

Responses to sugars and their behavioural mechanisms in the starling (*Sturnus vulgaris* L.)

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Summary. The response of the starling to sugar solutions was investigated as this species, which eats sweet fruits, does not prefer sugar solutions according to the literature.

In choice tests using two identical fountains, moderate preference for higher concentrations (0.5 M and 1 M) of glucose and fructose to water was demonstrated. The same concentrations of sucrose were rejected. Lower concentrations (0.25 M and less) of all three sugars were neither preferred nor rejected. In choice tests using two differently coloured fountains the subjects did not generally respond more sensitively to sugar solutions. In learning experiments with differently coloured fountains the starlings developed very marked preferences for 0.5 M glucose and 0.5 M fructose and a corresponding rejection of 0.5 M sucrose in the course of 1–2 days. In a learning experiment with identical fountains they also developed a pronounced preference; the preference values obtained, however, are higher if secondary cues such as the colour of the fountain or its position are available. In short time tests immediate responses to sugar solutions could not be demonstrated.

The rejection of sucrose is attributed to illness-induced aversion learning, the learned preference for glucose and fructose to the preference according to gain in energy per unit of time as postulated by the optimal foraging theory. Taste sensations play, if any, only a minor role. The learning mechanisms operating in the experiments could be employed by the starling for the selection of fruits.

Introduction

Many species prefer sugar solutions to water (Dethier 1963; Kare 1971). These preferences are

based in insects on the sensitivity of specialized sensory cells in hair sensilla (Dethier 1963), in vertebrates, however, where most sensory cells of the taste buds respond to more than one taste quality, on the different response profiles of different classes of gustatory nerve fibers (Sato 1971). In the taste sensitivity to sugars considerable quantitative and qualitative differences are found in different species. The honey bee, e.g., responds almost exclusively to those sugars common in nectar and honey dew and primarily to those concentrations from which a durable honey can be prepared (von Frisch 1965). If the response to sugars is interpreted in this way as an adaptation to the diet of the species in question, it becomes plausible that cats, for example, which are strict carnivores, do not normally prefer sugars (Beauchamp et al. 1977).

There are relatively few investigations into the response of birds to sugars (Reviews: Kare 1965; Wenzel 1973; Gentle 1975; Kare and Rogers 1976). In the most studied species of all – the domestic chicken – the results are unequivocal: whereas some authors reported positive responses, others found only indifferent ones. The conflicting results may on the one hand be attributed to different testing procedures (Wenzel 1973); on the other hand they may be caused by the fact that in the chicken the preference for sugar depends on its nutritional state (Kare and Ficken 1963; Kare and Maller 1967). This calls to mind that behavioural responses to taste solutions are determined not only by the sense of taste (Kitchell et al. 1959).

The results from the different species of birds investigated by various authors were summarized by Kare (1965; Kare and Rogers 1976) in the following rule: nectar and fruit-eating species are more likely to respond positively to sugars than are insectivorous or granivorous or graminivorous

species, which respond negatively or not at all. The rule does not say in which way those species should be classified which eat insects and additionally berries, as do many songbirds (Brensing 1977). As an adaptation to the berries in their diets, preference for sugars should be expected. Therefore it is astonishing that Kare (1965, 1971) enumerates the European starling (*Sturnus vulgaris* L.) among those species which failed to select avidly the common sugars in solution, especially since the starling eats sweet fruits such as cherries and grapes thereby causing considerable economical problems in cherry plantations and vineyards (Brown 1974; EPPO 1978; Feare 1980). It is in agreement with Kare's statement that Weischer (1953) could not successfully demonstrate preferences for sugar solutions in two young starlings. As the negative findings of these experiments could have resulted from inadequate testing conditions, I started testing starlings with a method that had been used successfully in tests with quinine solutions (Schuler, in preparation). At first the aim of these experiments was to demonstrate unequivocal responses to sugar solutions. Later, the behavioural mechanisms which form the basis of the responses to sugars and probably simultaneously the basis for the choice of sweet fruits in this species were investigated.

In the experiments the response to glucose, fructose, and sucrose was examined, as only these sugars are normally found in fruits in considerable amounts (Whiting 1970).

