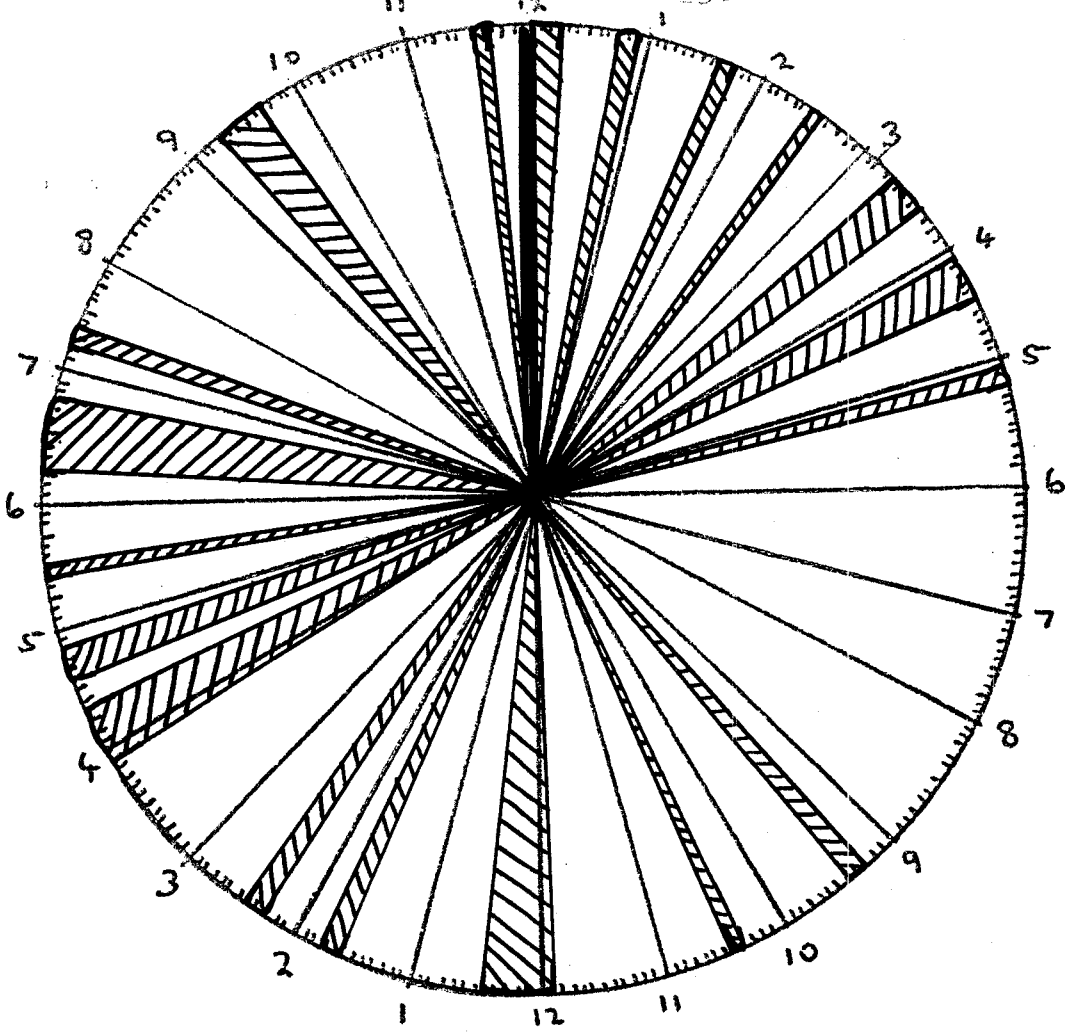


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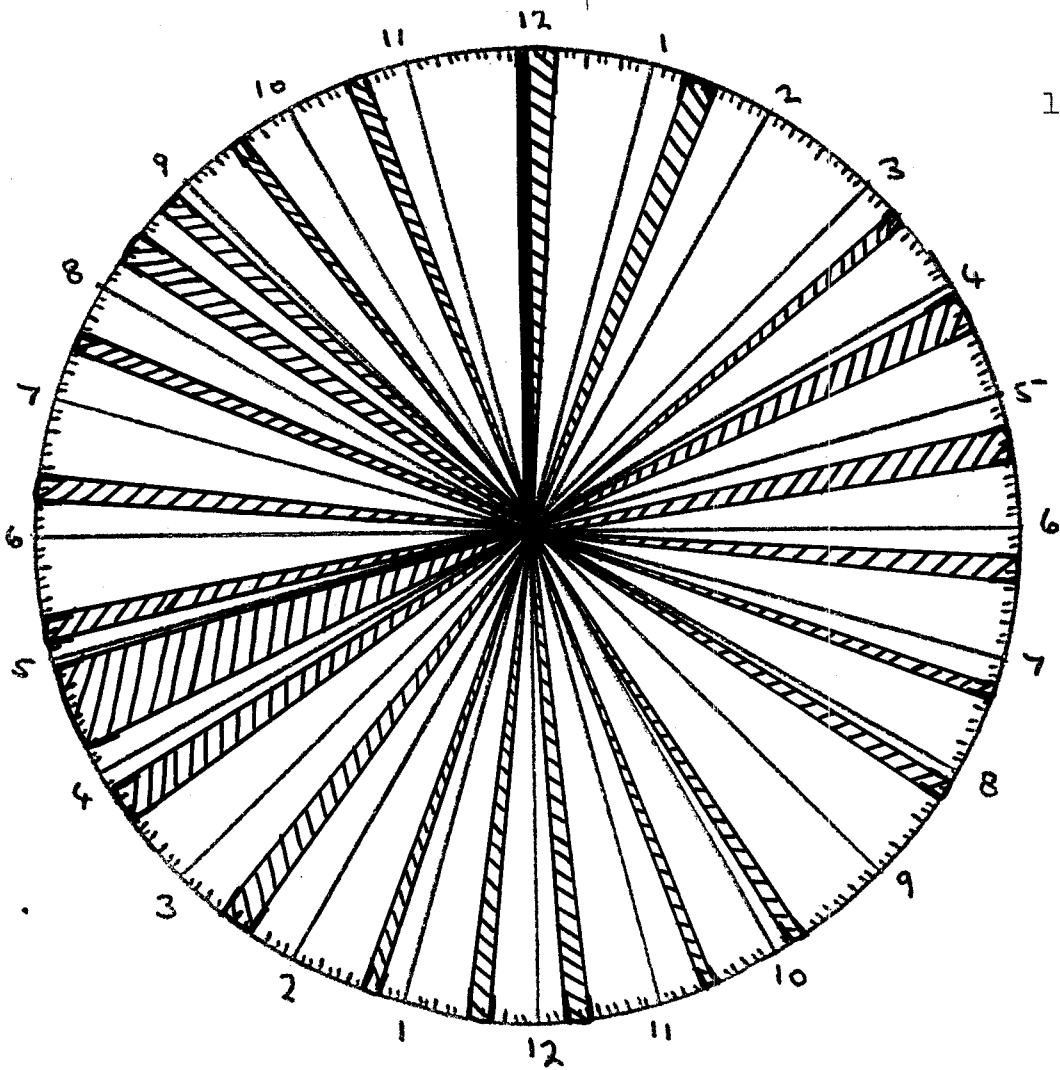


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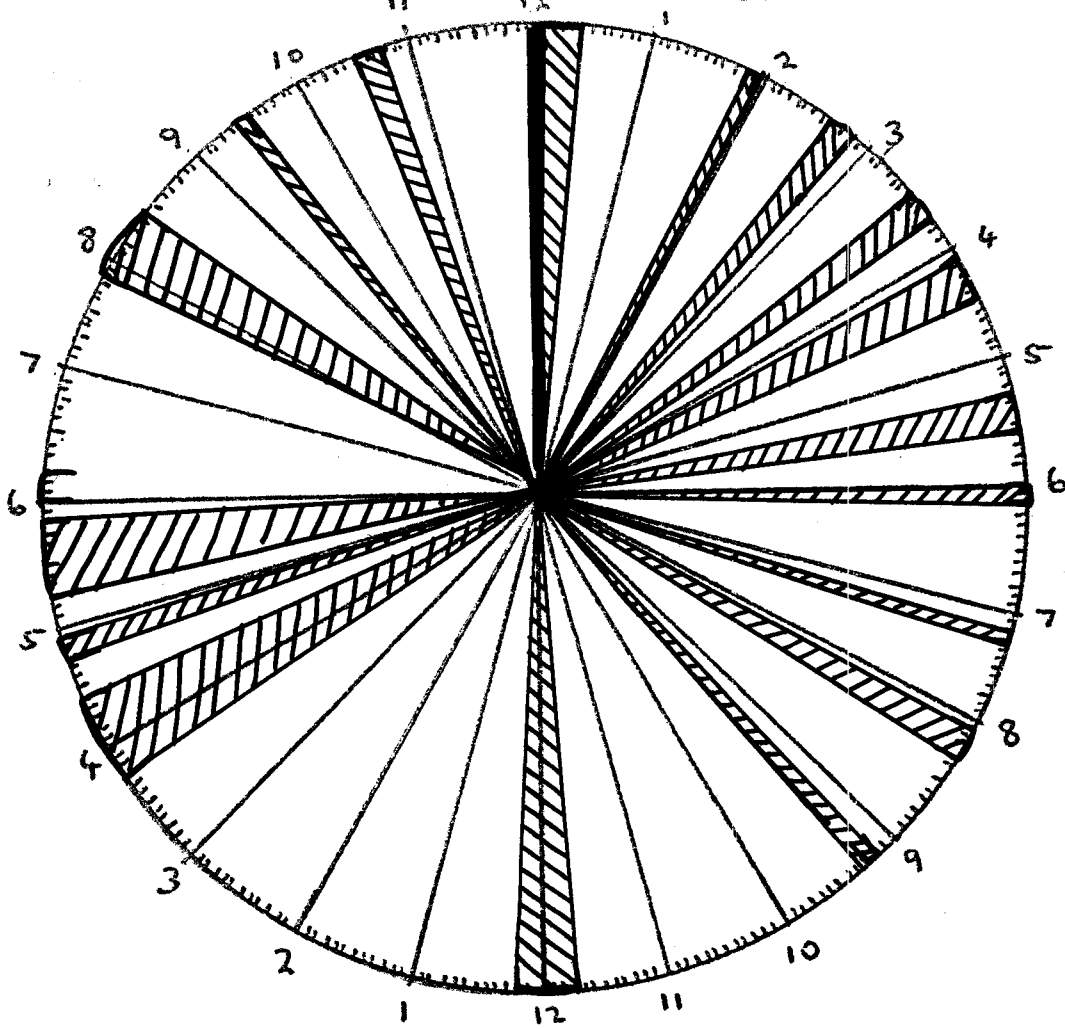


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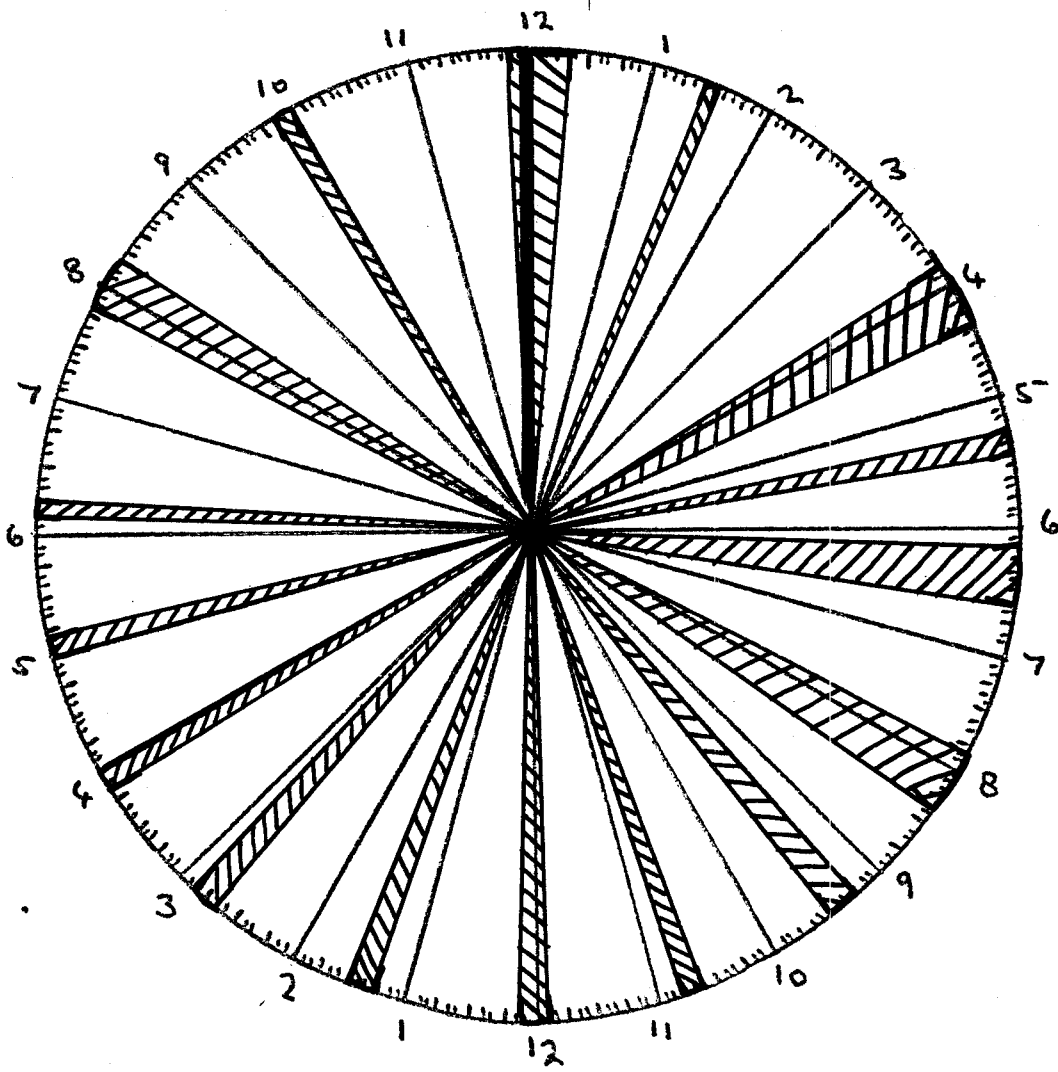


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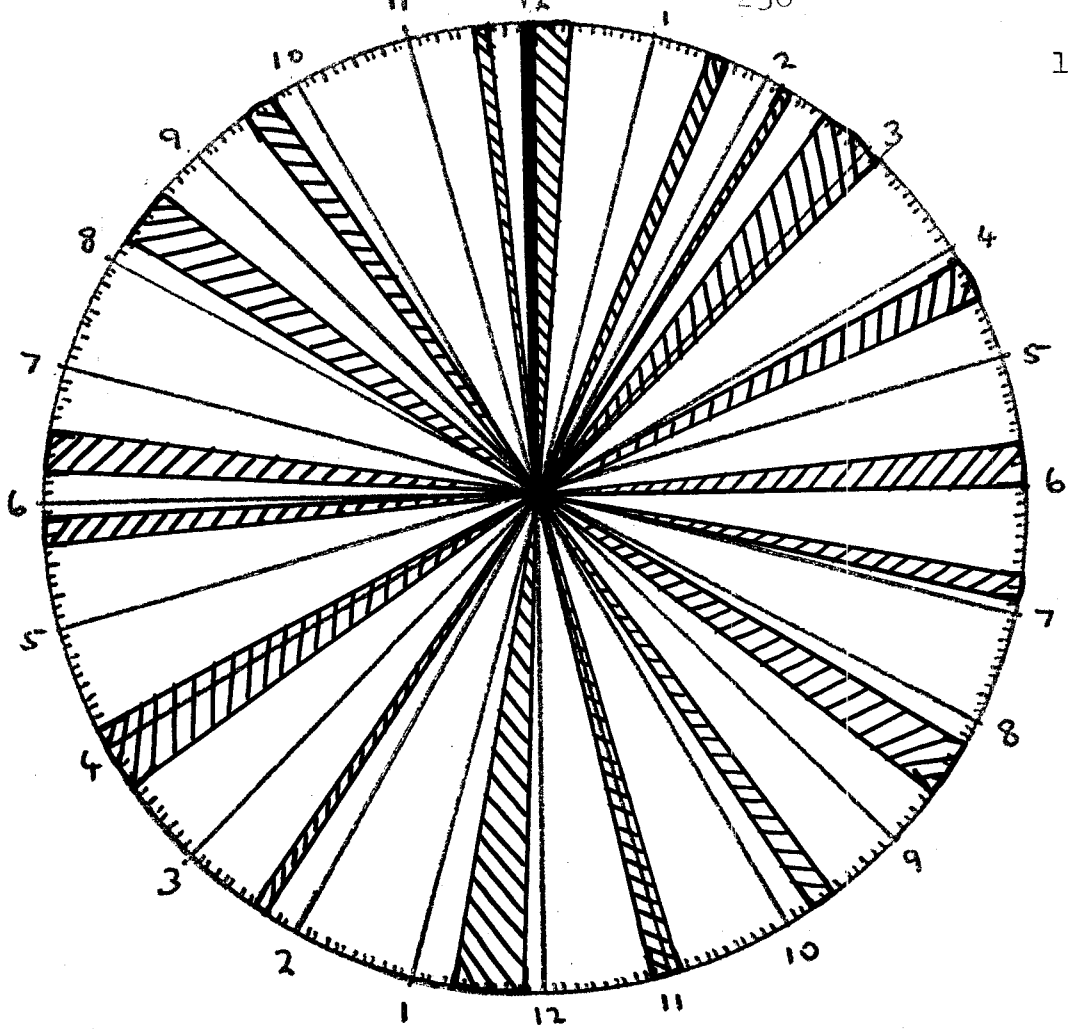


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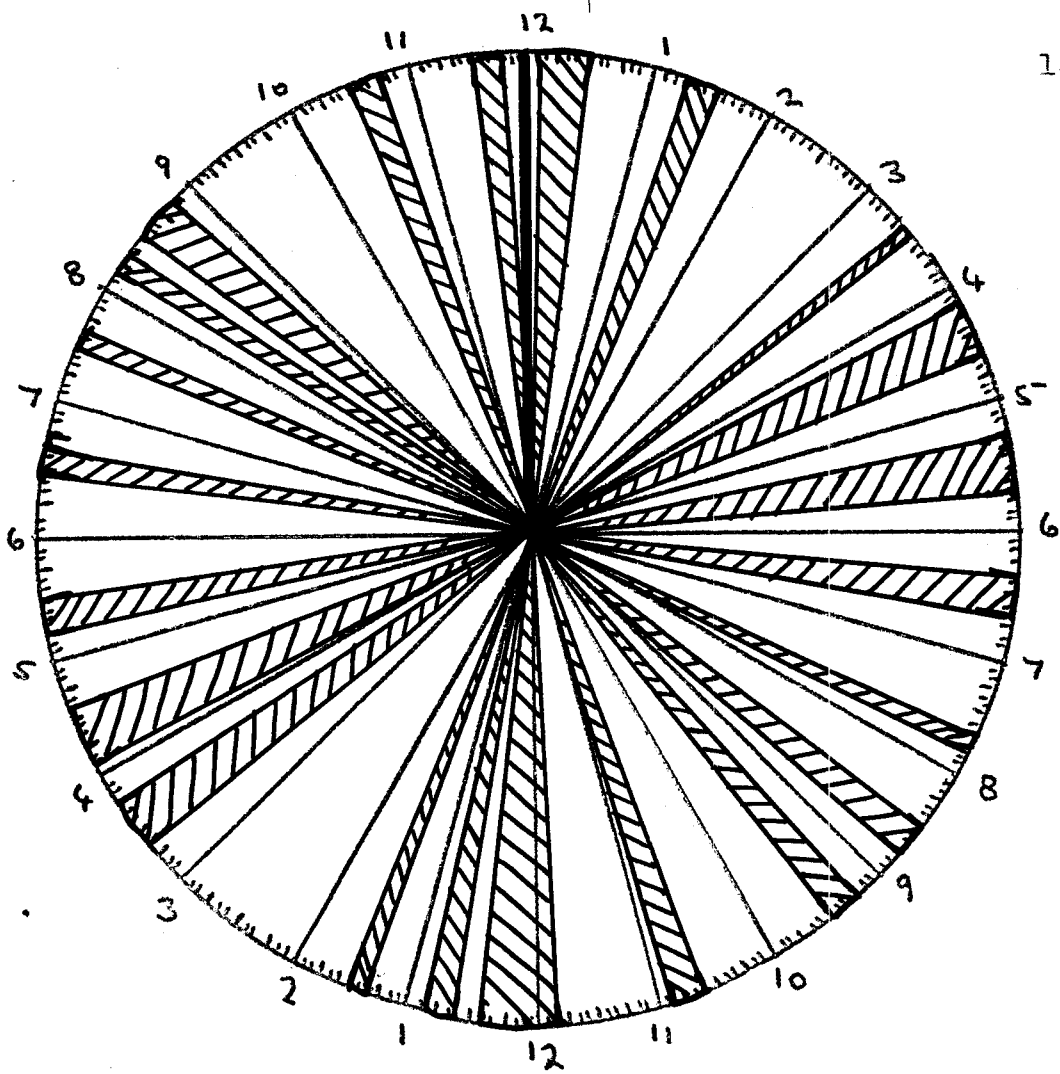