Materials and methods

Experimental subjects were a total of 36 wild-caught adult starlings. They were kept for a prolonged period in an outdoor aviary, then accustomed to single cages and tested in other behavioural experiments. Some of them were tested in several experimental series. For the experiments they were kept singly in cages (96 × 46 × 76 cm) which were illuminated by natural daylight and simultaneously by fluorescent tubes. The cages were made of wire netting (Bekaert Casanet plastic), their front of Plexiglas. Two drinking fountains could be attached to the outside of this surface. Their basic drinking troughs extended through two holes (3.8 cm apart) into the cage at the height of the perches. Thus the starlings could drink when sitting on the anterior perch. This arrangement avoided spoiling of the test fluids with food, which was given in a dish placed on the cage floor. The birds were fed with turkey starter pellets (P.St. 28, Hemo, Scheden, or Club, Hamburg) ad libitum. In the morning they were given the opportunity to bathe in a dish. After the tests two fountains with yellow bases containing tap water were attached to each cage until the following morning.

The following sugars were used for the preparation of the solutions: D(+)-Glucose (Monohydrate) (Merck 8342), D(-)-Fructose (Merck 5321) and Sucrose (Merck 7653). For the tests each starling was provided with two fountains containing test

solution and water, respectively (two bottle drinking test). Both fluids had the same temperature and both fountains were filled to the same height. Each experiment consisted of a series of single tests, which were carried out according to an experimental design determined previously. To exclude the effects of position preferences each solution was delivered at the same frequency on the right and left sides. The consumption of test solution and of water was determined by weighing the fountains before and after each test. From these data the preference value, i.e. test solution, as percentage of total fluid intake was calculated.

Choice tests without colour cues. The fountains used were made of glass in the usual shape, i.e. consisting of a vertical storage tube with a small drinking trough attached to its base. Solutions were prepared with distilled water which was given also in the second fountain. Fluid consumption was determined to the nearest 0.1 g. Each bird was given each of the concentrations once on each of the four experimental days, whereby the sequence of the concentrations was fixed by the method of randomized latin squares according to Linder (1959).

Choice tests with additional colour cues. Here plastic drinking fountains with clear tubes and coloured bases (Vitakraft Feeding and Water Automat No. 31022) were used. Each bird had a light-blue and a light-green fountain except for the first two experiments of the section 'The effect of colour cues in tests with different concentrations' where four of the ten birds had a red and a green one. For all these experiments, which extended over several weeks, the solutions were made using tap water, which was also offered in the second fountain. Solutions were prepared two times a day. Fluid consumption was determined to the nearest 0.01 g. On each experimental day, only one concentration was given in four tests, each of 1.5 h duration. The positions of the fountains were changed regularly.

The data were treated statistically according to Siegel (1956), Dixon and Massey (1957), and Sachs (1969).

Results

Choice tests without colour cues

The classical 2-choice 24 h preference test (Richter and Campbell 1940; Cagan and Maller 1974) successfully used in quinine tests with starlings before (Schuler, in preparation) is inappropriate for testing with sucrose: No preference for a 0.5 M solution was found in a pilot experiment. Moreover this solution is detrimental to starlings: Two of the five birds died after having drunk this solution almost exclusively for one day.

Two-choice 1 h preference tests gave useful results in preliminary experiments with different concentrations of sucrose as well as fructose. Therefore ten birds were tested subsequently with this method for glucose, fructose and sucrose.

In the *glucose experiment* the concentration of the solution had a significant effect on the relative intake according to a two-way analysis of variance with repeated measurements ($F_{4,150} = 5.8$; $P < 0.001$). In contrast, the differences between the individual birds and the interaction of birds and con-

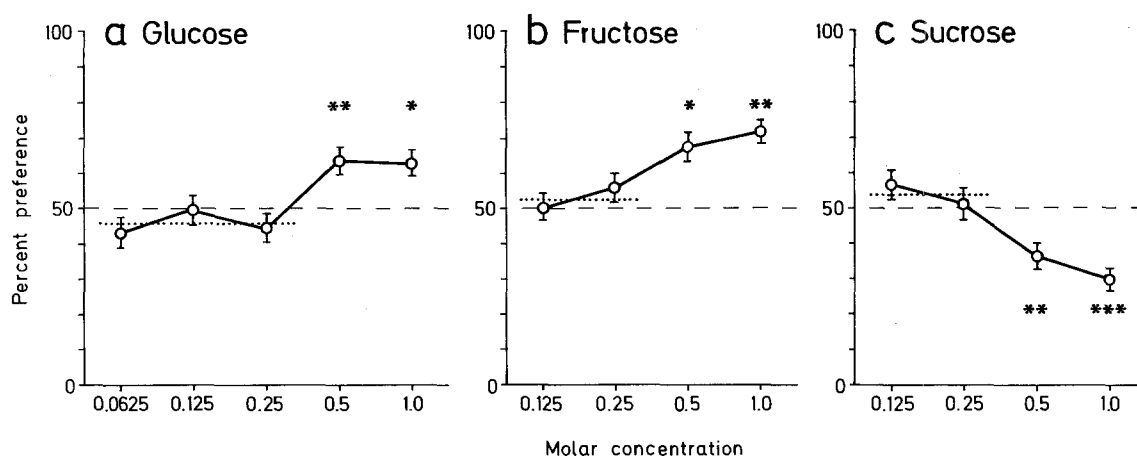


Fig. 1. Preference values for sugar solutions in choice tests without colour cues. Mean \pm SE is shown for $n=40$ one hour tests per concentration (four with each of ten birds).average of the concentrations with mean values near 50%, indicating an indifferent response. * $P<0.05$; ** $P<0.01$; *** $P<0.001$ for the distance to this average (Scheffé test subsequent to analysis of variance)

concentrations were not significant. Figure 1a shows that the preference values of 1 M and 0.5 M solutions were significantly higher than the average of the three lower concentrations, the mean values of which were near 50%, indicating an indifferent response.

In the *fructose experiment* the effect of the concentration of the solution was also significant ($F_{3,120}=5.7$; $P<0.001$). Here, too, the differences between birds and the interaction of birds and concentrations were not significant. Figure 1b shows that the preference values of 1 M and 0.5 M fructose were significantly higher than the average of the lower concentrations, the mean scores of which were near the 50% indifference value.

In the *experiment with sucrose* the analysis of variance yielded again a significant influence of the concentration of the solution ($F_{3,120}=9.1$; $P<0.001$) and no significance for the differences between birds and the interaction. Figure 1c shows that preference values of 1 M and 0.5 M solutions were here *lower* than the mean of the inefficient 0.25 M and 0.125 M concentrations. From this it follows that 1 M and 0.5 M sucrose were – in contrast to equimolar concentrations of glucose and fructose – rejected compared to water.

Choice tests with additional colour cues

In the subsequent experiments it was investigated whether the starlings show stronger responses if they can associate the sugar solution with the colour of a fountain. Birds may show more pronounced reactions when tested with this method (Weischer 1953, see also Brindley 1965; but compare Pick and Kare 1962).

The effect of colour cues in tests with different concentrations

Ten starlings were tested for 0.25 M, 0.5 M, and 1 M sugar solutions with two differently coloured fountains in a series of experiments. In each experiment the three concentrations of one sugar were offered on three consecutive days in ascending order after a day with control tests, in which water was given in both fountains to determine the colour preference of the individual birds.

The preference values for 0.5 M and 1 M solutions obtained in these experiments were not generally higher than in the tests without colour cues, in some cases they were even smaller. However, since the response is influenced by colour preferences here, the difference of a solution's preference value to that of a lower concentration is a better index than the preference value itself. Figure 2 shows that this difference was significantly greater than in the tests without colour cues *only if* a preferred solution was offered in the fountain with the rejected colour and vice versa. This treatment extends the range of possible scores by lowering the baseline for the preferred solution and raising it for the rejected one.

The effects of colour and of solution are not summated in a simple additive manner. Table 1 shows that the colour preference of the birds was altered by each experiment as a whole. This means that colour preferences were changed by learning processes during repeated sugar tests. Thereby glucose and fructose, which increase the preference value of a colour, are positive conditioning stimuli, whereas sucrose, which decreases it, is a negative conditioning stimulus.