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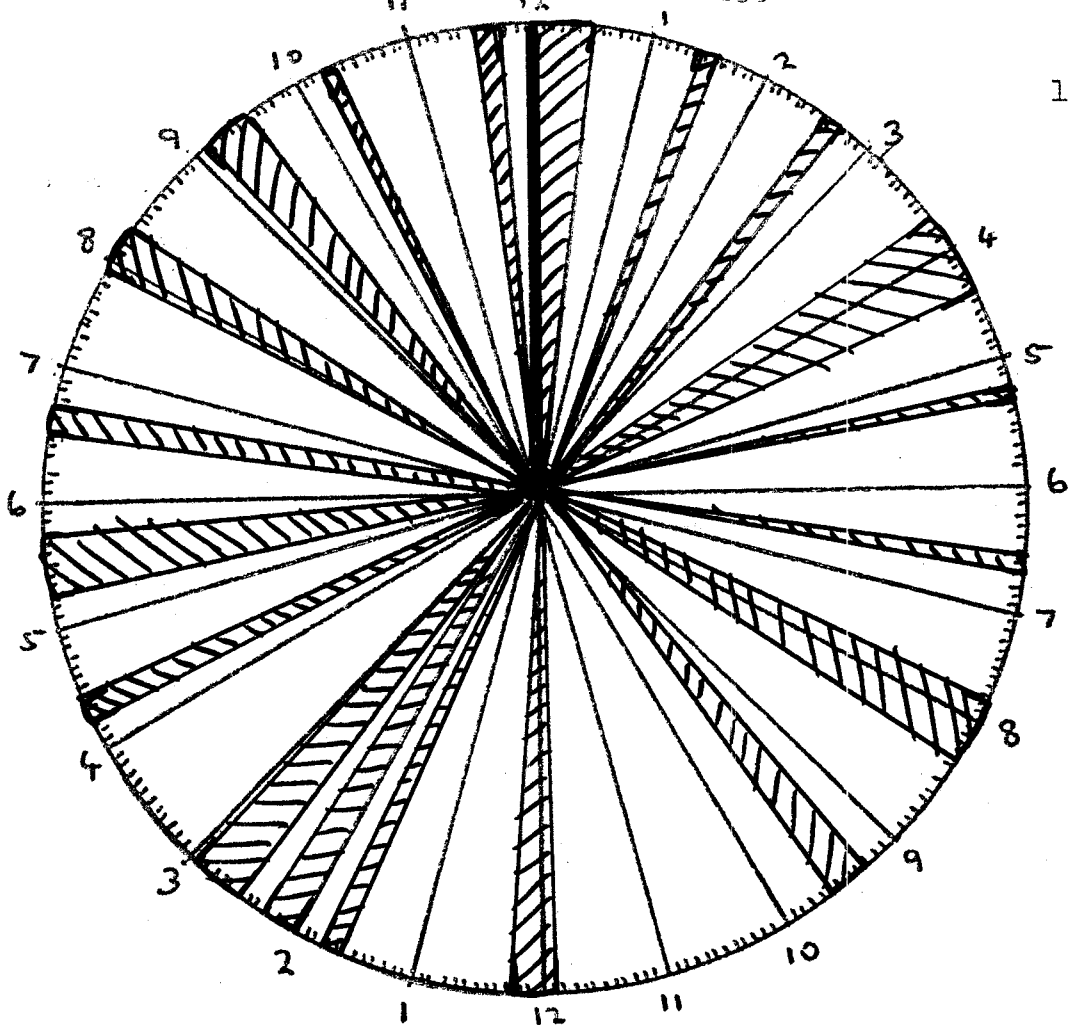


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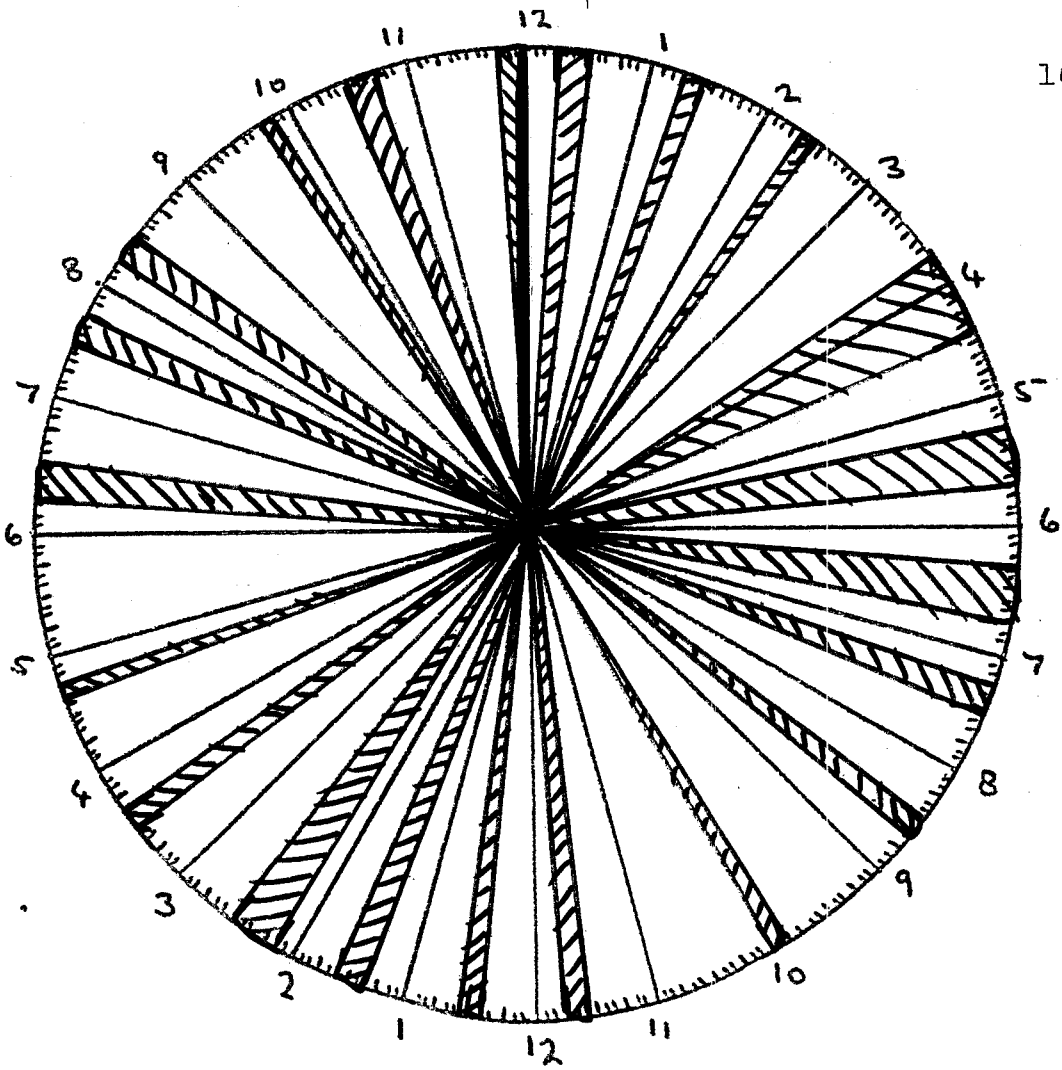


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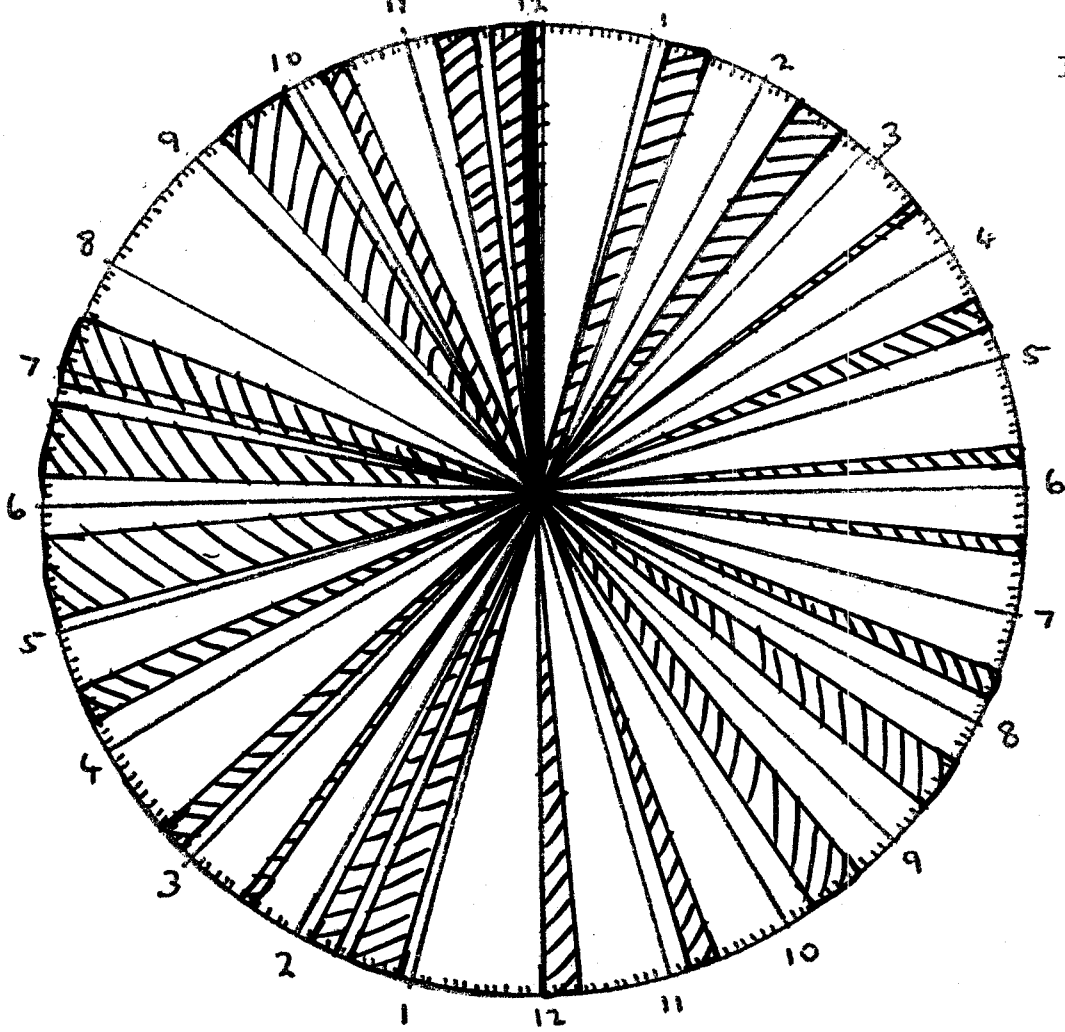


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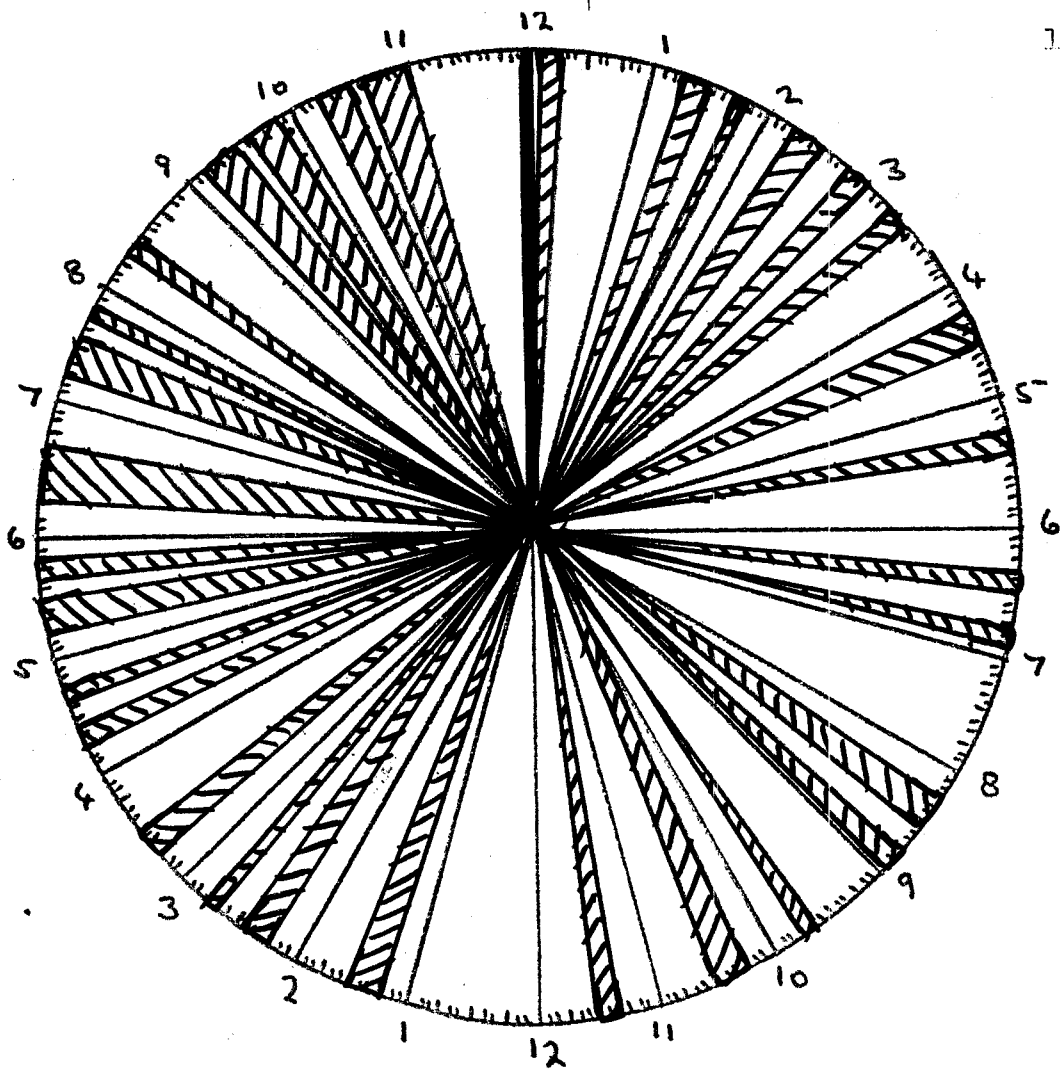


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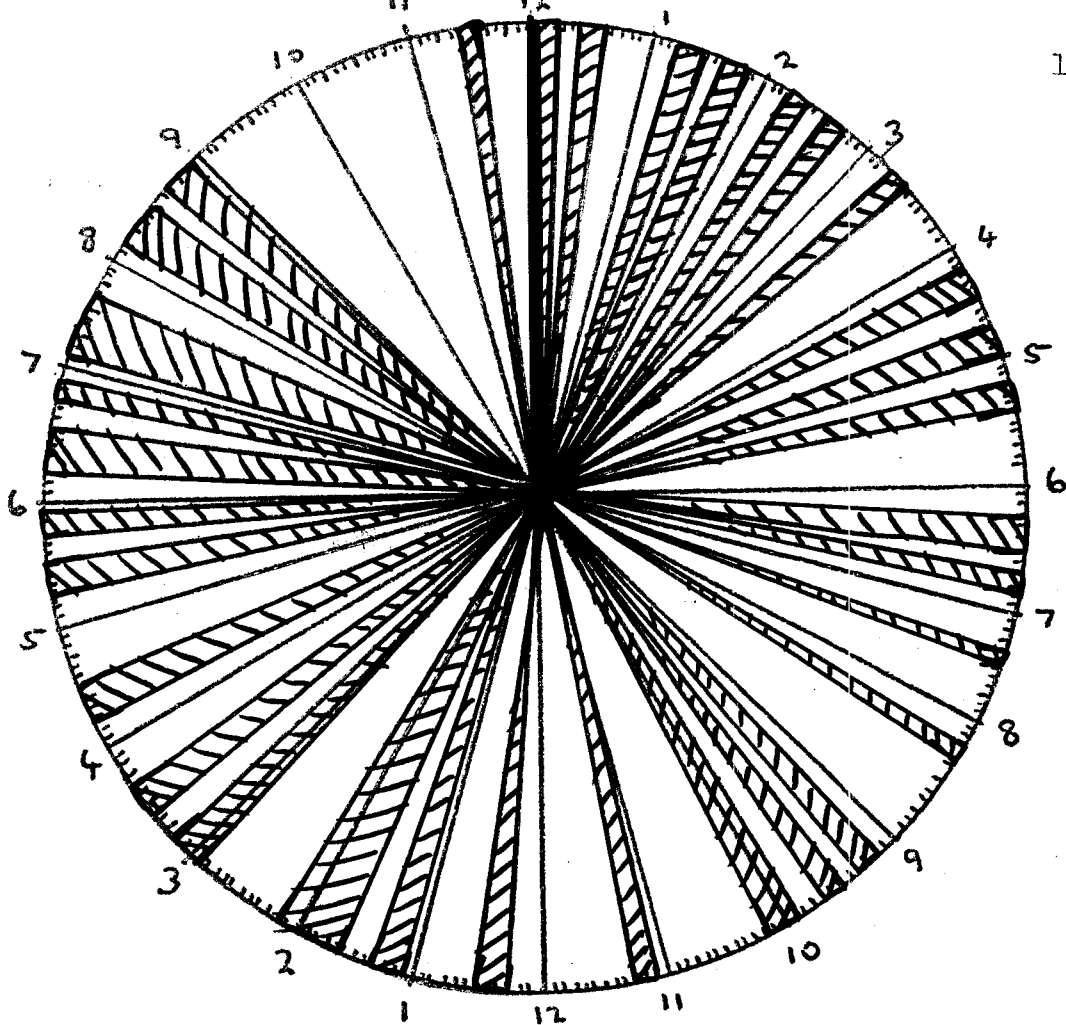


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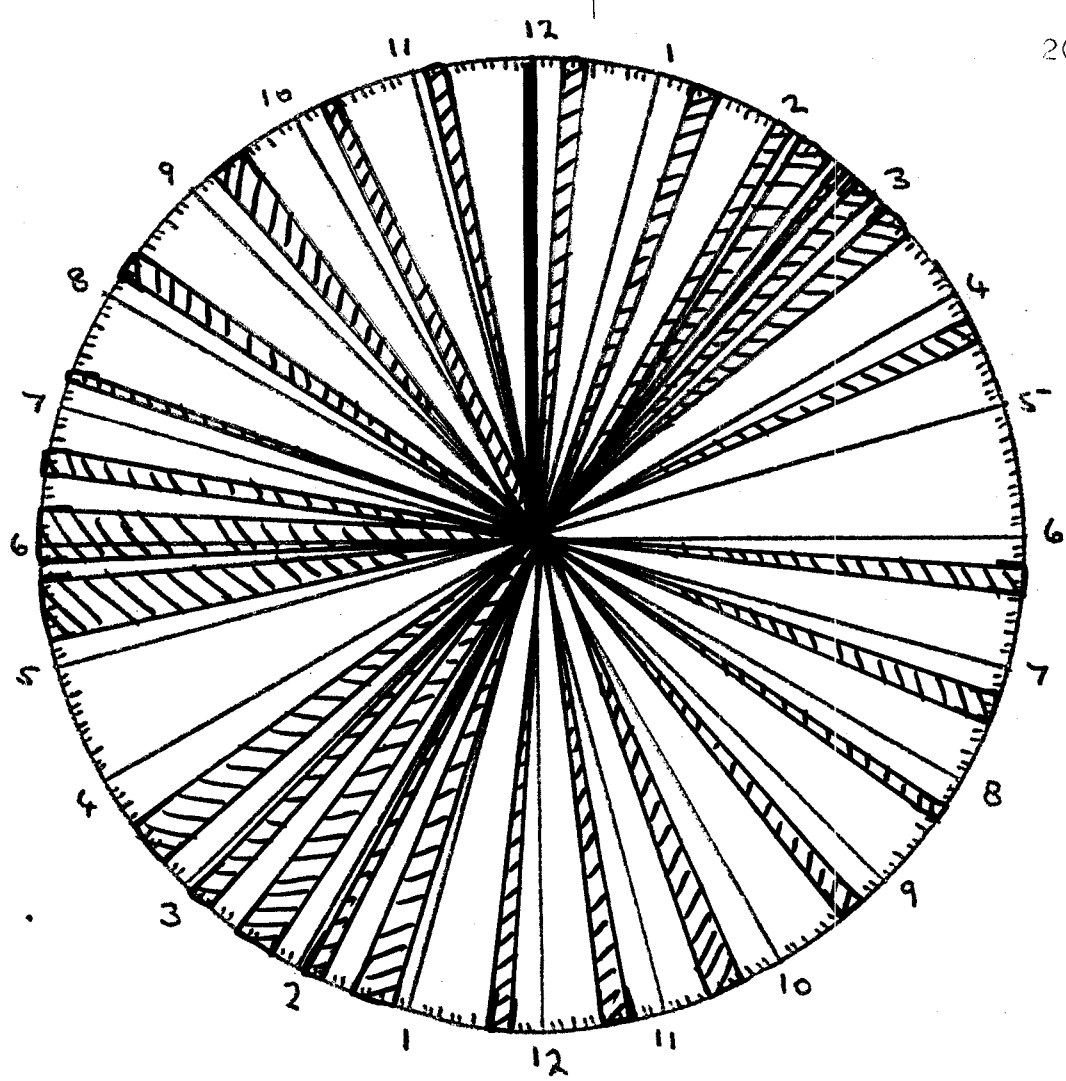


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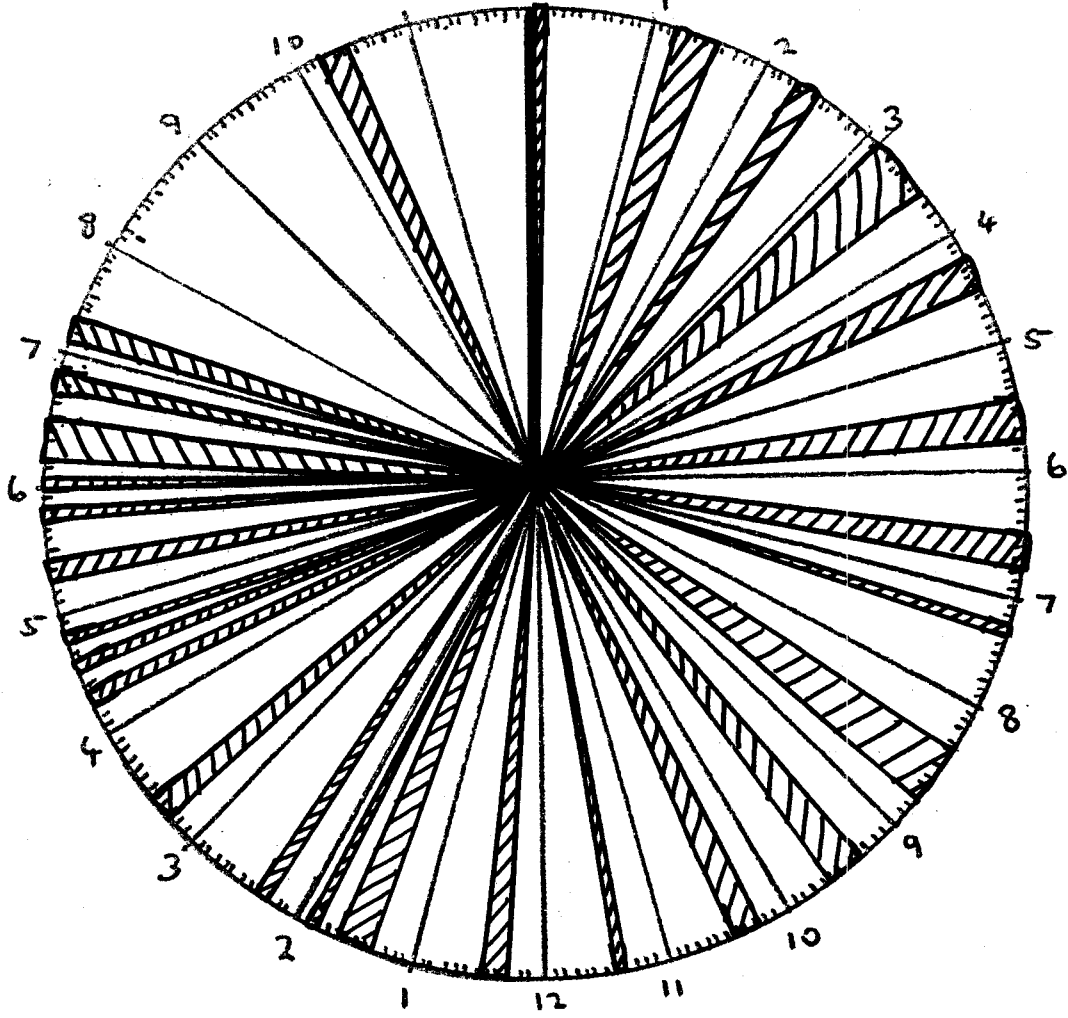