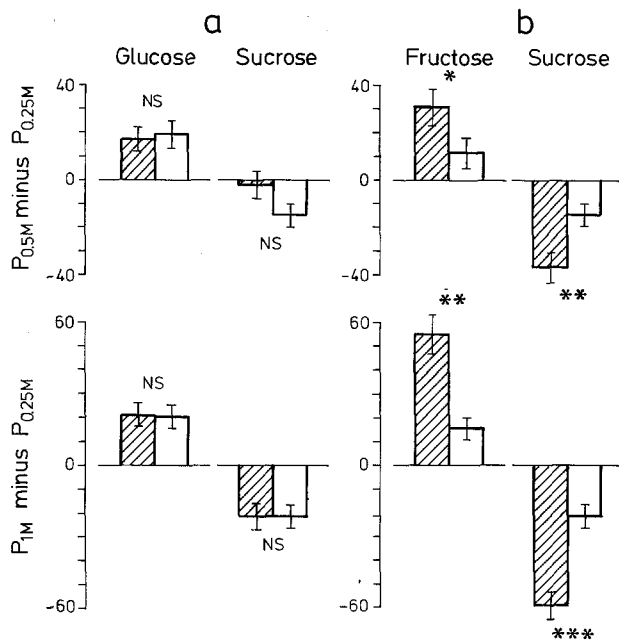


Fig. 2a, b. Comparison of choice tests with additional colour cues to those without colour cues. *Hatched*: tests with two differently coloured plastic fountains; *white*: tests with two identical glass fountains. The difference (mean \pm SE) between the preference values *P* of higher concentrations (0.5 M and 1 M, respectively) and of 0.25 M sugar solutions is shown for $n_1 = n_2 = 10$ starlings. **a** In the choice tests with additional colour cues solutions preferred before were offered in the fountains with the colour preferred by the individual Ss, rejected solutions in the fountains with the rejected colour. **b** Solutions preferred before were given in the fountains with the rejected colour and vice versa. *NS* not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (Mann-Whitney *U*-tests, one-tailed)

Table 1. Influence of sugar tests on the colour preference as measured in control tests with water in both fountains. The data of the control tests at the beginning of the experiment are compared to the data of the control tests at the beginning of the following one. The preference values refer in each case to the fountain which contained the sugar solution during the experiment. Wilcoxon matched-pairs signed-ranks tests

Experiment	Preference value ($\bar{x} \pm$ SE)		<i>n</i>	<i>P</i> (one-tailed)
	Before	After		
Glucose	61.7 \pm 5.3	84.4 \pm 3.3	10	≤ 0.0025
Fructose I	22.4 \pm 3.2	71.7 \pm 6.1	6 ^a	< 0.02
Fructose II	30.1 \pm 4.3	70.9 \pm 3.2	10	< 0.0025
Sucrose	29.1 \pm 3.2	20.7 \pm 4.7	10	< 0.05

^a In the following experiment only 6 out of 10 starlings had the same combination of colours

The effect of colour cues in the learning experiment

To investigate the learning processes more completely one sugar concentration was offered for several days. Ten birds were first tested with 0.5 M

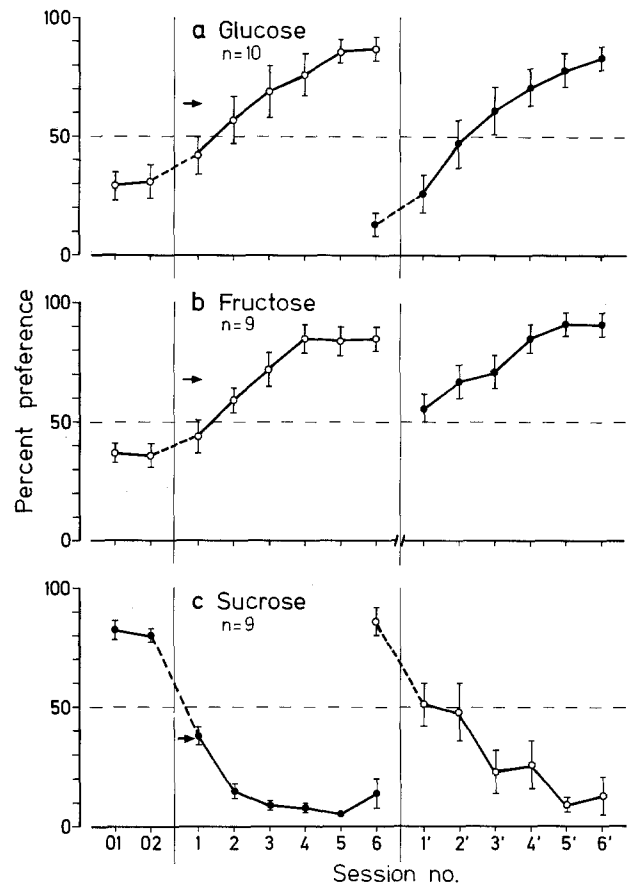


Fig. 3. Preference values for sugar solutions in learning experiments with two differently coloured fountains. Mean \pm SE preference values for 0.5 M sugar solutions are shown. *White dots*: fountains with the colour rejected by the individual S in the control sessions (01, 02) with water in both fountains. *Black dots*: fountains with the preferred colour. During sessions 1 to 6 glucose and fructose solutions were offered in the fountain with the rejected colour, sucrose solution in the preferred one. After that the colours of the fountains containing sugar solution and water were exchanged. Two sessions were performed per day, each consisted of two 1.5 h tests. *Arrows*: Preference values from the choice tests without colour cues (see Fig. 1)

glucose, then with 0.5 M sucrose and finally with 0.5 M fructose. For a maximum effect glucose and fructose were offered in the fountain with the colour rejected on the control day, sucrose in the preferred one. To ensure that the colour preference had not changed spontaneously, the solutions were given in the second half of each experiment to each bird in the fountain with the other colour. To deal with the time course of the preference value as exactly as possible without abandoning the balance of position preferences two subsequent tests were always combined to form one session.

Figure 3a shows that in the *experiment with glucose* the starlings first learned to prefer the fountain with the colour rejected initially; when the solution was offered afterwards in the other fountain, they chose increasingly that one. The relative

intake from the initially rejected fountain was in session 1 somewhat higher than in the previous control session ($P < 0.05$; Wilcoxon test, one-tailed). Thereafter it increased permanently until session 5. In session 1' the relative intake from the initially preferred fountain was not significantly higher than in the preceding session (number 6) (26% vs. 13%; $P > 0.05$). After that it increased rapidly at first and then progressively more slowly. The graphs demonstrate first, that the predilection for the fountain containing glucose developed gradually, i.e. that the response is a learned preference. They show second, that after the colour change the starlings at first did not choose solution but colour, and third, that they learned afterwards anew to select the fountain containing solution.

In the first half of the *experiment with fructose*, nine birds learned to choose the fountain rejected initially, in the second half – which followed after a pause of 3 days – to choose the initially preferred one again (Fig. 3b). (One bird chose according to colour only: During the whole experiment it drank almost exclusively from the green fountain). The relative intake of the nine birds was not significantly higher in session 1 than in the preceding control session ($P > 0.10$); it increased, however, to 85% in session 4. In the first session with changed colours (number 1') the relative intake from the other fountain was 56%; it rose to 91% in session 5'. It can be concluded that – as with glucose – the preference for the fountain containing fructose is a learned response, and that the birds after the colour change also had to learn anew.

In the first half of the *experiment with sucrose*, all ten birds rapidly learned to reject the initially preferred fountain; in the second half, after changing colours, only nine succeeded. They learned more slowly here than they had in the first half (Fig. 3c). Only the data of these nine were included in the computation. Their relative intake was much lower in session 1 than in the previous control session ($P < 0.0025$); it fell to less than 10% in session 3. In session 1' the relative intake from the other colour was significantly lower than in session 6 ($P < 0.01$); a value of less than 10% was reached, however, only in session 5'. The graphs demonstrate that the rejection of sucrose is also a learned response. As the preference shift after the colour change is not greater than that at the start of the experiment, it can be concluded that the birds here, too, at first did not choose solution but colour and relearned subsequently.

0.5 M sucrose again proved to be fatal. One bird died after having drunk 17.8 g of the solution in the first 1.5 h after the colour change; this was 96% of its total fluid intake. The other nine, which

endured the same test without damage, drank to a maximum of 8.8 g; four of them had similar relative intake values (88 to 99%).

The preference values reached do not depend on the specific colour of the fountain containing the solution: In all three experiments there was no significant difference between the values reached in the green fountains (session 6 or 6' depending on the individual bird's initial colour preference) and those reached in the blue ones (glucose: $81.0 \pm 4.2\%$ vs. $89.2 \pm 4.6\%$; *NS*; fructose: $89.6 \pm 4.2\%$ vs. $86.6 \pm 4.0\%$; *NS*; sucrose: $19.7 \pm 8.3\%$ vs. $6.7 \pm 1.2\%$; *NS*; Wilcoxon tests, two-tailed).

From the comparison of these experiments to those of the choice tests with identical fountains, it can be seen that the preference values stated there (arrows in Fig. 3) were exceeded in most of the learning experiments in the third session. In the sixth sessions (number 6 as well as 6') they were significantly more pronounced: Higher with glucose and fructose, and lower with sucrose (in each case $P < 0.01$; *U*-tests, one-tailed).

To test whether starlings develop marked preferences only if they can identify the fountain containing the sugar solution by its colour two groups of five birds each were compared, one having two identical green fountains the other two differently coloured ones. Following two control sessions 0.5 M fructose was offered for twelve sessions in the less preferred fountain. Four additional sessions were performed without the regular change of the fountains' positions, to see whether the position of the fountain, too, could be used by the starlings as a secondary cue.