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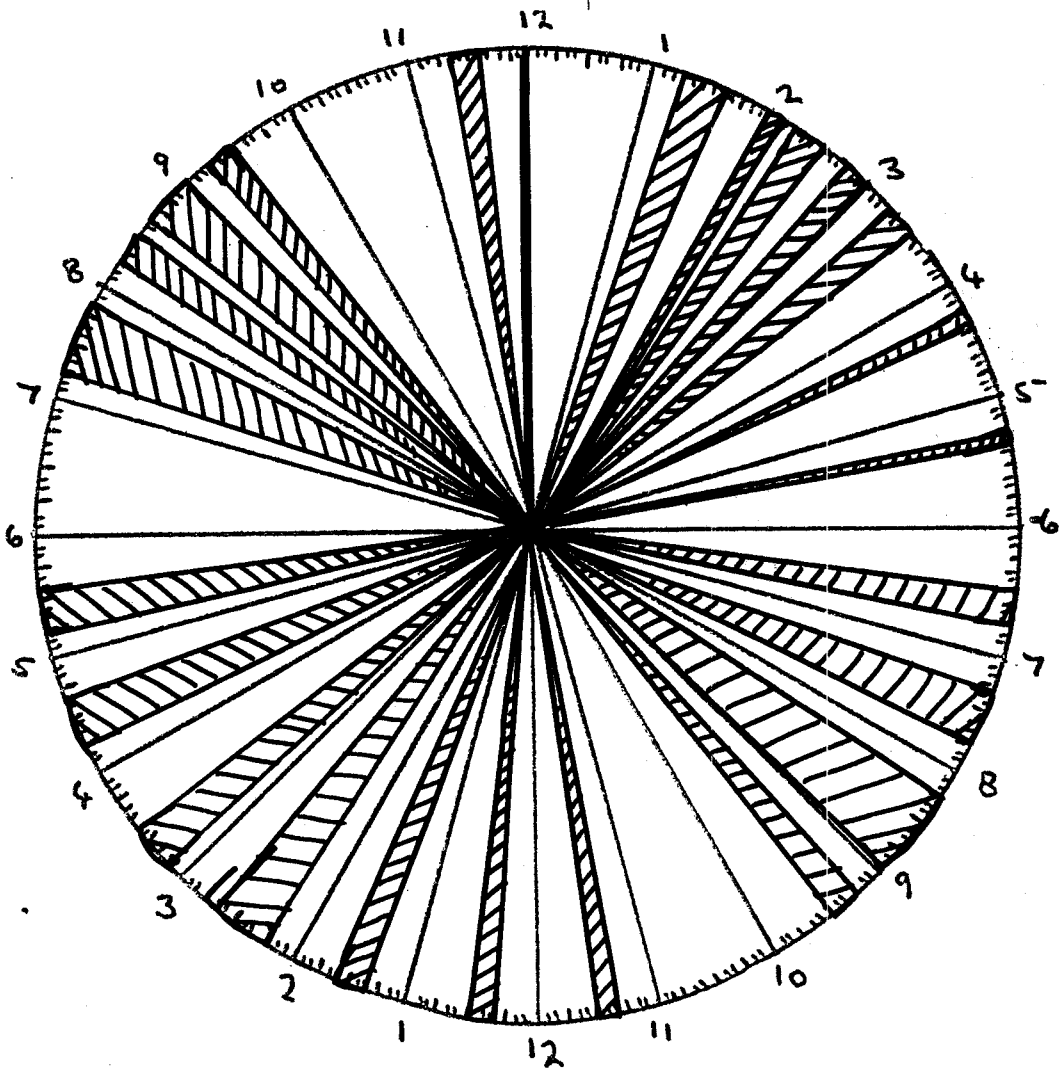


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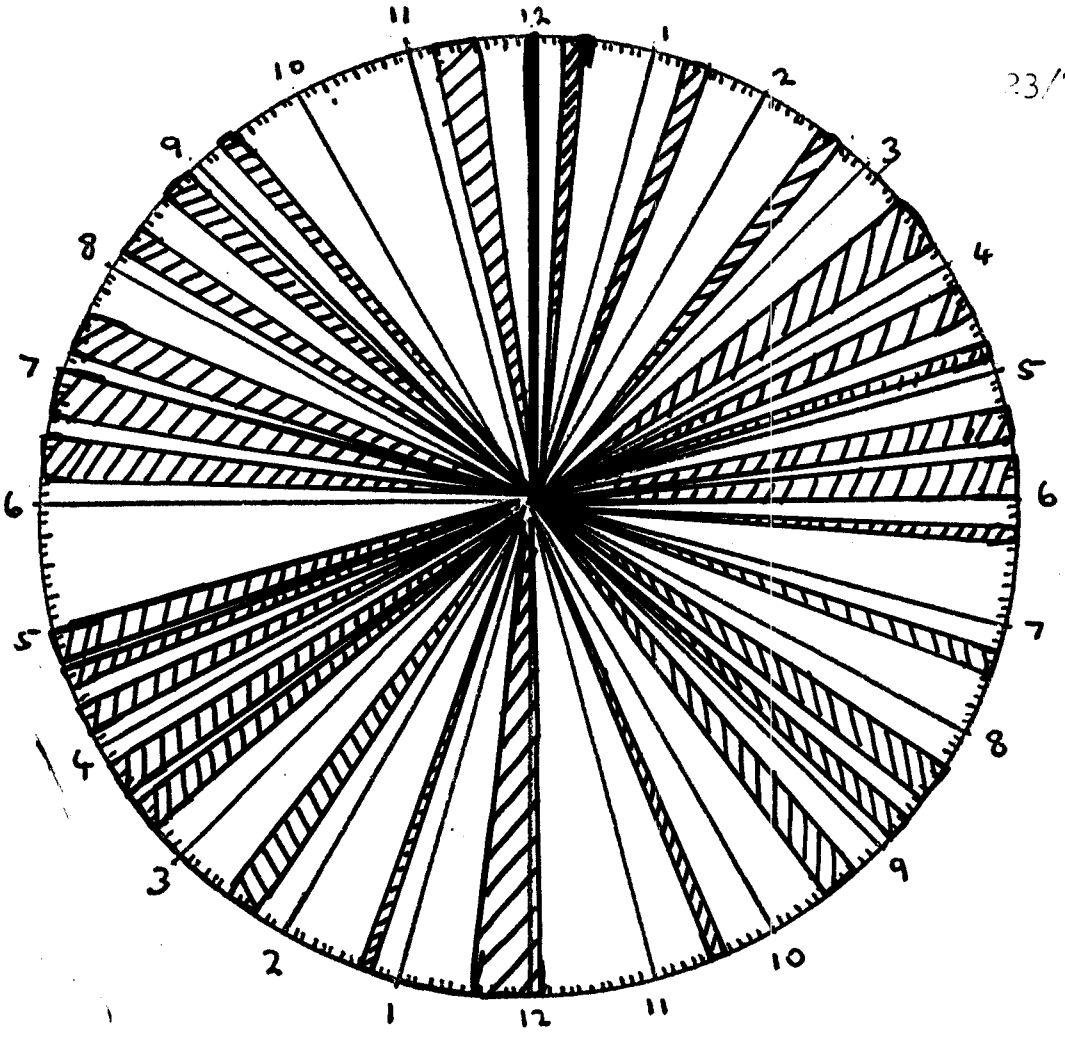


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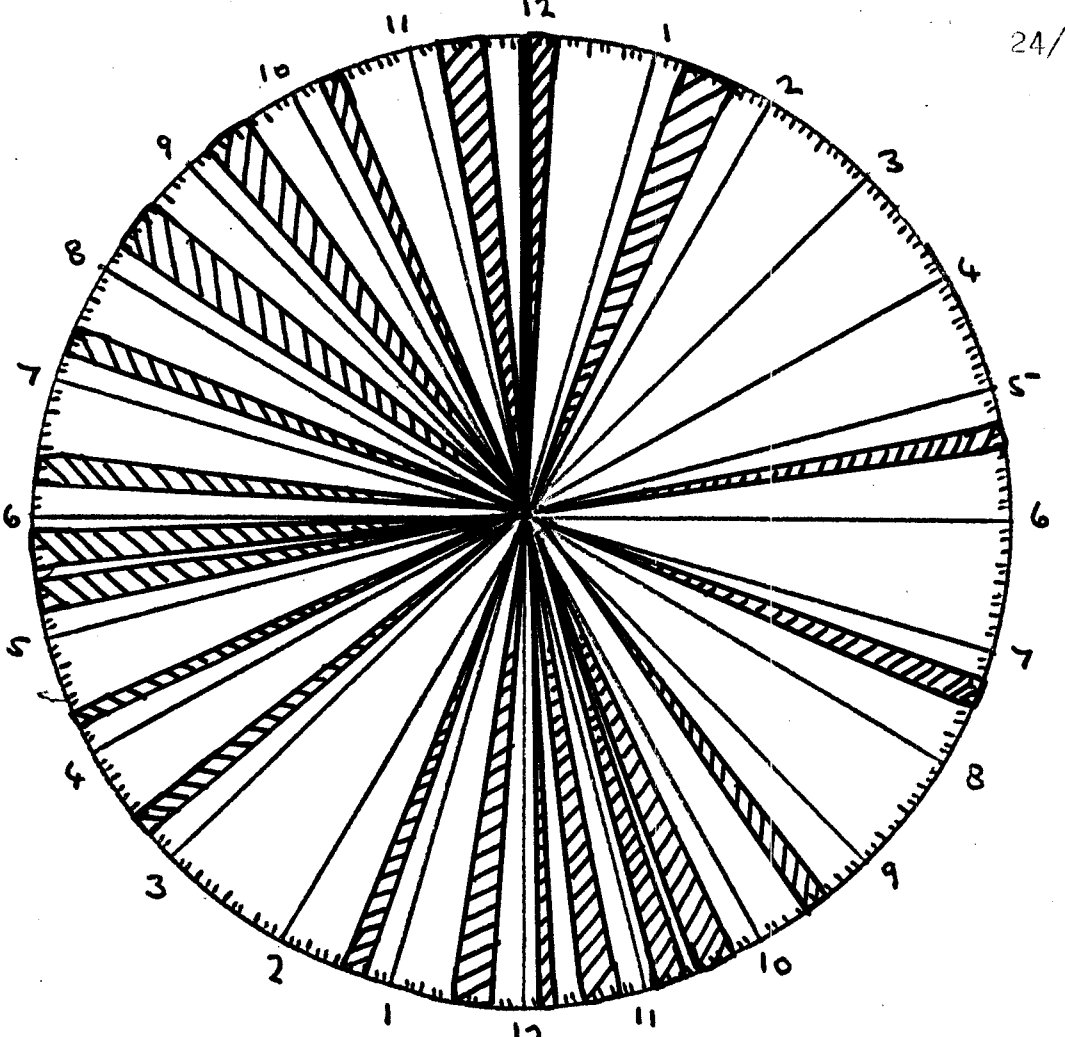


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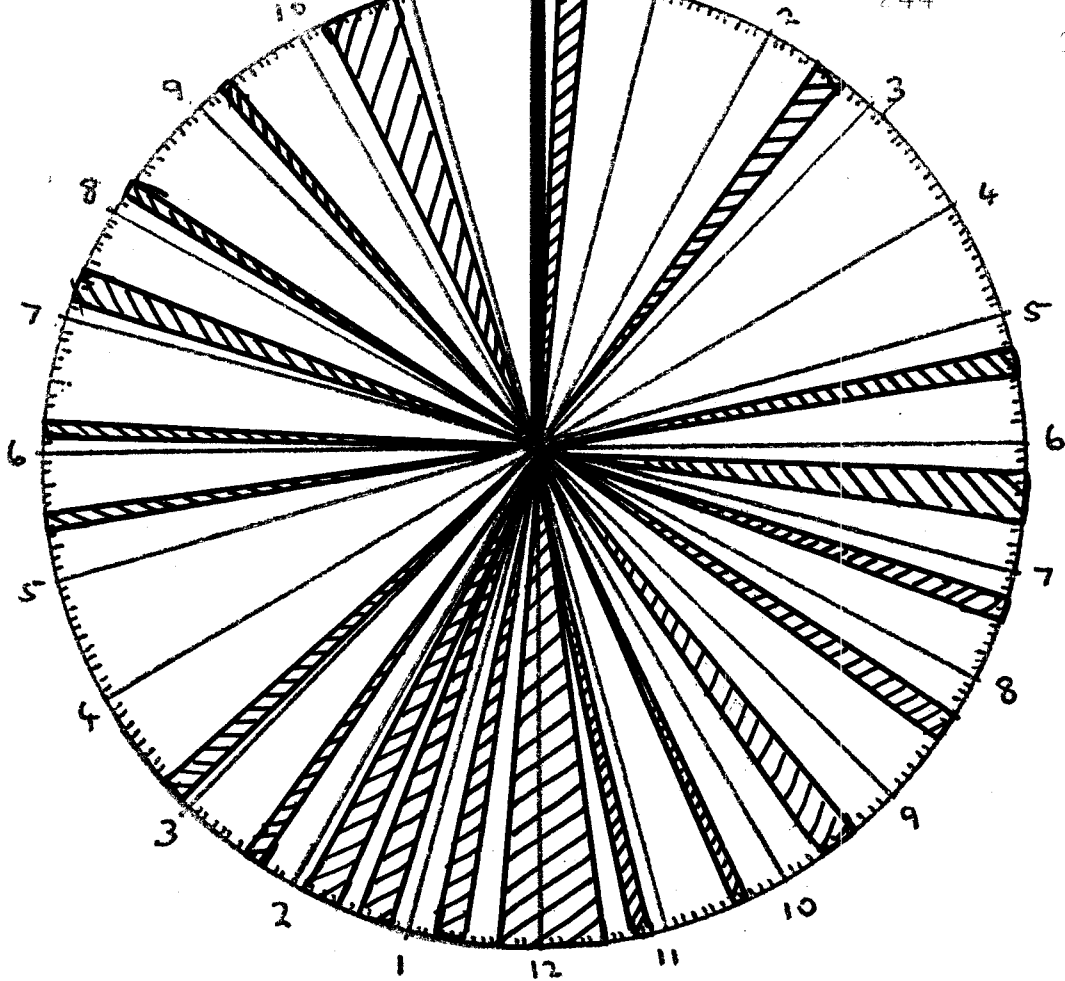


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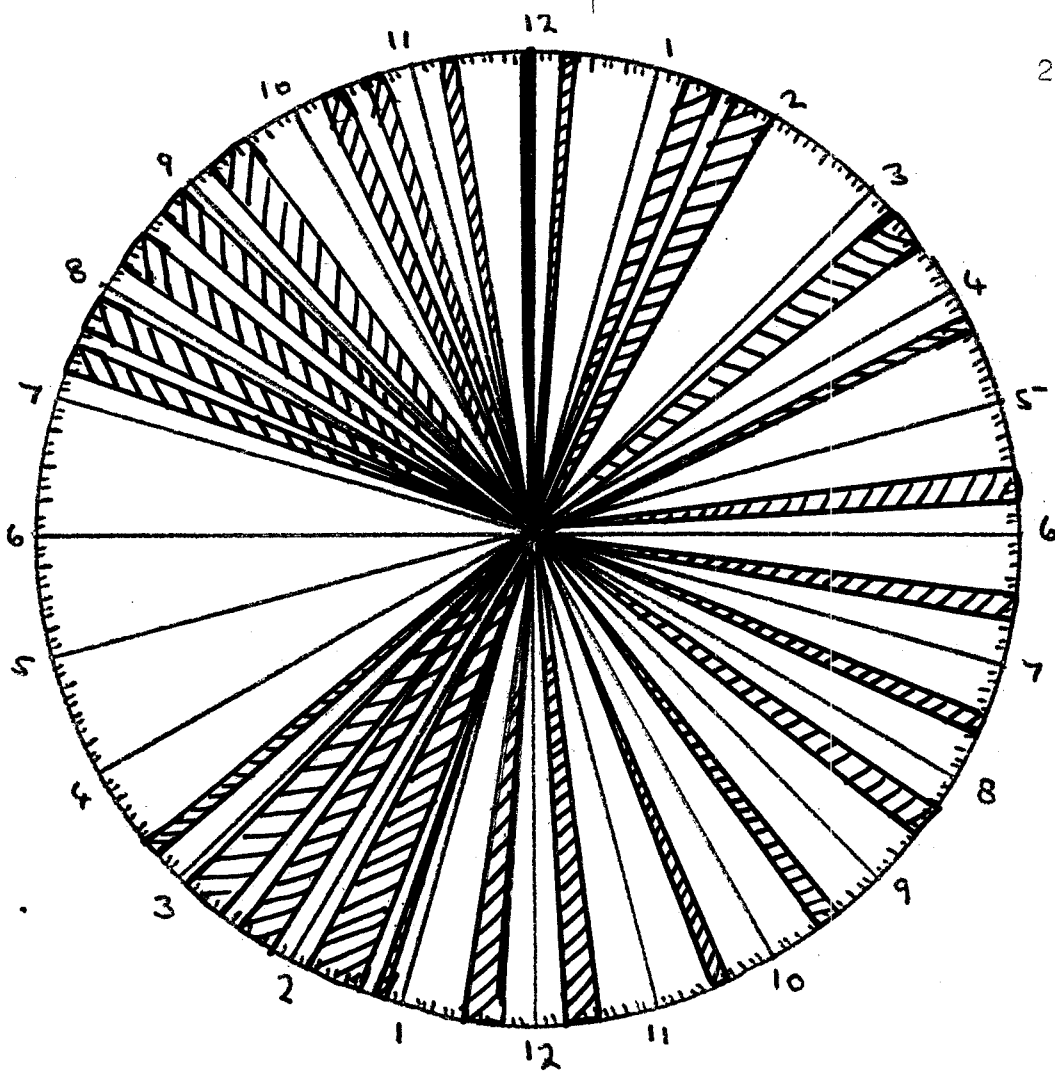


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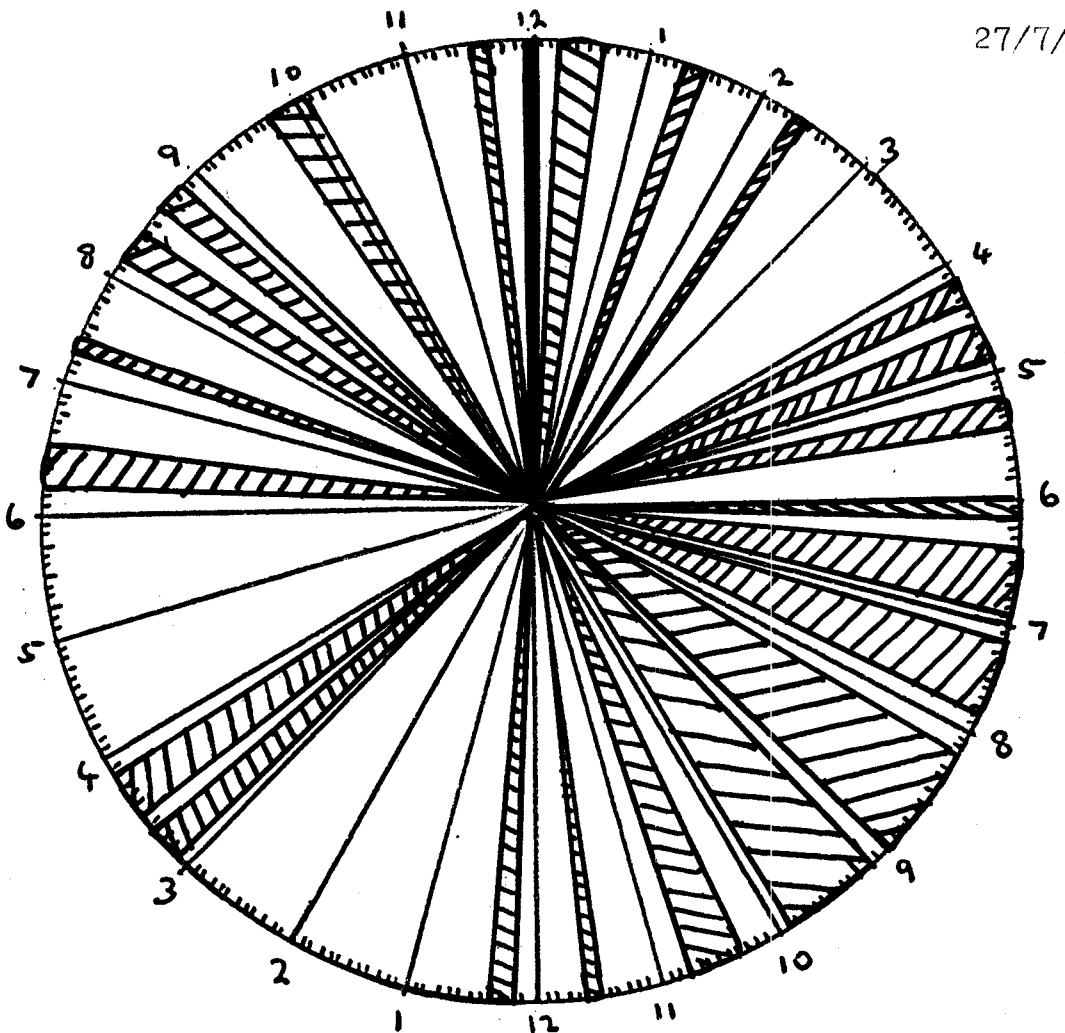
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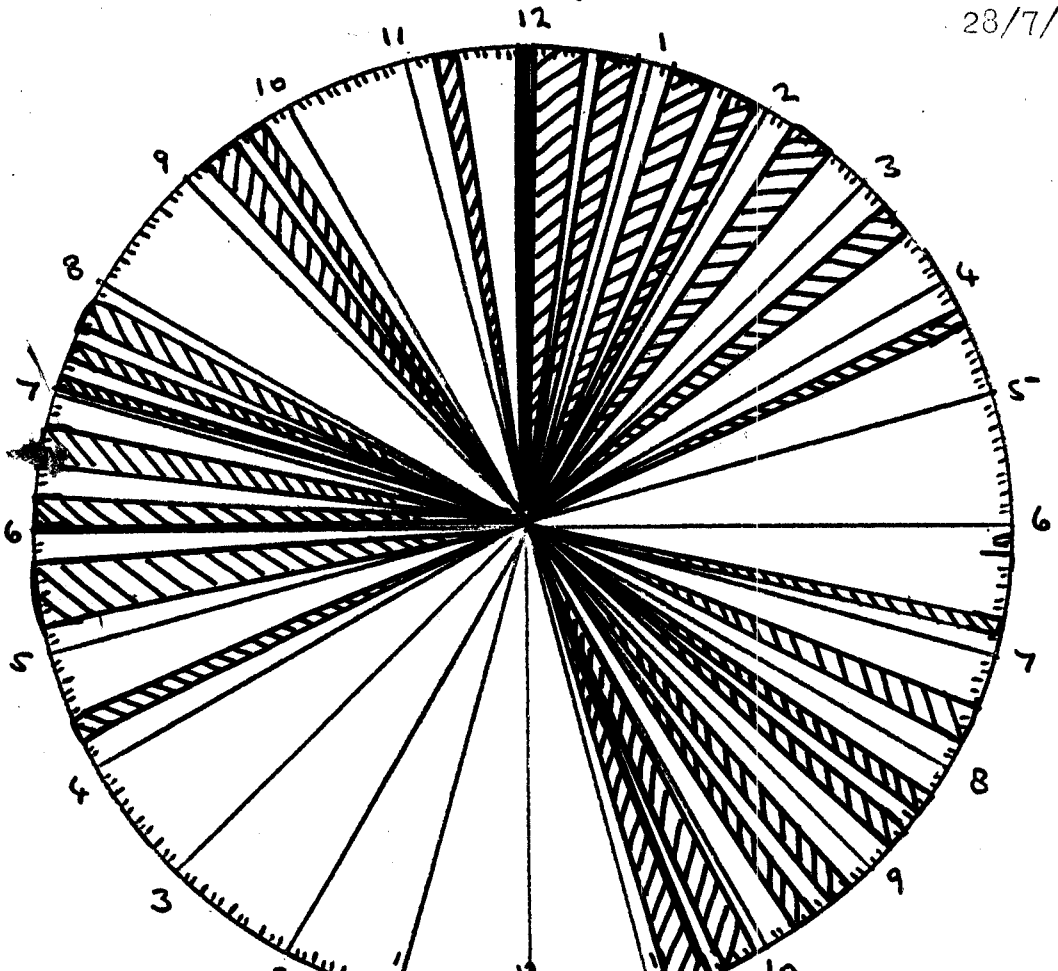
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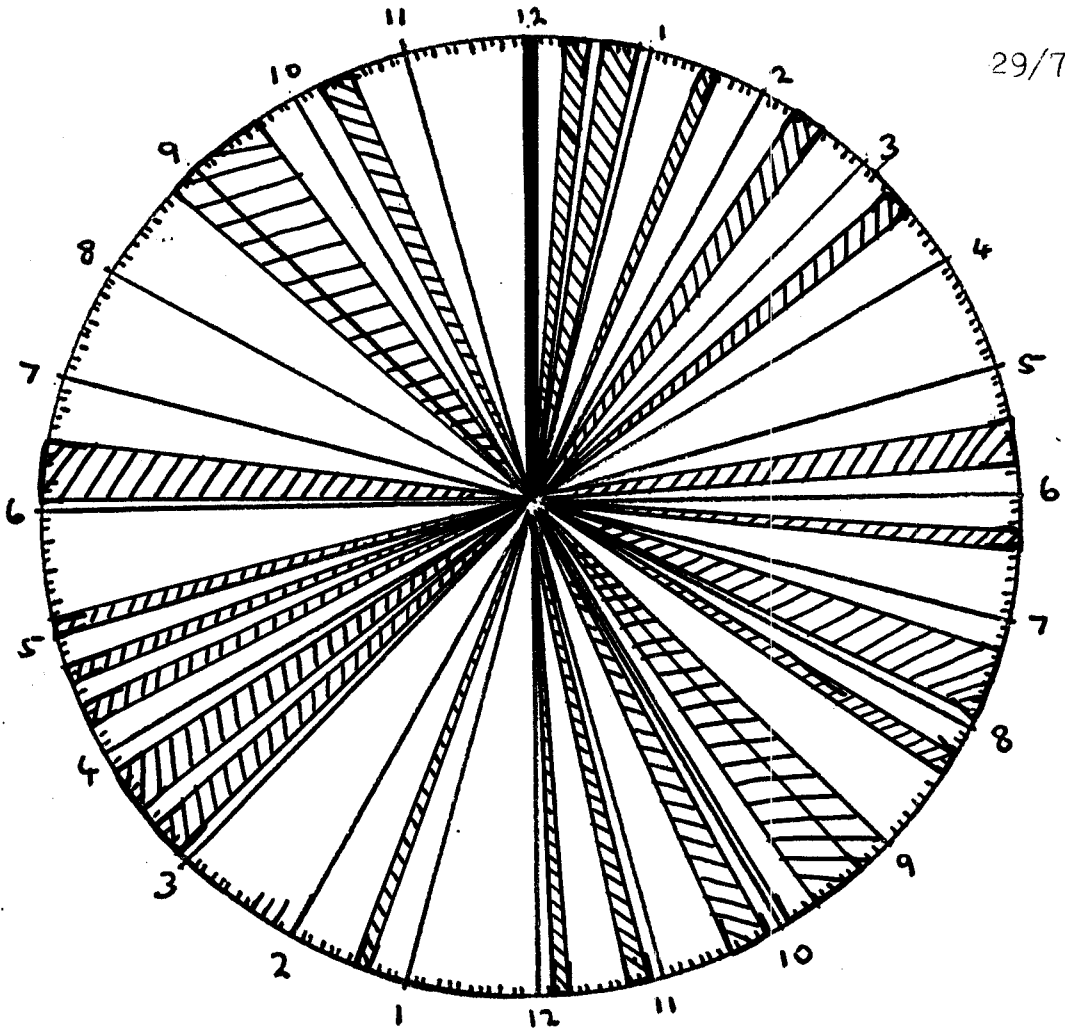
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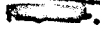




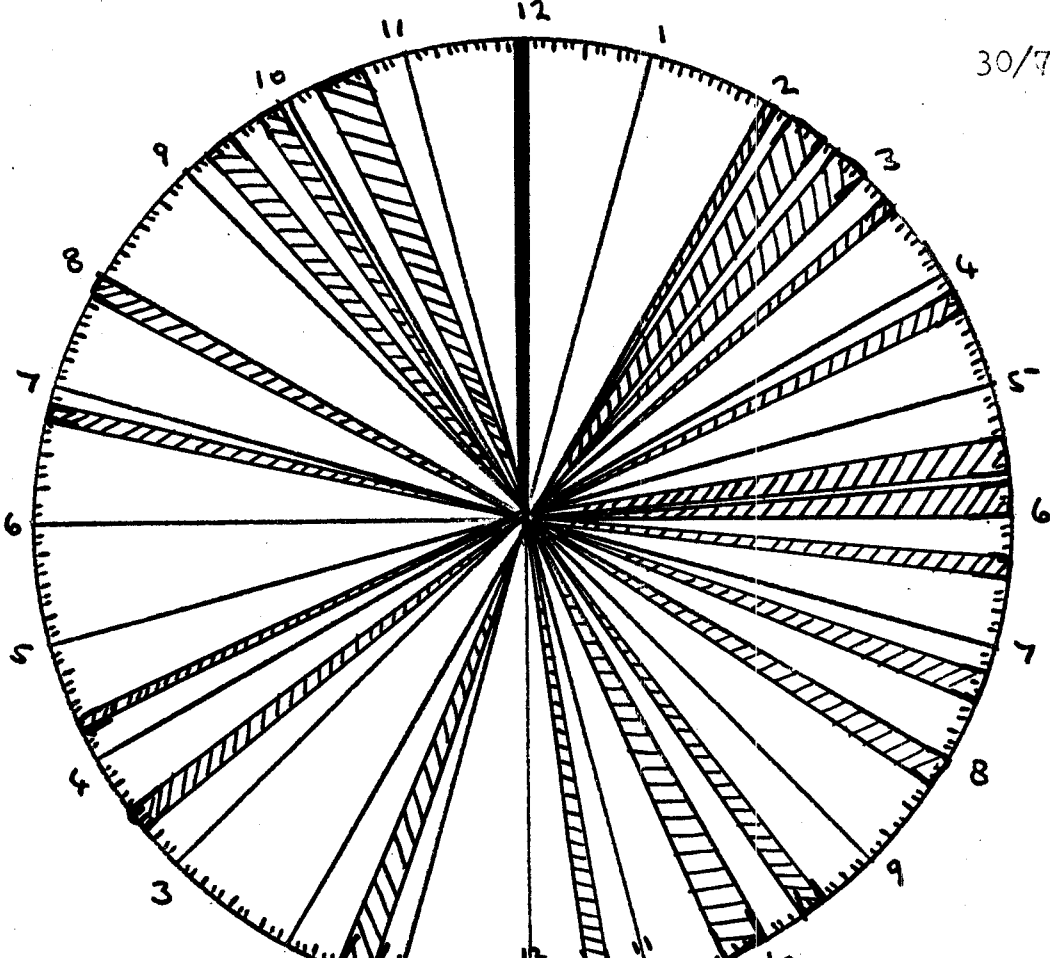
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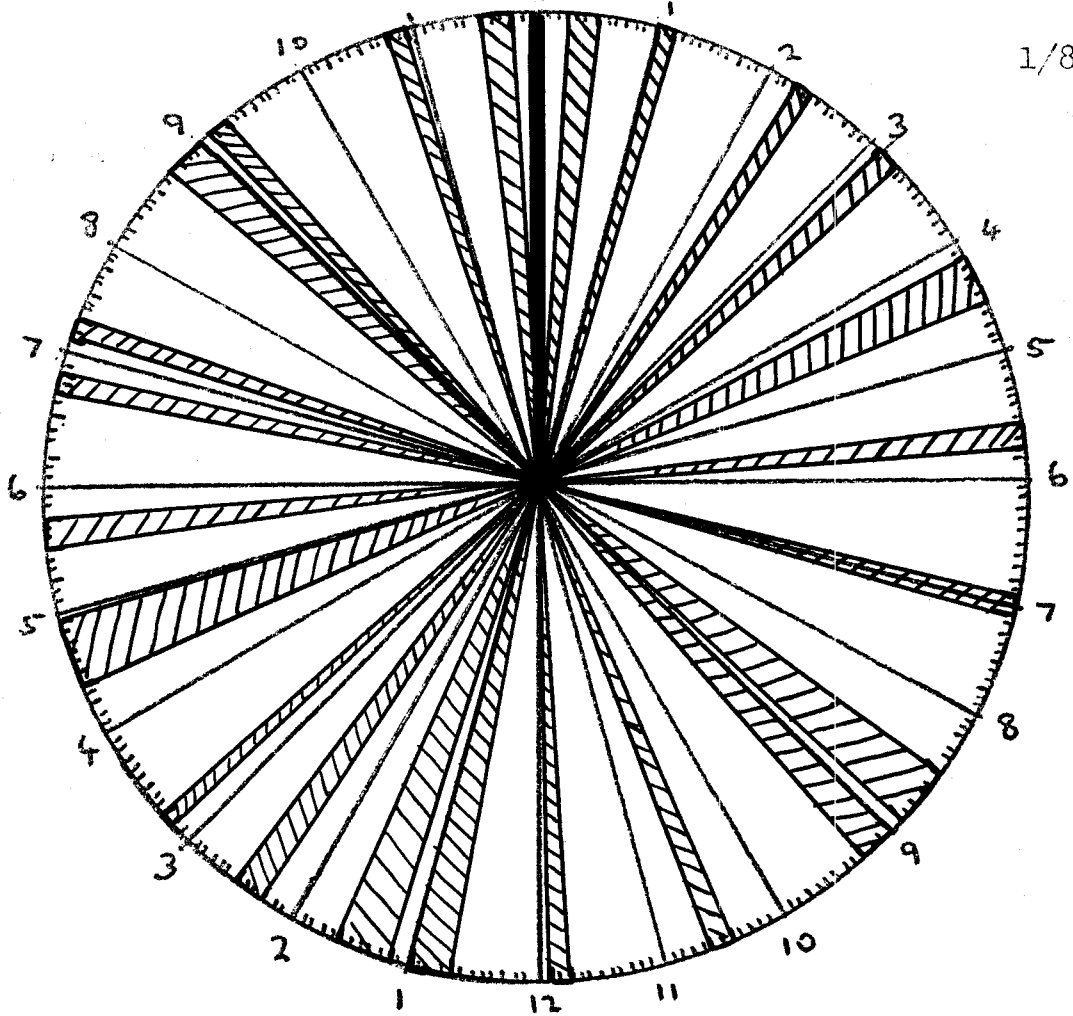
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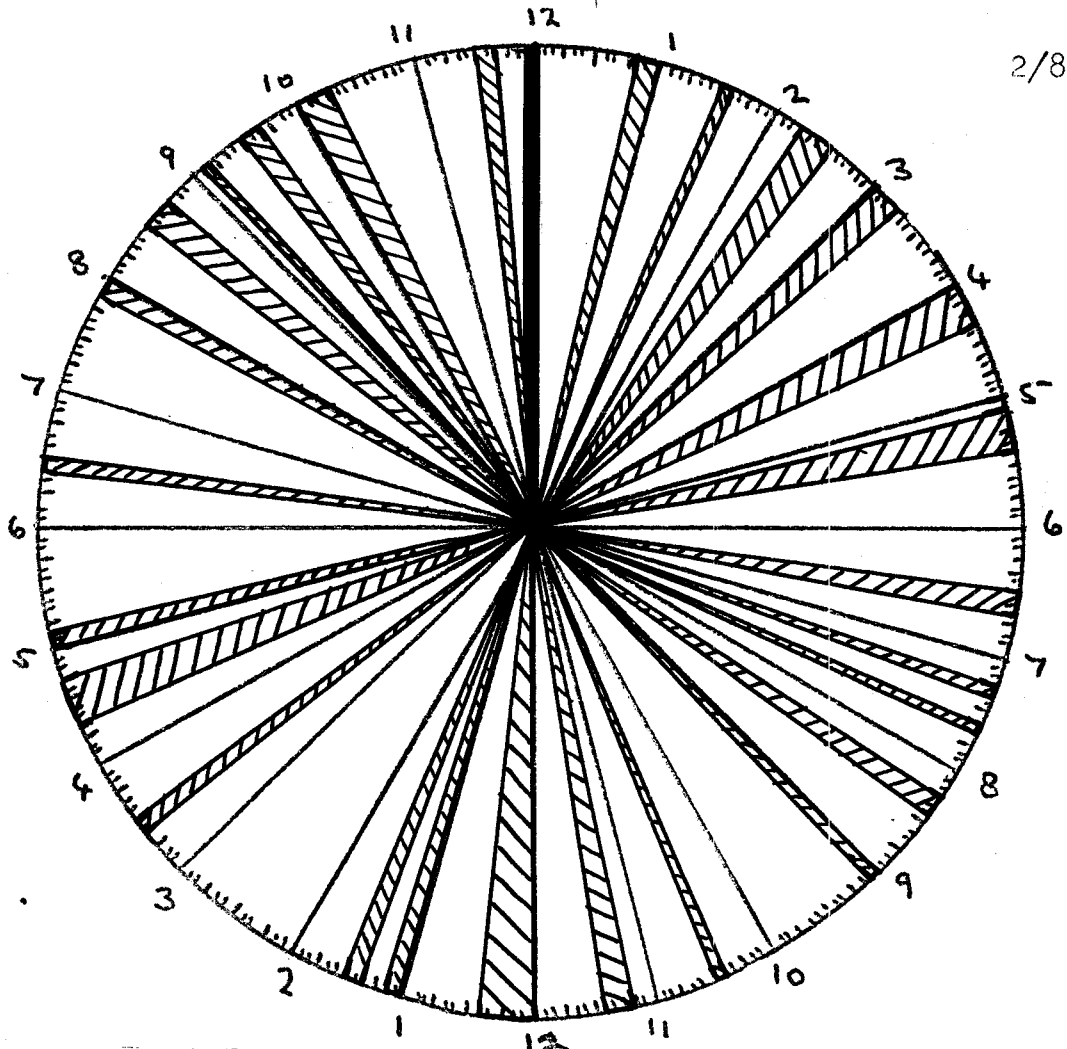


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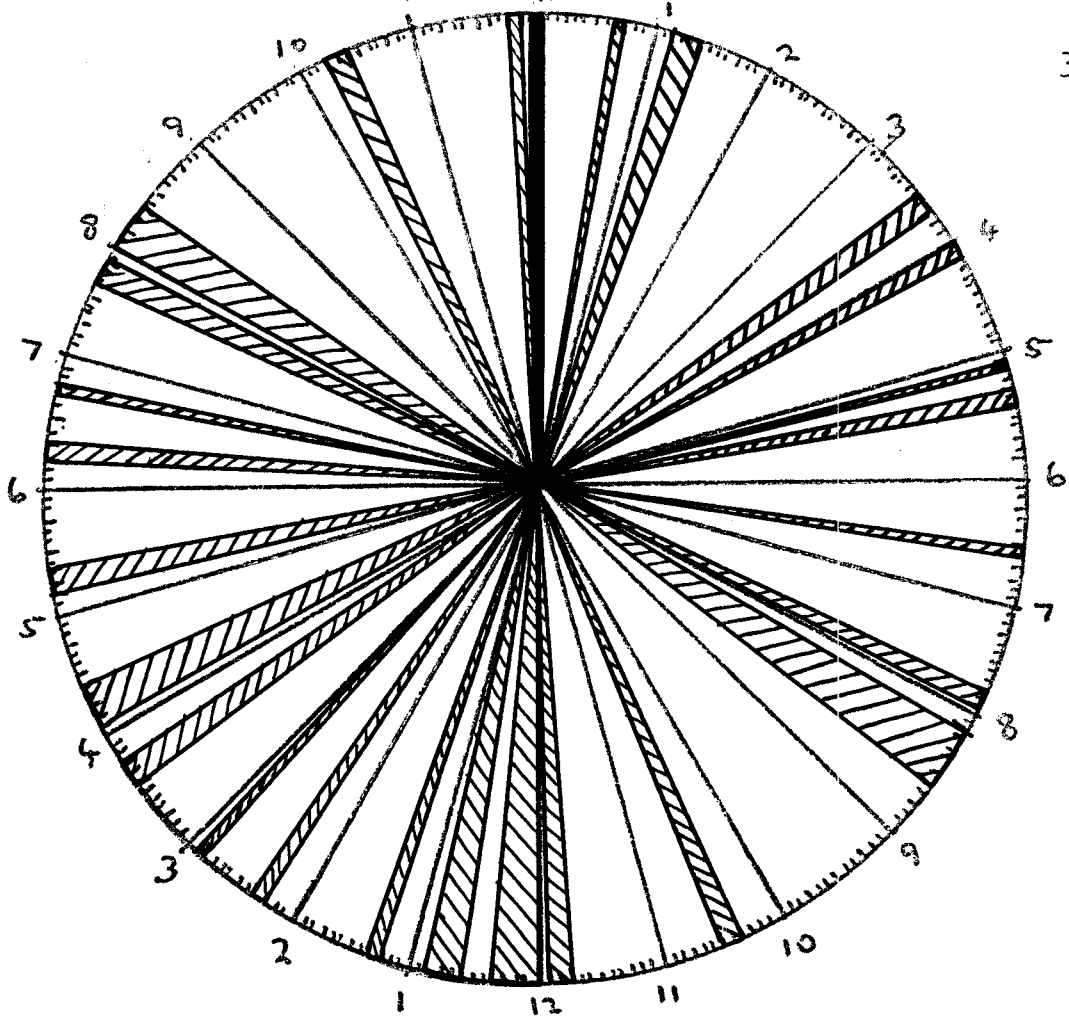


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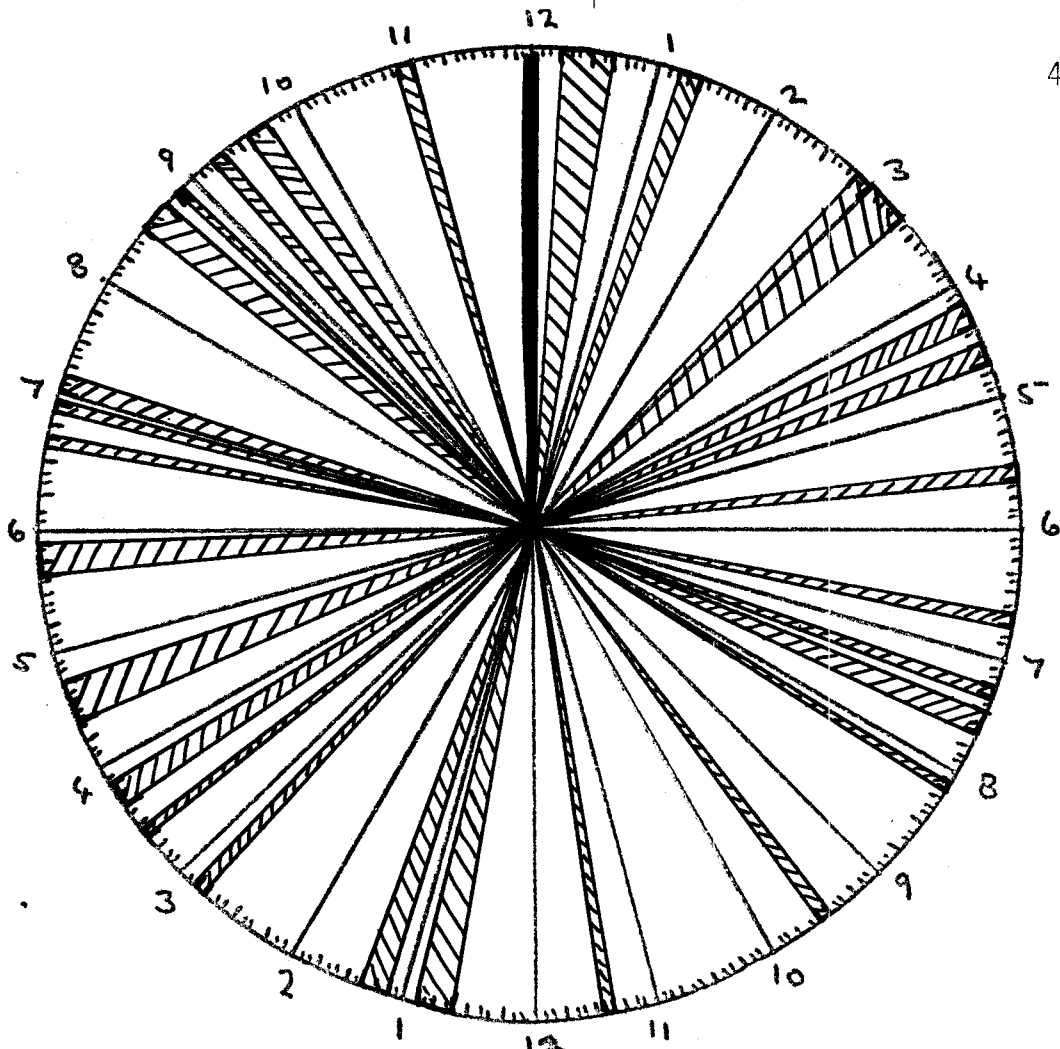