Both groups learned to prefer the fountain containing fructose (Fig. 4). During the first three sessions their preference values were very similar, after that, however, it was distinctly lower with the group having identical fountains (mean \pm SE for sessions 9 to 12: $79.8 \pm 2.7\%$ vs. $96.6 \pm 1.4\%$; $P < 0.001$; *U*-test, one-tailed).

During sessions 13 to 16, when the positions of both fountains remained constant, the preference value of the group having identical fountains increased significantly to $90.0 \pm 3.9\%$ ($P < 0.05$; Wilcoxon test, one-tailed) it did not reach, however, the value of the group with different fountains ($97.1 \pm 0.9\%$; $P < 0.05$; *U*-test, one-tailed).

This result shows that starlings develop marked preferences even with identical fountains. The preference is, however, more pronounced if they can use the position or the colour of the fountain as a secondary cue to identify the sugar solution, whereby colour is more efficient.

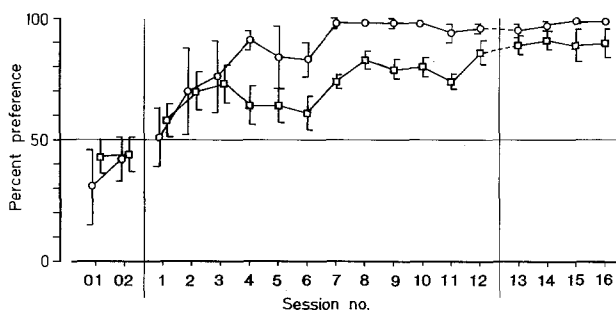


Fig. 4. Influence of secondary cues on the sugar preference in a learning experiment. The mean \pm SE preference value for 0.5 M fructose of two groups of starlings ($n_1 = n_2 = 5$) is shown. *Circles*: birds tested with two differently coloured fountains (i.e. with colour as a secondary cue). *Squares*: birds tested with two identical fountains (no colour cue). 01, 02: control sessions with water in both fountains; 1 to 12: experimental sessions in which the position of the fountains were exchanged regularly (no position cue); 13 to 16: experimental sessions in which the positions of the fountains remained constant (i.e. with position as a secondary cue). Two sessions were performed per day, each consisted of two 1.5 h tests

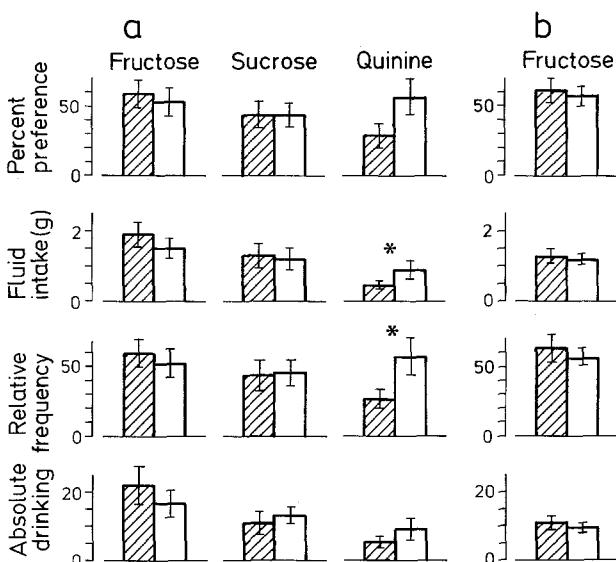


Fig. 5a, b. Responses to taste solutions in short time tests as measured by four different indices. *Hatched*: 5 min choice tests between solutions and water. *White*: Control tests with water in both fountains. **a** Tests performed in January and February; $n = 10$ tests (two with each of five starlings). **b** Tests conducted in September; $n = 18$ tests (two with each of nine starlings). Fluid intake and absolute drinking frequency refer only to the fountain containing the test solution. *Experimental and control tests are significantly different ($P < 0.05$; Wilcoxon test one-tailed)

Do starlings show an immediate response to sugar solutions?

The experiments above demonstrated that starlings can show very marked learned preferences to sugars. From these findings the following question arose: Are the preferences shown in the tests with-

out colour cues also learned responses? These tests were controlled for learning by randomizing the sequences of concentrations, positions and fountains. The possibility, however, that the starlings were learning the position of the solution *within* a single test, the duration of which was 1 h, cannot be excluded. Therefore the attempt was made to detect immediate responses of the starlings to sugar solutions by measuring over a short time (short-time tests) and by observing their drinking behaviour.