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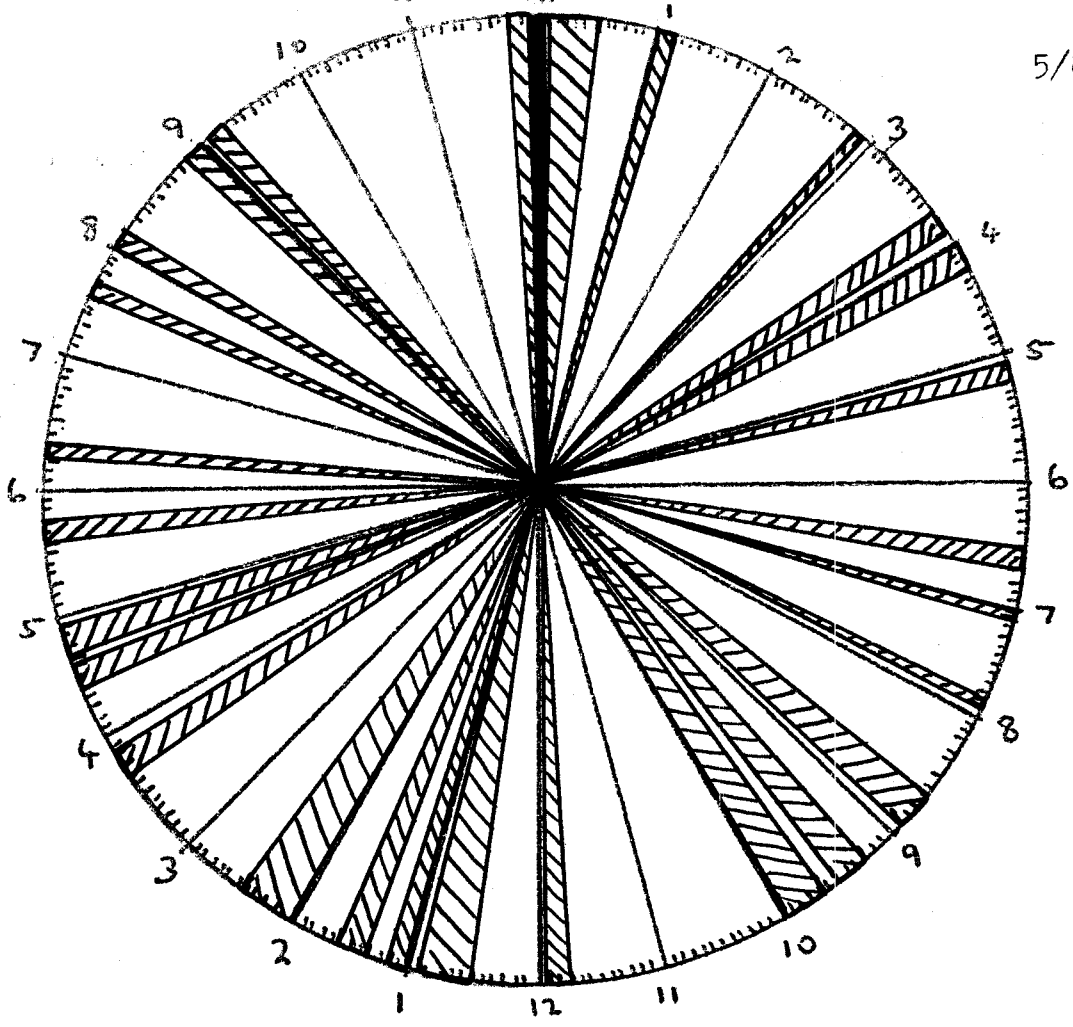


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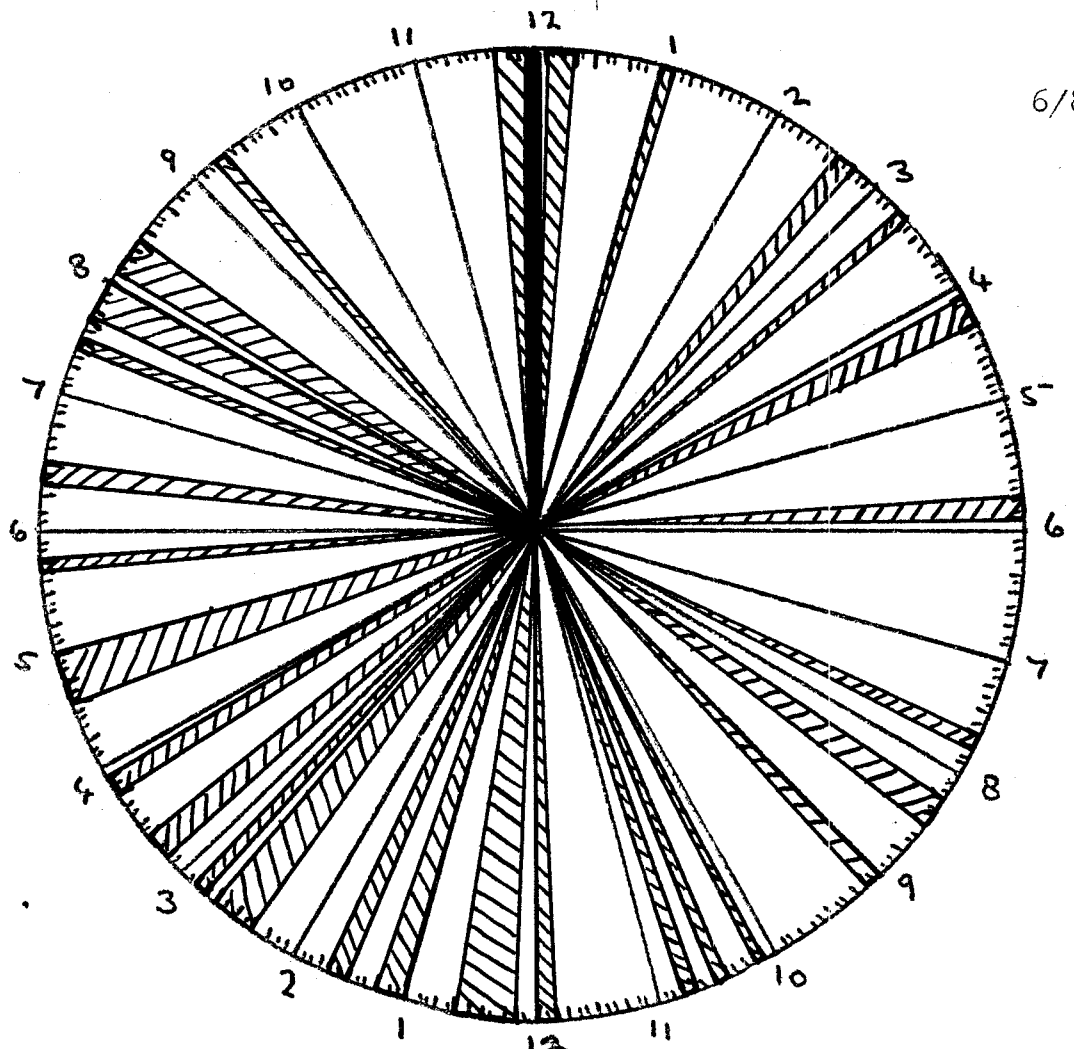


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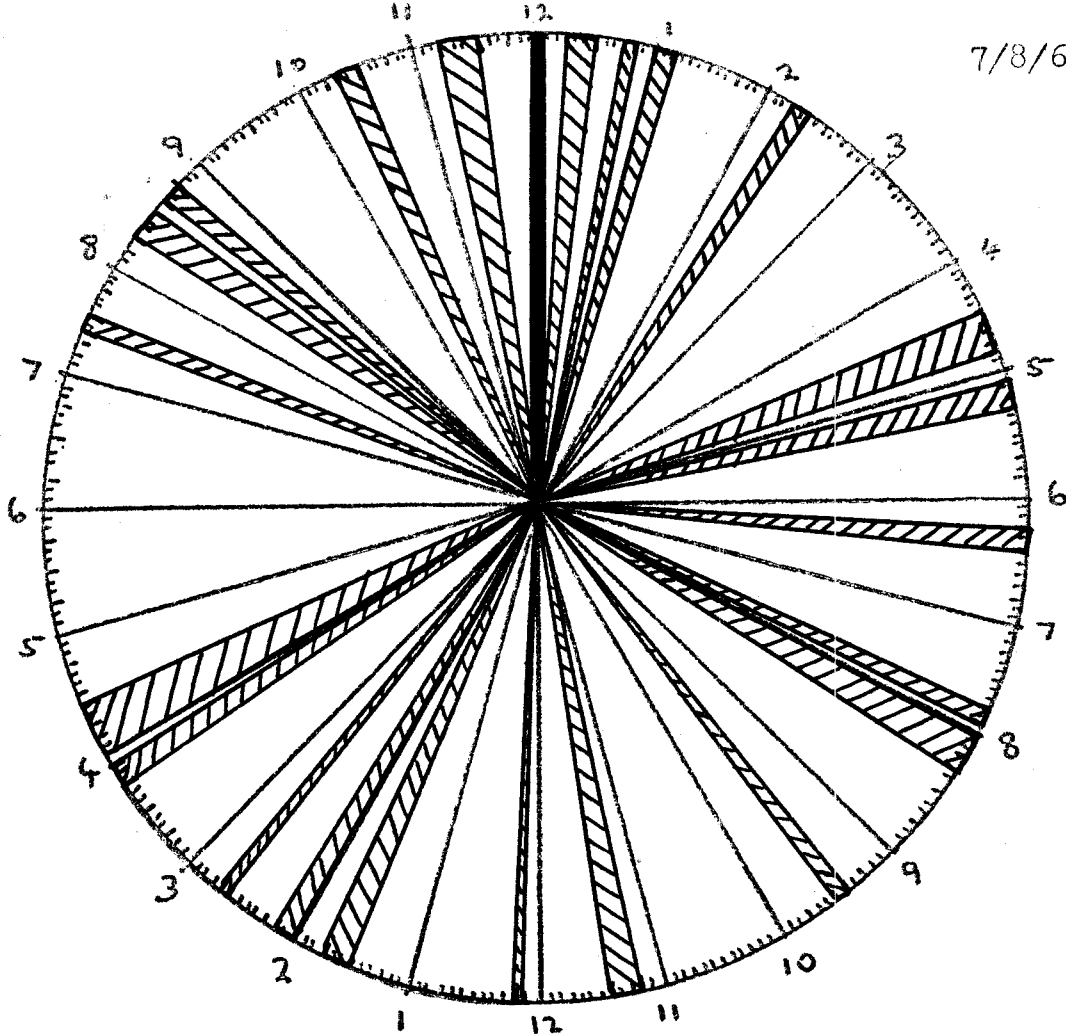


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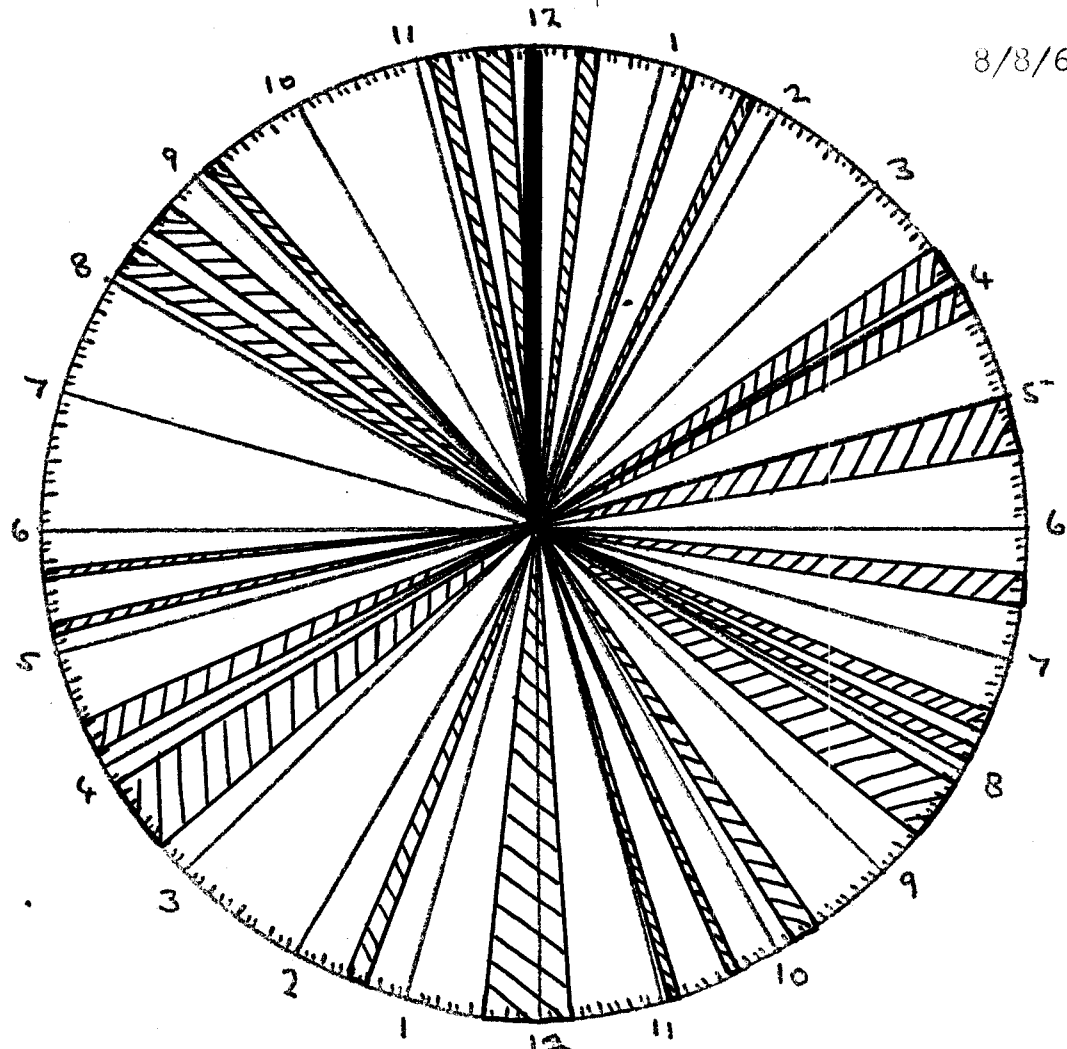


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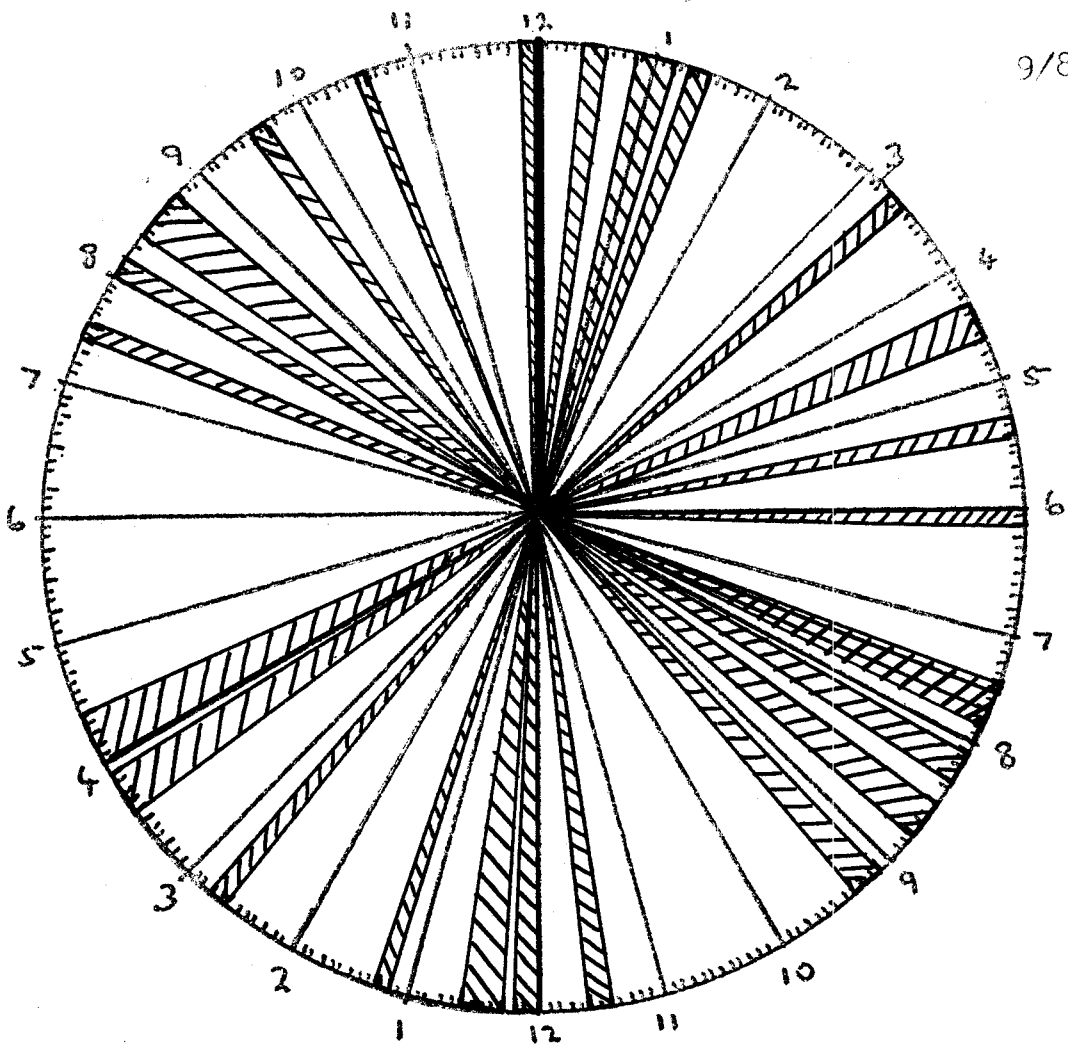


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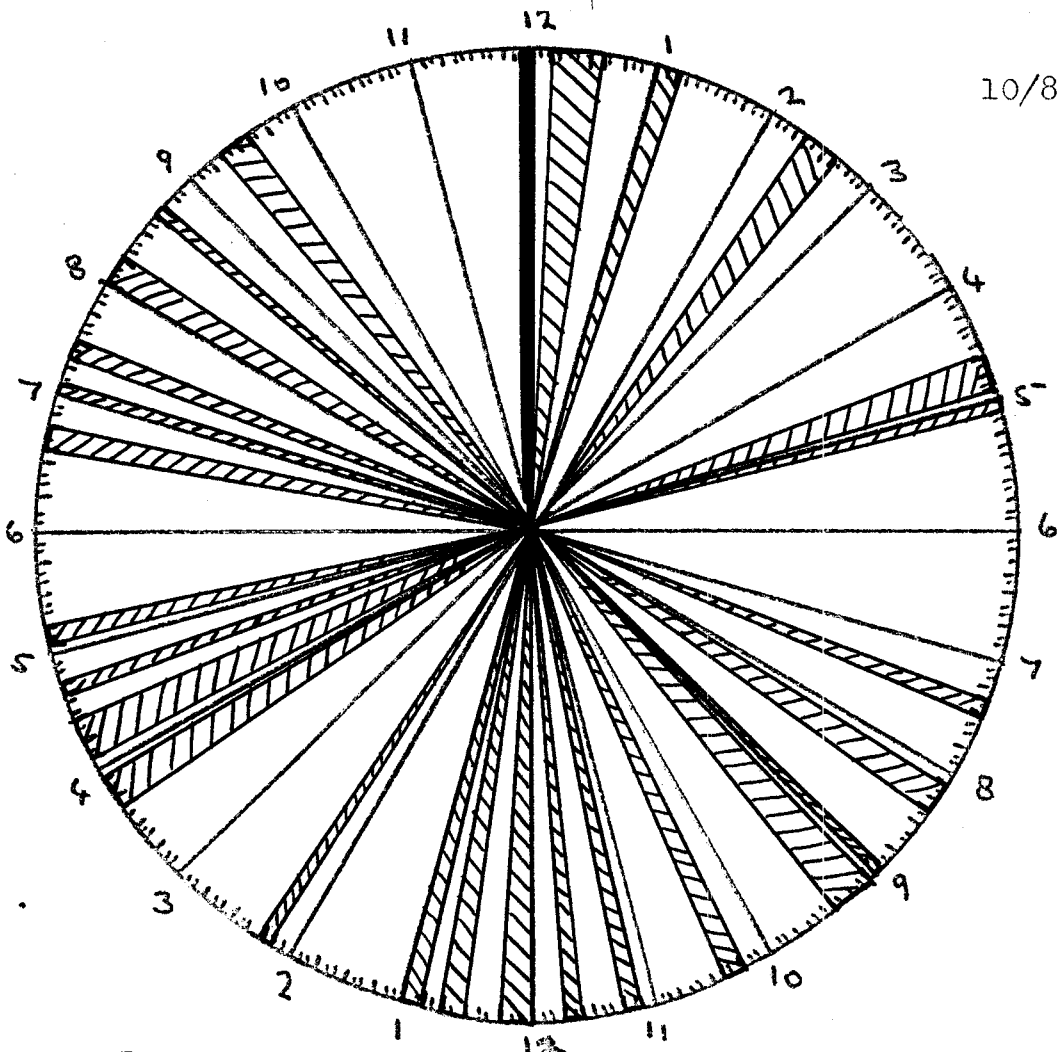


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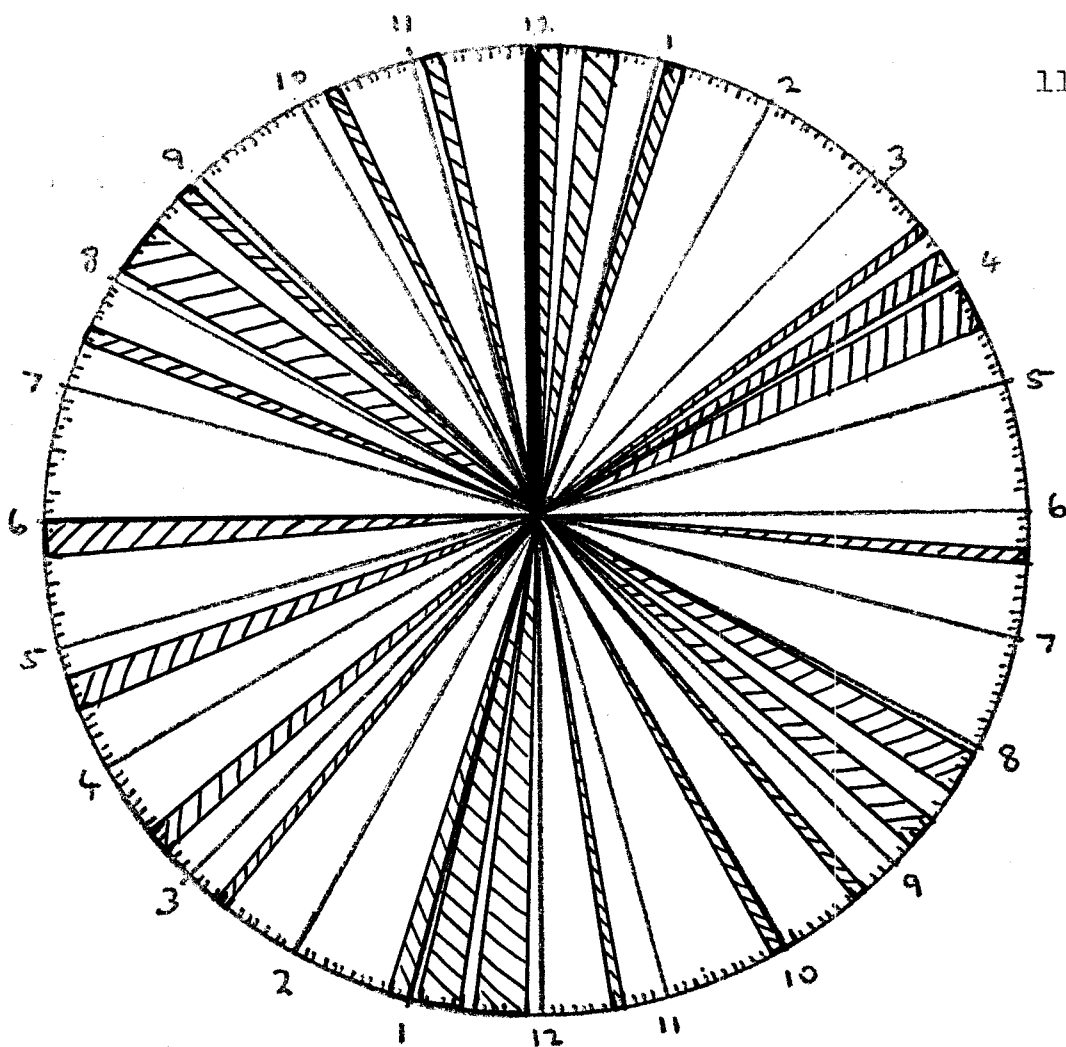


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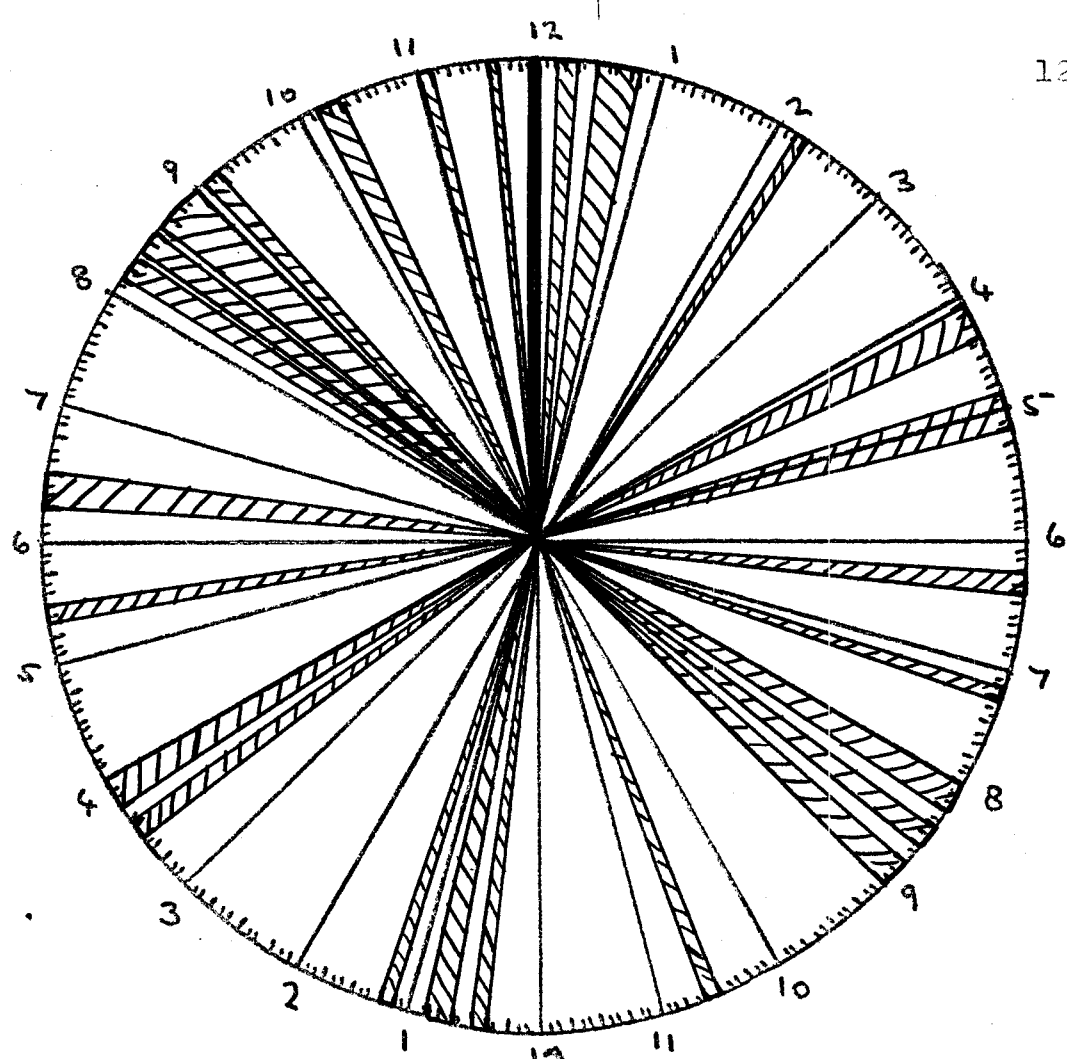


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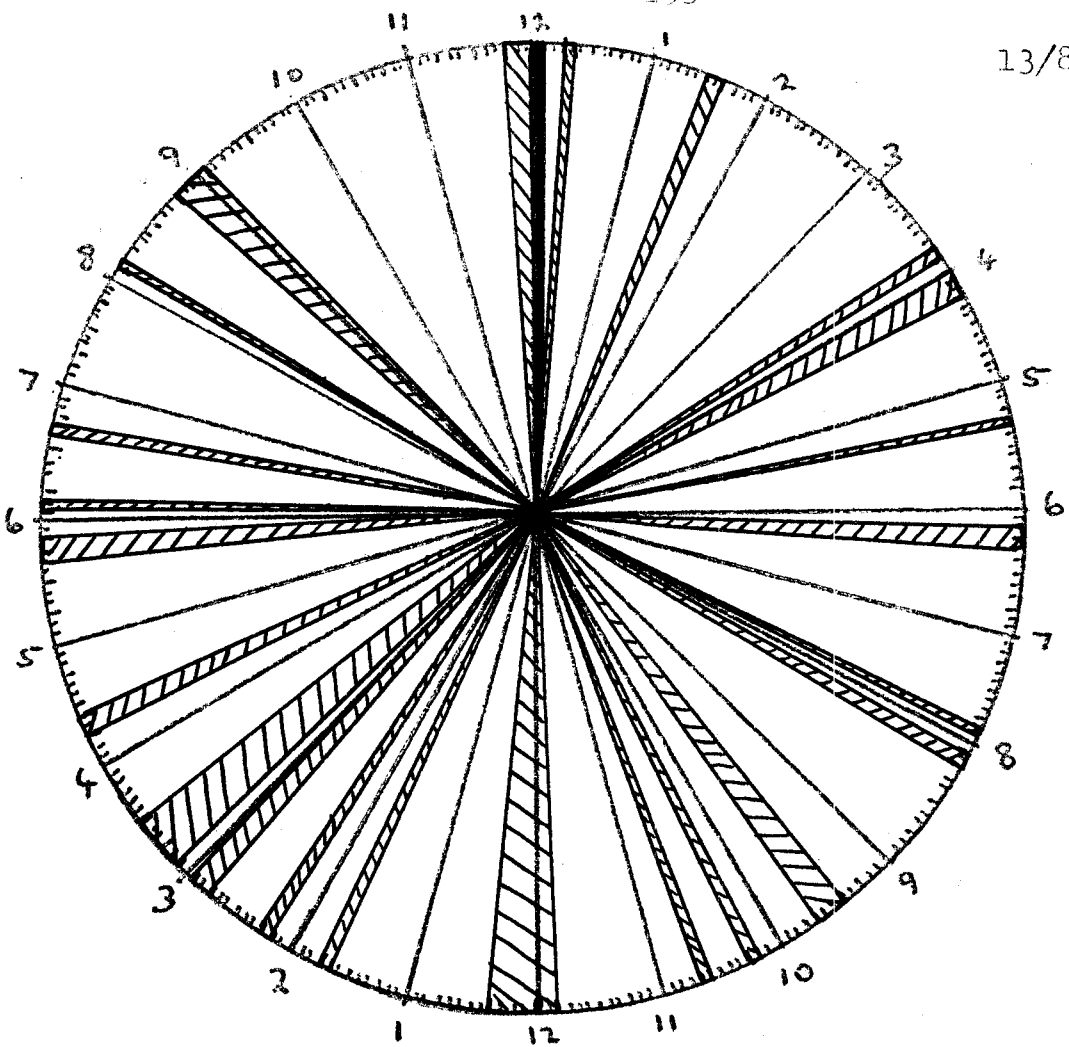


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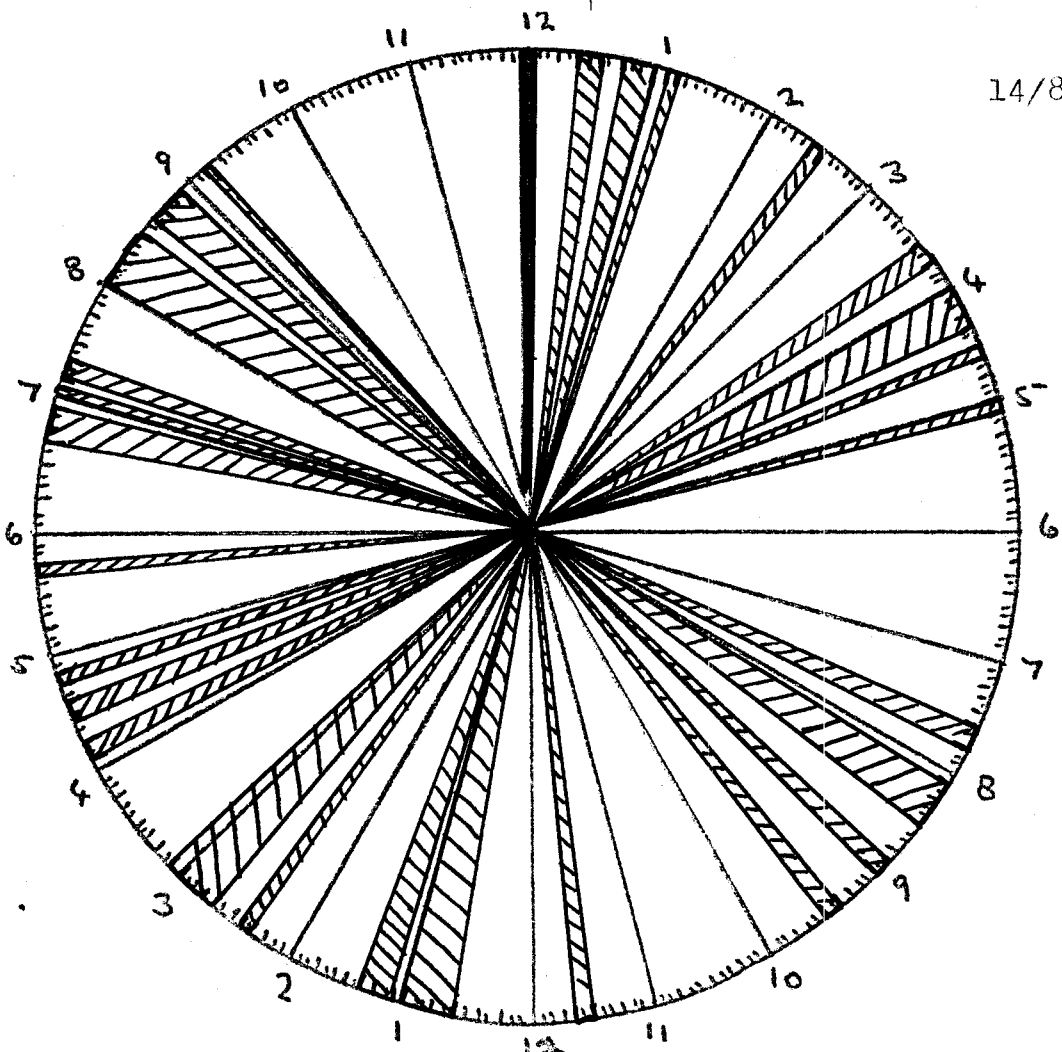


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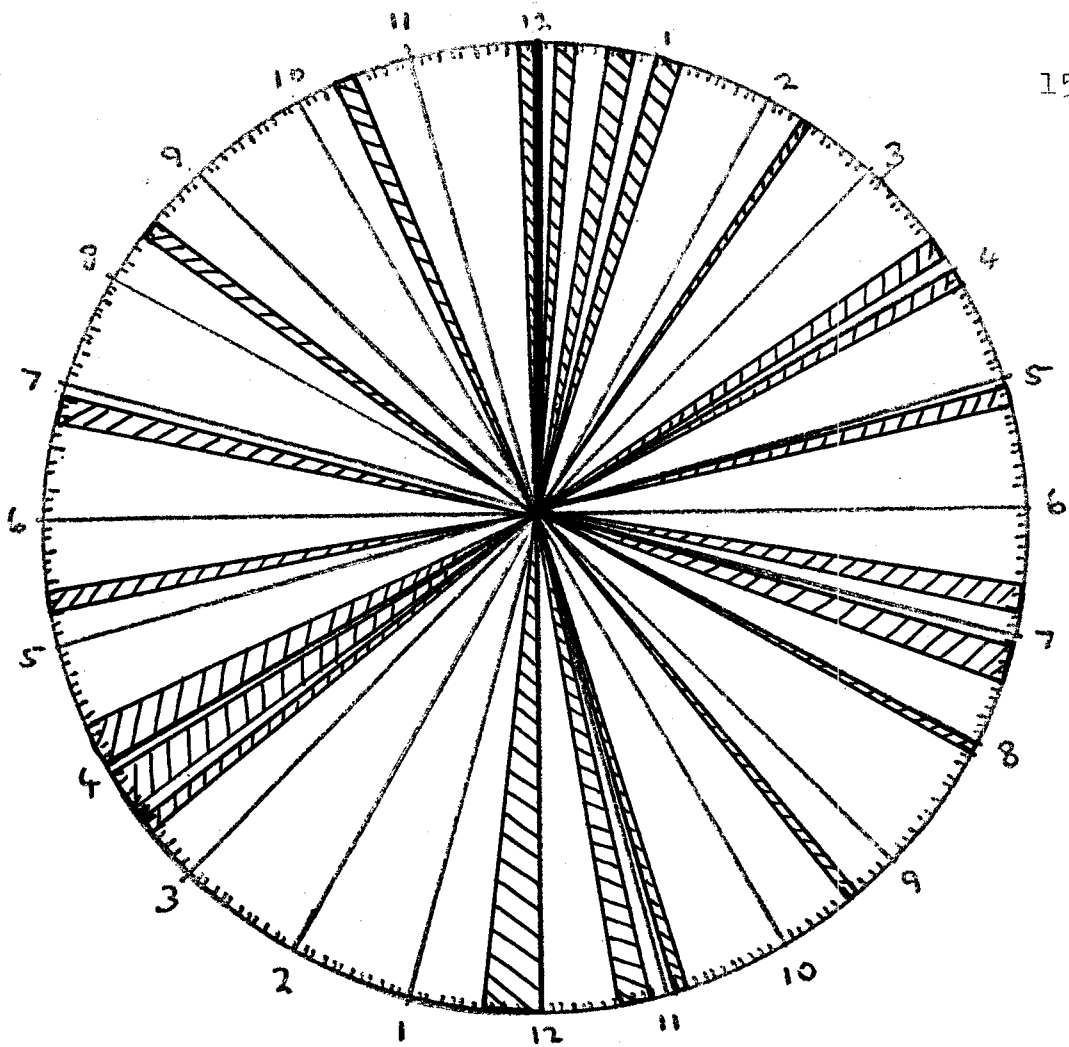


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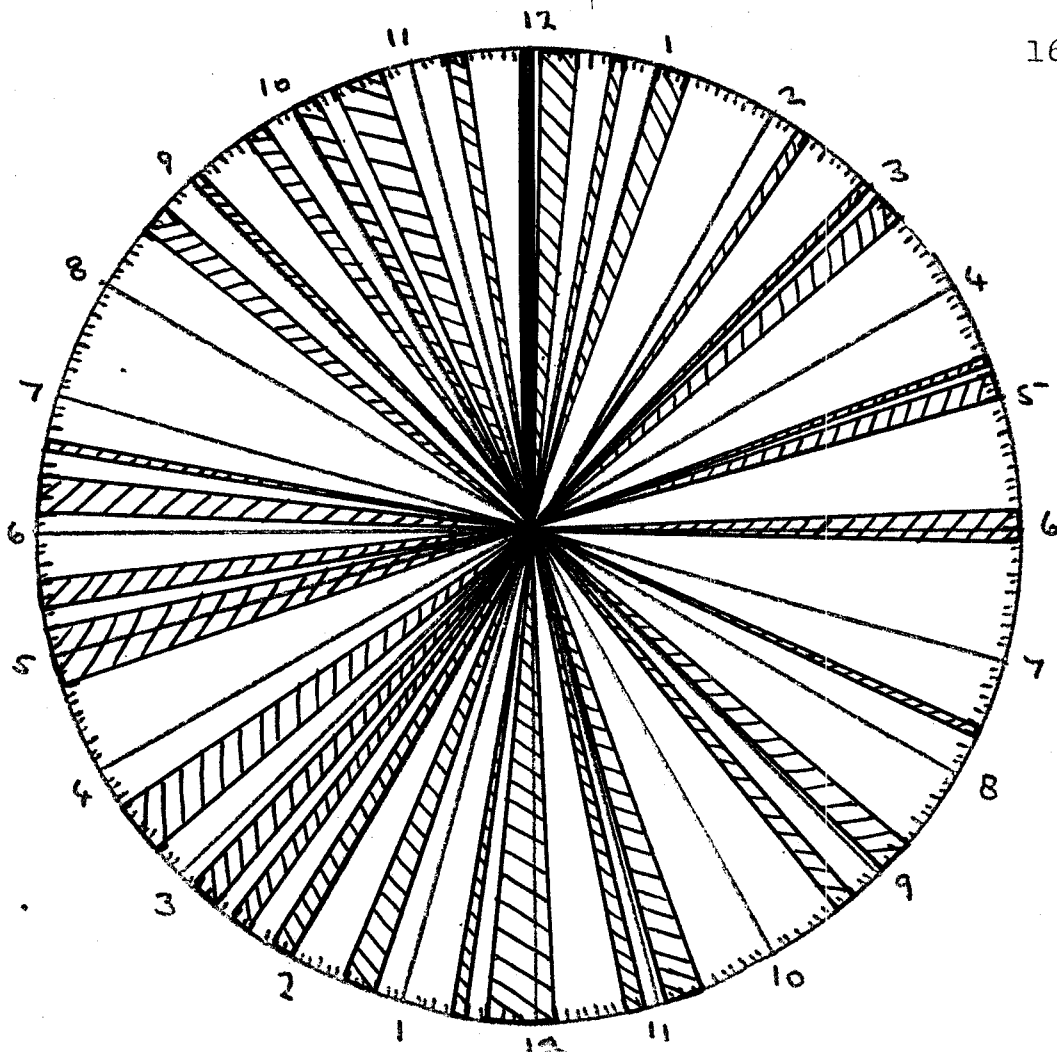


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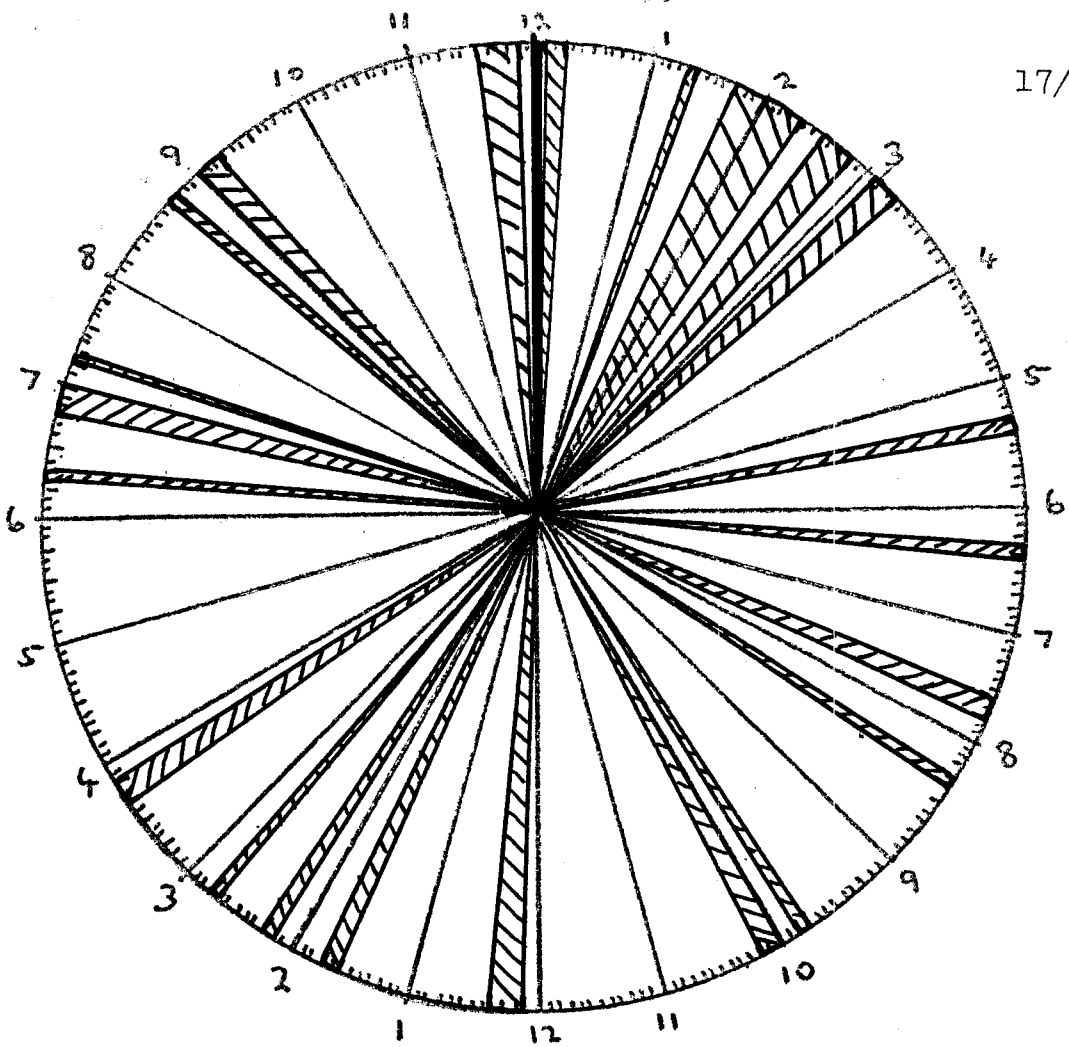