Short-time tests. Five experienced birds were tested with 0.5 M fructose, 0.5 M sucrose, and – as a secondary control – 0.1% quinine-dihydrochloride. The two differently coloured fountains were given four times at intervals of 1 h for only 5 min, each time in the same position. During the second test the left one contained the solution, during the fourth test the right one, in the first and third tests water was given in both of them as a control. Besides the fluid consumption the number of drinking acts was noted.

Figure 5a shows that in the experiment with fructose a significant difference between experimental and control tests could neither be found for the relative or absolute fluid intake nor for the relative or absolute drinking frequency. The same holds true for the experiment with sucrose. As the starlings showed a response to quinine under equivalent conditions – the absolute fluid intake and the relative drinking frequency were significantly different from the control tests –, it can be concluded that they did not show an immediate response to sugar solutions here.

Since these experiments carried out in January and February had negative results, the experiment with fructose was repeated with nine starlings in September, i.e. in a season in which starlings in the field eat berries and should therefore be most sensitive to sugars. Figure 5b shows that here, too, there were no significant differences between experimental and control tests.

Observations of drinking behaviour. During the experiments no differences in behaviour between starlings drinking sugar solutions and water, respectively, were noticed. Direct observations and analysis of films showed the following results: When drinking water the starling dips in its beak and then raises it, as do most bird species, above the horizontal plane for swallowing. Drinking is followed now and then by ruffling and shaking feathers, moderate headshaking and bill-wiping by which the bird removes drops hanging on the beak.

The same behaviour patterns could be observed when the birds were drinking 0.5 M sugar solutions. When drinking quinine solution, they behaved quite differently: Immediately after having taken it, they violently shook their heads, whereby the beak was held at a right angle to the longitudinal axis of the body, describing an angle of approximately 270°. This behaviour pattern obviously has the function to remove the badly tasting fluid from the inside of the throat and beak. Subsequently they wiped their beaks intensively.

The indifferent, immediate responses of the birds to sugar solutions are in accordance with the hypothesis that the preference for higher concentrations of glucose and fructose and the rejection of sucrose are learned rather than immediate responses even in those tests not designed as learning experiments.

When the birds were observed for a prolonged period, about 10–20 min after having drunk 0.5 M sucrose they showed the violent head-shaking described above for quinine, a diarrhoea-like evacuation and occasional vomiting. Their sitting quietly with fluffed feathers indicated absence of bodily well-being. Thus, 0.5 M sucrose solution obviously causes heavy disturbances in the function of the gastro-intestinal tract. If the starlings were offered sucrose solution after that, they did not touch it, even if their drinking water had been removed for a longer period.

Discussion

The experiments described demonstrate for the first time specific preferences for sugar solutions in the starling (see also Schuler 1980a). These preferences were in each case statistically significant and under appropriate conditions very pronounced: the percentage preference may rise to nearly 100% (Fig. 4). However, three restrictions are valid: First, from the sugars frequently present in fruits, starlings prefer only glucose and fructose, whereas they reject sucrose. Second, they prefer only higher concentrations. Third, all marked preferences – and probably the moderate ones, too, – were learned responses. These restrictions do not support the notion of a response based only or even primarily on the taste sensation. Since this is especially evident in the rejection of sucrose, its mechanism shall be discussed first.

The mechanism of the rejection of sucrose

The taste of sucrose is not an unconditioned negative stimulus because the starlings showed no im-

mediate response when drinking sucrose solution. The negative stimulus is apparently the disturbance of the alimentary tract commencing some minutes after drinking. Thus the rejection of sucrose is caused by illness-induced aversion learning, the well-studied mechanism (see Milgram et al. 1977) by which animals learn to avoid poisonous food.

The aversion to 0.5 M sucrose does not result from its high concentration by weight because 1 M glucose and 1 M fructose, which have similar concentrations by weight, were preferred.

The detrimental and in certain cases even fatal effect of sucrose depends on the concentration of the solution, on the amount consumed and on the amount of water taken simultaneously. Therefore the concentration affecting the alimentary canal seems to be the decisive factor. This leads to the hypothesis that the prime effect is a disturbance of the water balance caused by osmotic forces. This hypothesis is further supported by the fact that the solutions rejected had osmotic pressures (≥ 500 mosmol/l) higher than that of avian blood plasma (in chickens 312–341 mosmol/l, Skadhauge and Schmidt-Nielsen 1967).