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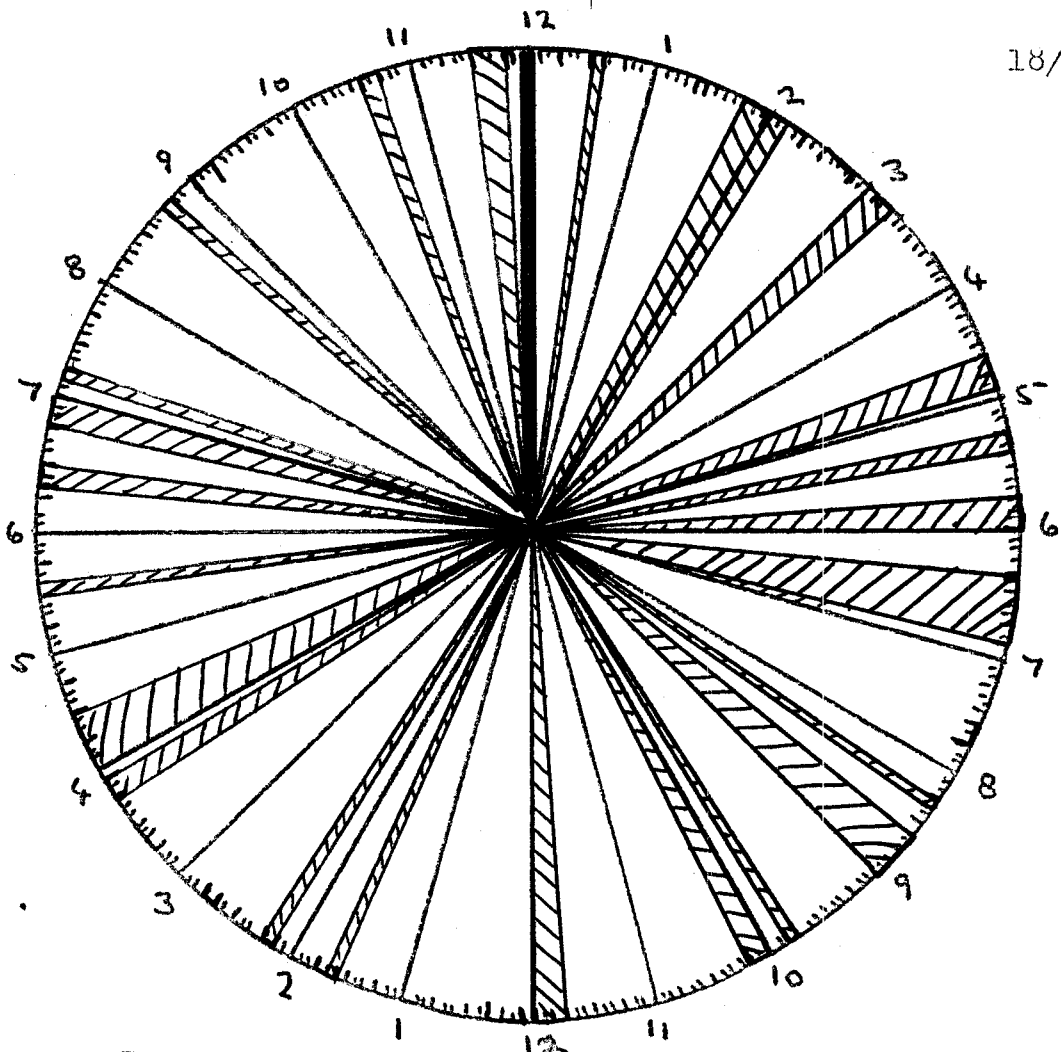


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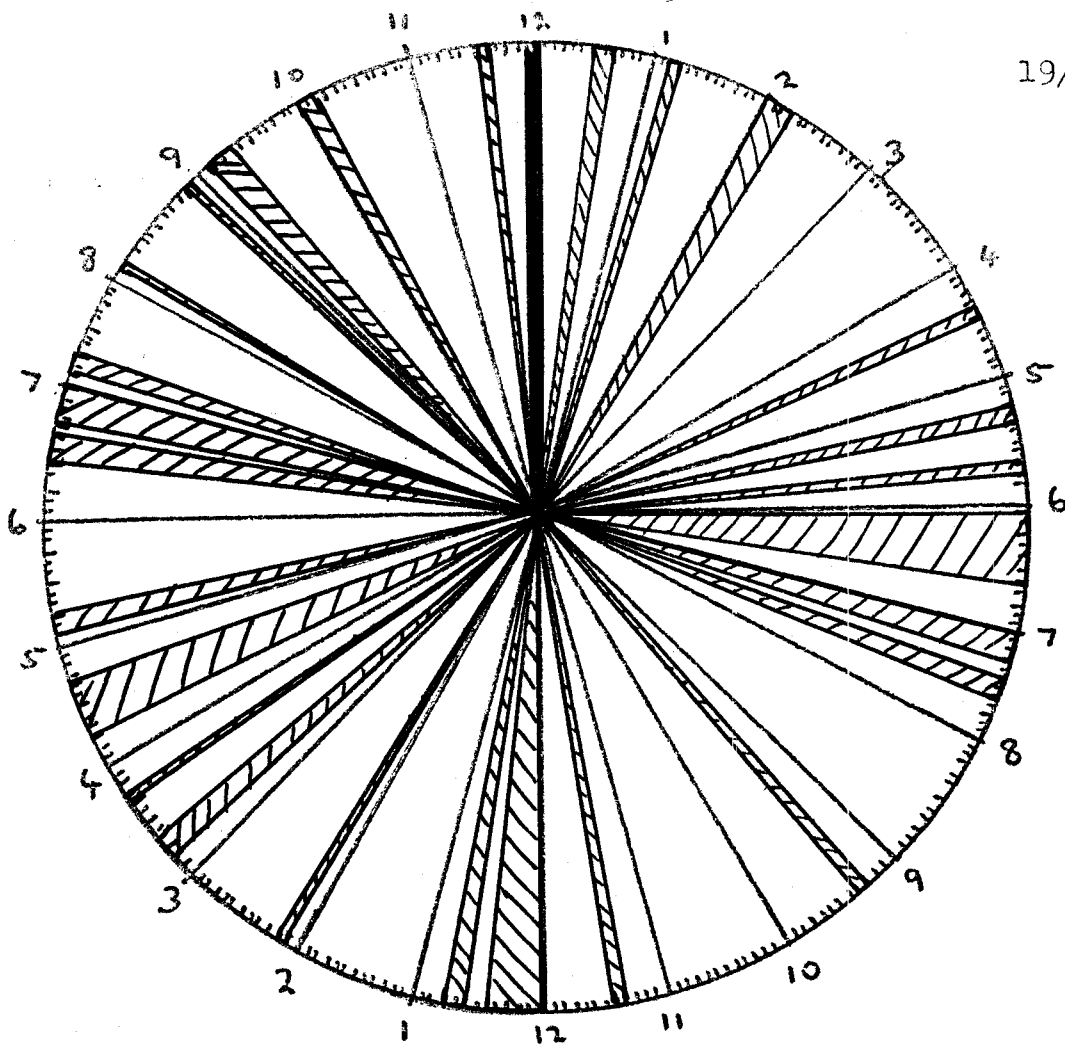


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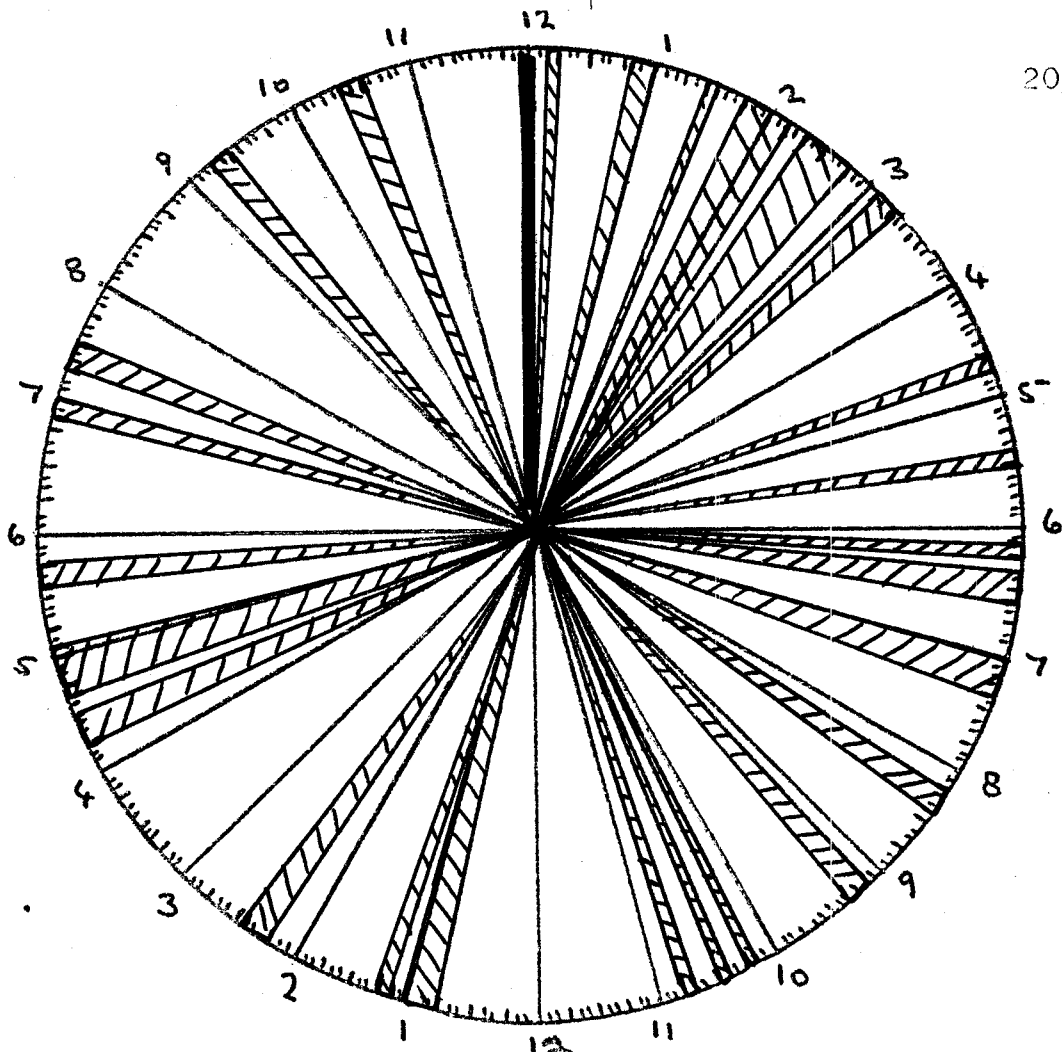


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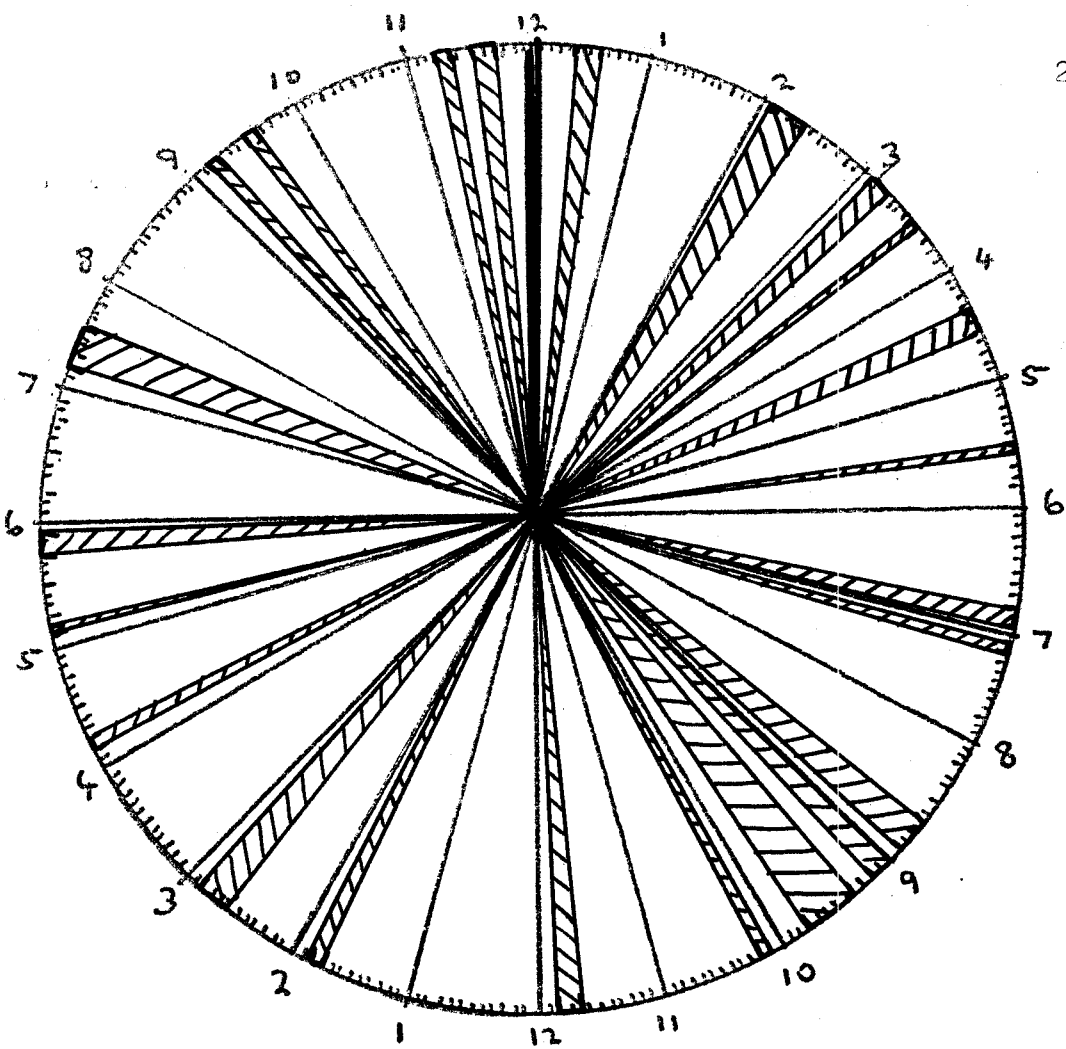


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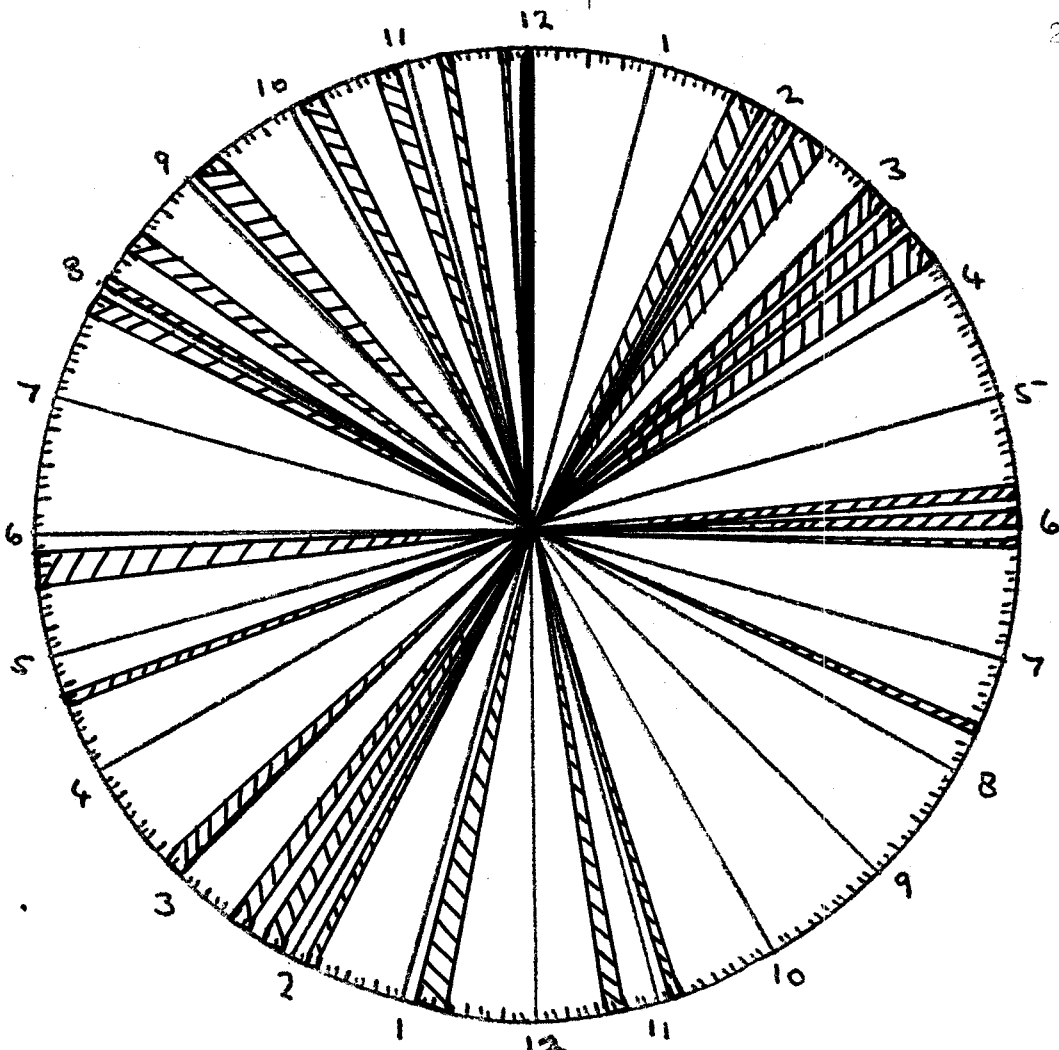


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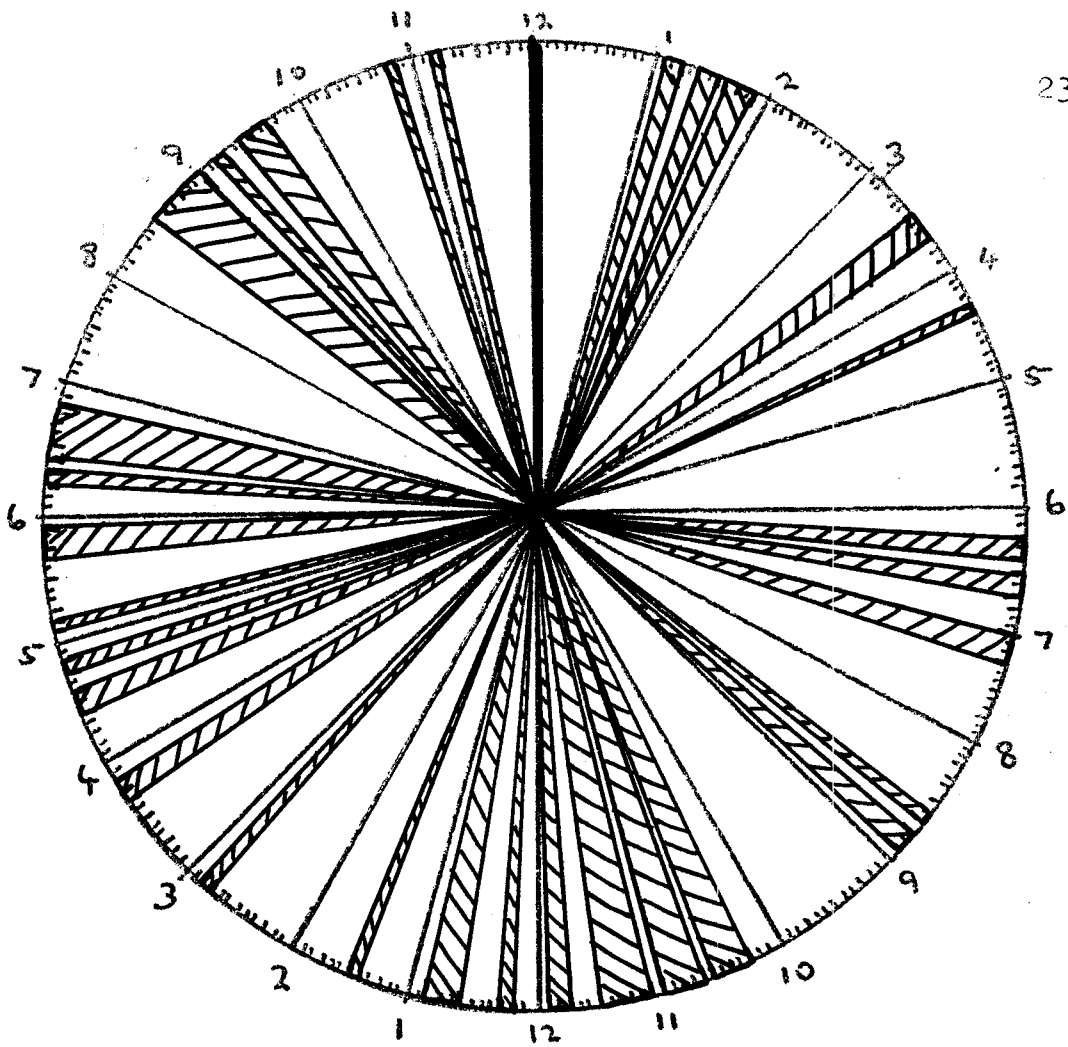


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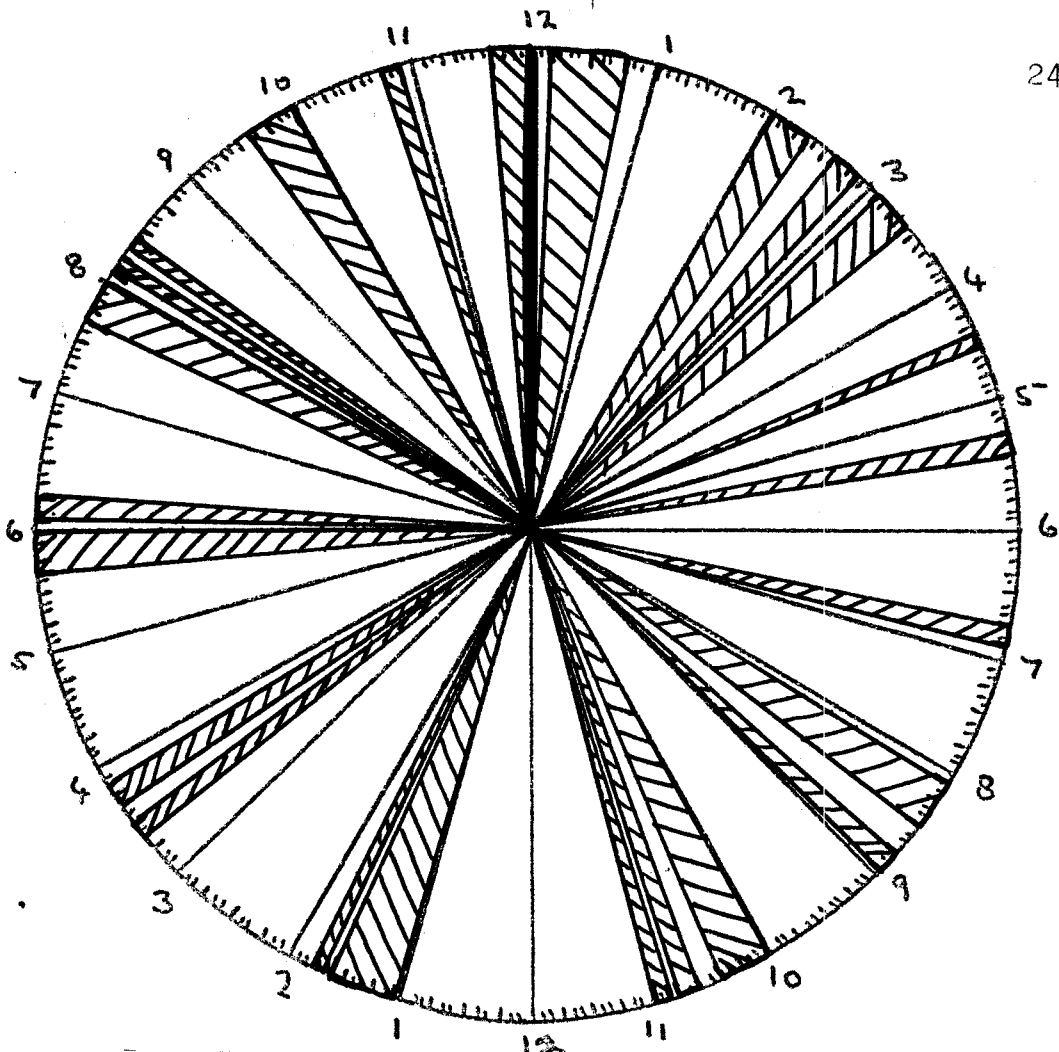


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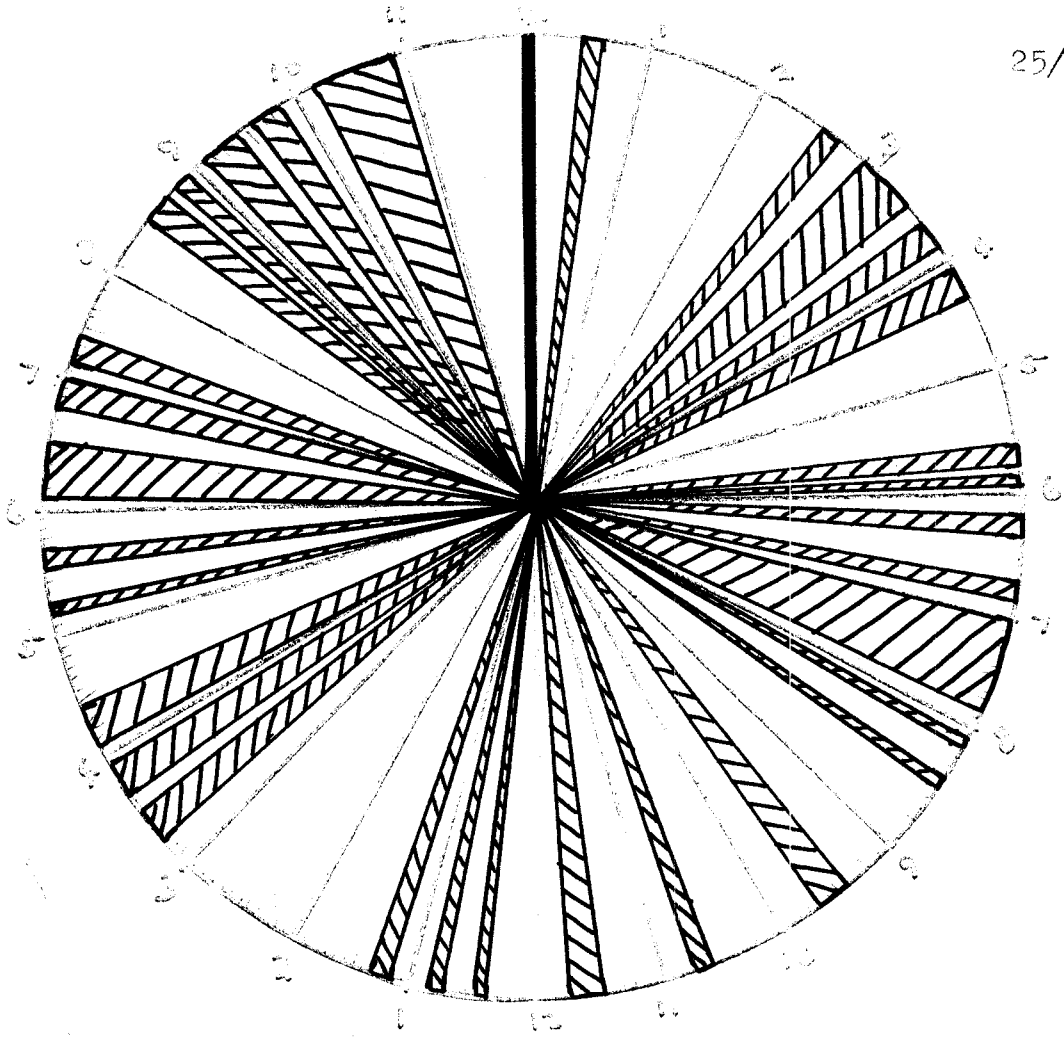


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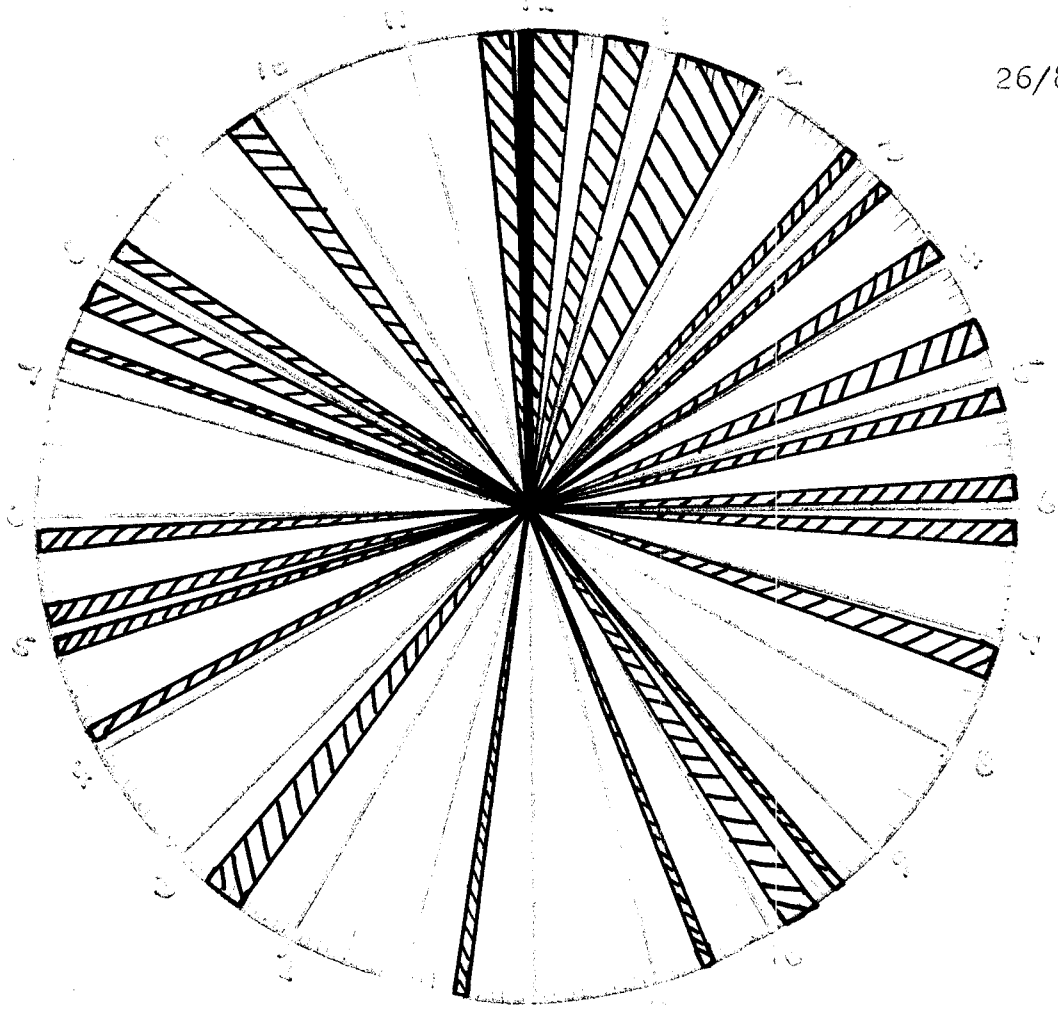


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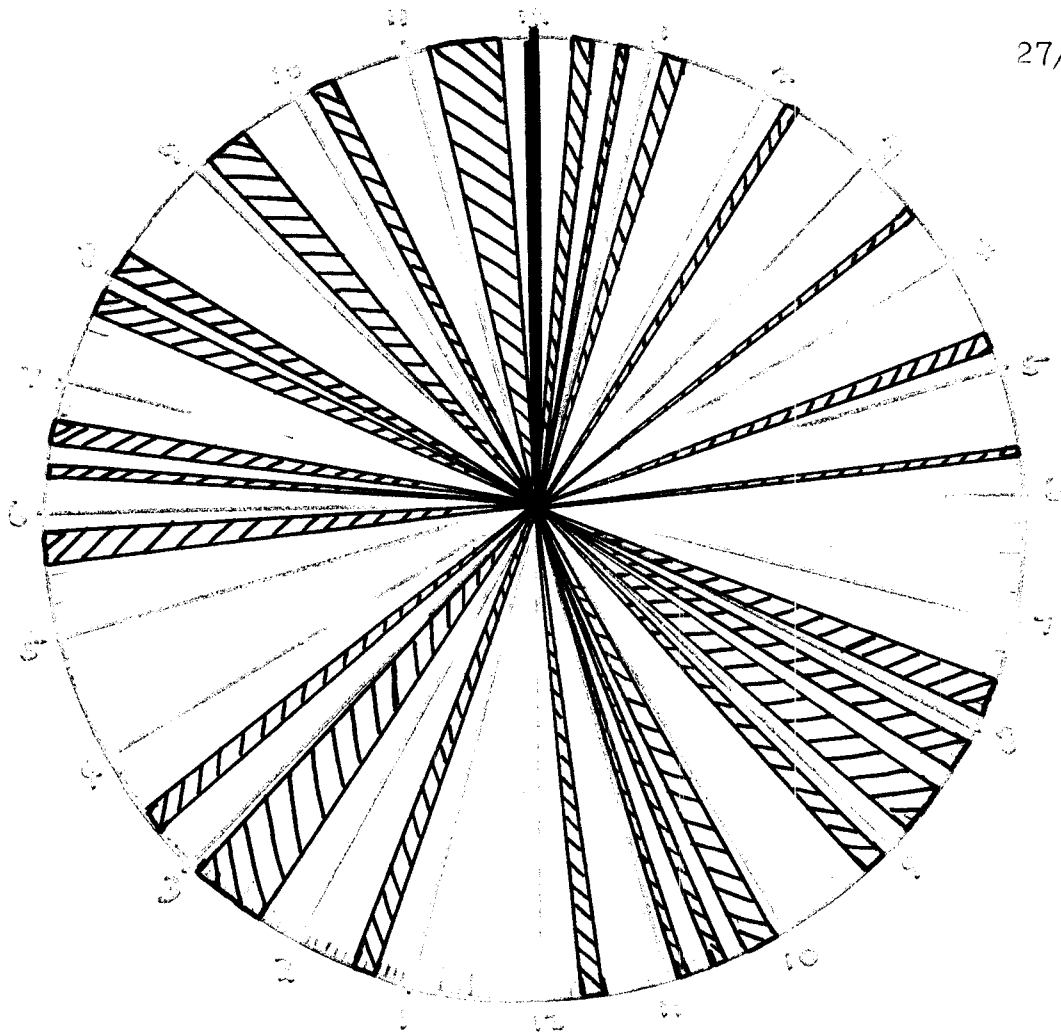


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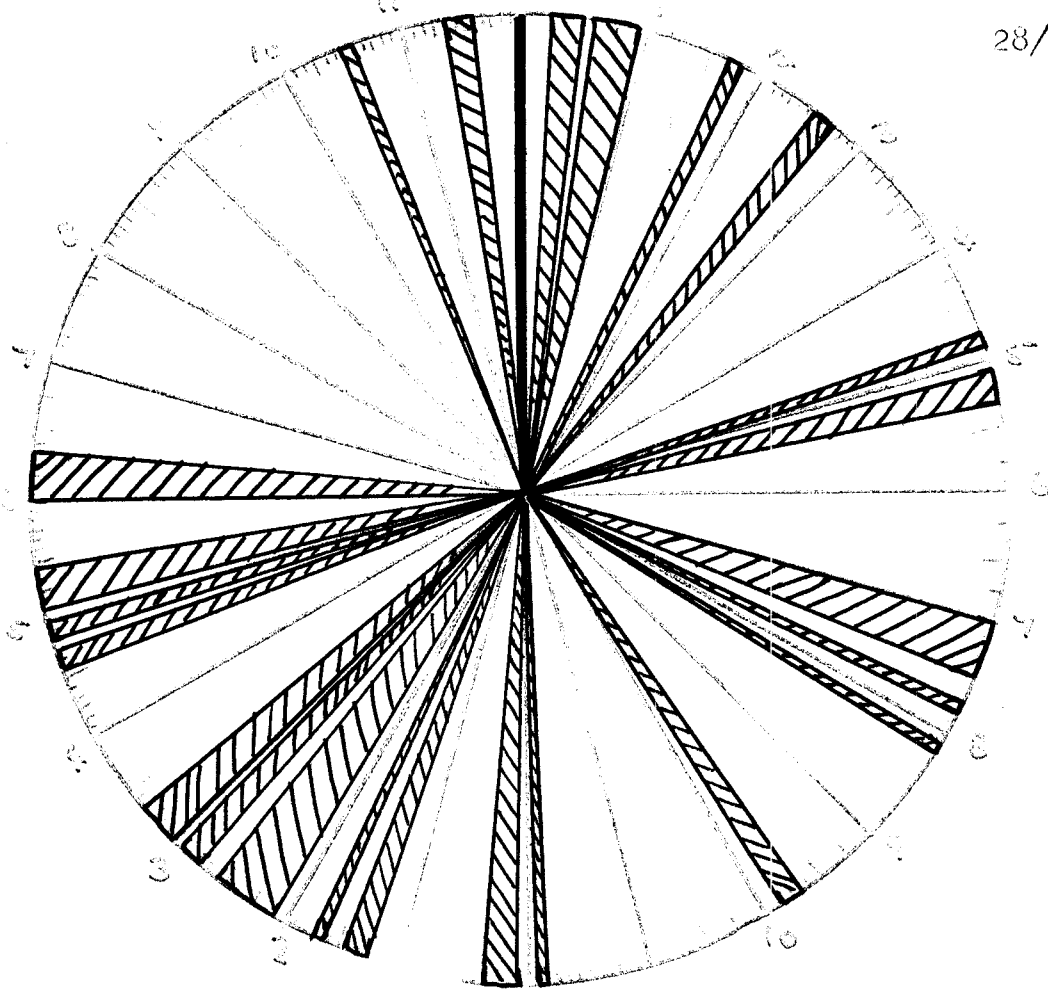


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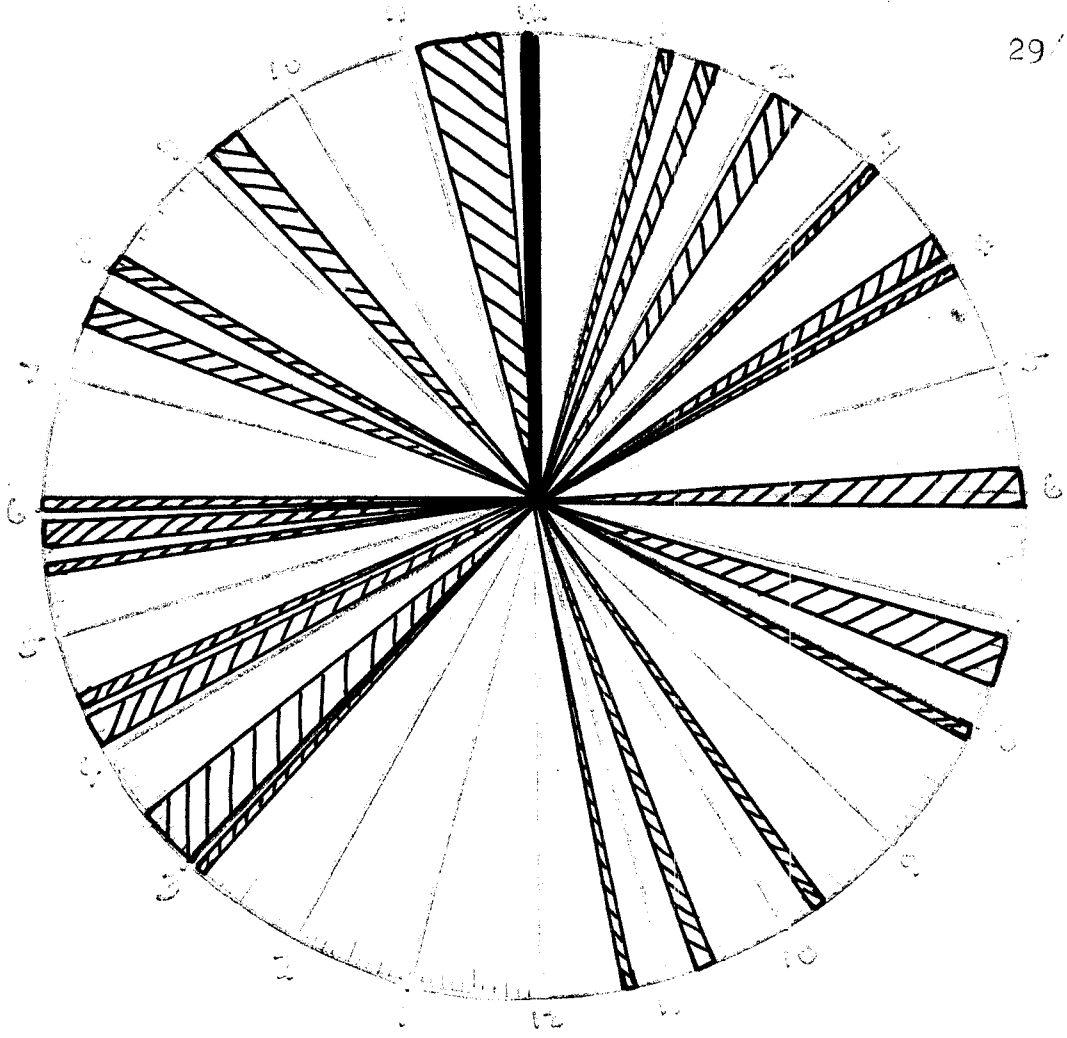


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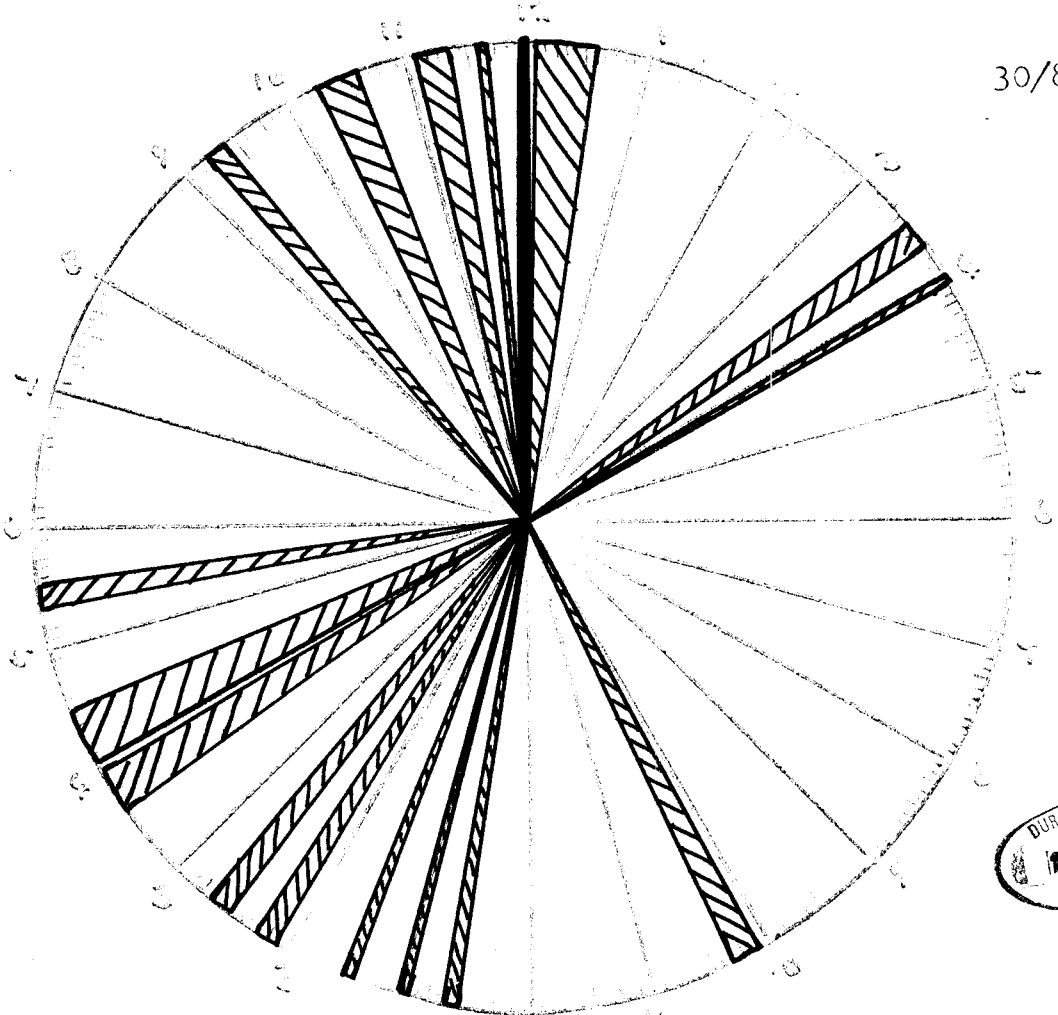


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