After the learning process the starlings recognized the sucrose solution primarily by the colour of its fountain. Whether gustatory cues played an additional role cannot be decided definitely from the present experiments. Quails similarly chose primarily according to colour after illness-induced aversion learning (Wilcoxon et al. 1971).

The mechanism of the preference of glucose and fructose

The taste of fructose is apparently not an unconditioned positive stimulus, as the starlings showed no immediate response to fructose solution. The same holds true for glucose according to pilot tests. Therefore both sugars must act as rewarding stimuli in a different way. Here one has to think of positive feedback from the digestive system or from metabolism, e.g. of an increase of the level of blood glucose. Such post-ingestional effects play an important role in the control of feeding (e.g. Morgan 1965). Furthermore they can act as delayed unconditioned stimuli (Rozin and Rozin 1981). The optimal foraging theory (see Krebs 1978) is based on the hypothesis that animals can adjust foraging efforts as well as choice of food items according to profitability measured, e.g. in gain in energy per unit of time. Since the starling makes such foraging decisions (Tinbergen 1981), one can assume that its sugar preference results

from the gain in energy per unit of time coming from drinking solutions of easily digestible sugars.

Domestic chickens prefer sugar solutions only if experiencing caloric deficit (Kare and Ficken 1963; Kare and Maller 1967). This explanation does not fit the starling, as it can fulfill its energy requirements from the type of food given here (Taitt 1973), even though it is not easily digestible for this species (Thompson and Grant 1968).

As with sucrose the starlings recognized the solutions of glucose and fructose after the learning process primarily by the colour of the fountain containing the solution. Here, too it cannot be decided definitely whether gustatory cues played an additional role.

The function of the sugar responses and of the underlying mechanisms

Cherries and grapes, which the starling is fond of, contain considerable amounts of glucose and fructose, but no or almost no sucrose (Whiting 1970; Schön, personal communication). The molar sugar concentration within these fruits conforms to 0.29–0.44 M glucose plus 0.33–0.44 M fructose for cherries and to 0.50 M glucose plus 0.45–0.5 M fructose for grapes (estimated by using additional data on water contents from Souci et al. 1973). These concentrations correspond to those preferred in the experiments, at least for both sugars together. Therefore the starling eats cherries and grapes probably because of their sugar contents. Whether it rejects fruits containing sucrose is questionable since the highest sucrose concentration in domestic fruits (peaches: 0.23 M; estimated as above) is lower than those rejected in the experiments.

Since the starling's response to sugars is to be attributed to learning mechanisms, the question arises whether its reaction to fruits is determined in the same way. Actually this reaction is not innate but learned (Schuler, unpublished data). Furthermore, eating olives (e.g. Steinbacher 1960), which contain oil and taste bitter, conforms to the hypothesis that it takes fruits primarily because of their energy contents. Considered as a whole, fruits are probably only a supplementary food for this species (Havlin and Folk 1965), as was demonstrated for other songbirds by Berthold (1976).

The selection of food by means of the learning mechanisms discussed has advantages compared to selection by means of a taste receptor alone (Schuler 1980b): These mechanisms can be applied to very different substances. Furthermore, they cannot be deceived by chemicals stimulating the

taste receptor and simultaneously being metabolically neutral or even detrimental. On the other side they need classes of analogous objects, such as the numerous fruits of trees and bushes, because they cannot examine each single food object separately.

Comparison to the response of other bird species

In the present experiments the first avian species, and as far as I know the first species in general, was described which prefers solutions of glucose and fructose over water and simultaneously rejects sucrose solutions. It may well be that other birds also behave in this manner, since only few species have been tested and some of these apparently with one sugar only (e.g. Vince and Warren 1963; Rogers and Maller 1973).

For the chicken's response to sugars post-ingestional factors, too, are probably more important than the taste sensation (Gentle 1975). This possibility exists additionally in those species which have been tested only in tests of several hours duration each (e.g. Brindley 1965). It applies, however, surely not for nectar specialists, because sunbirds prefer sugar solutions even when offered for only 2.5 s (Dörr 1979) and because hummingbirds can distinguish between solutions of very similar concentrations (Schuchmann et al. 1979). On the other hand, post-ingestional factors play a part even in the sugar response of nectar specialists as their preference behaviour depends on the duration of the single test (Dörr 1979) and on the solution given on the day before (Stiles 1976). In addition the fact that their foraging as well as their territorial behaviour is determined by the amount of nectar available (e.g. Carpenter and MacMillen 1976; Wolf and Gill 1980) supports the view that they evaluate nectar sources not only by taste but also by gain in energy.

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