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DRINKING BY DOGS DURING AND AFTER RUNNING

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SUMMARY

1. Drinking by dogs has been studied during and after running on a treadmill, and compared with the drinking produced by NaCl given by stomach tube or intravenously.

2. When water was offered with a delay of more than 5 min after the end of a run producing loss of 30–90 g water by panting, the drinking was similar to that produced by NaCl, assuming that loss of 100 g water produces the same increase in plasma sodium as 15 m-mole NaCl. It is thus possible to explain drinking with a delay after the run as due to loss of water.

3. When water was offered immediately after a run or during pauses in the running there was drinking which cannot be explained as due to loss of water. Although the immediate stimulus to drinking is small, it may cause repeated small drinks by which the evaporative loss of water during running is matched by water intake.

4. Water (10–20 ml./kg body wt.) given by stomach tube before the run reduced or abolished drinking during running. Doses of water sufficient to stop drinking did not cause an increase in urine volume.

5. From these results a figure is produced placing in order mechanisms which may contribute to the control of water balance.

INTRODUCTION

O'Connor & Potts (1969) described the water exchanges of dogs living in metabolism cages. An important part of the exchanges depended upon the variable activity of the dogs in their cages which determined considerable variations in the water lost by evaporation. A substantial part of the water intake consisted of small drinks, usually 20–50 ml., taken during the periods of activity; thus activity, which could cause considerable loss of water by evaporation, was immediately associated with intake of water. Since activity seemed such an important factor in the water exchanges of laboratory dogs, in this paper evaporative loss and drinking have been studied during and after the controlled activity of running on a treadmill.

Loss of water by evaporation must be expected to produce increased concentration of the circulating blood. One mechanism which has been proposed as causing drinking is the stimulation by increased osmotic pressure or specifically by increased plasma Na of a receptor mechanism in the hypothalamus in a manner similar to the control of the release of antidiuretic hormone by 'osmoreceptors' (Verney, 1947). Evidence concerning this theory has been reviewed by Andersson (1971) and by Fitzsimons (1972). An example of the 'osmoreceptor' mechanism is that injection or ingestion of hypertonic NaCl causes in man the sensation of thirst (Arden, 1934; Wolf, 1950) and causes experimental animals to drink (Di Salvo, 1955; Fitzsimons, 1961, 1963; Holmes & Gregerson, 1950; Olsson, 1972; Wolf, 1950). In experiments on drinking, NaCl provides a stimulus which can be accurately reproduced and which is accepted as producing drinking by stimulation of the supposed receptors. In this paper the drinking produced by running has been compared to the drinking produced by small doses of NaCl with the hope of indicating whether the drinking from running can be explained by stimulation of receptors by increased concentration of the blood resulting from loss of water by evaporation.

O'Connor & Potts (1969) also found that the drinking by dogs in metabolism cages could be prevented by doses of water given by stomach tube and attributed importance to this as a factor controlling water balance. It has now been found that drinking during running can also be prevented by doses of water given beforehand.

Some of the findings have been communicated to the Physiological Society (O'Connor, 1972).

METHODS

The experiments were performed on five bitches – Lassie, Gina, Blackie, Sandy and Titch – also used in the observations of O'Connor & Potts (1969); in addition observations were made on another bitch, Betty. The preparation of the animals, their daily routine and feeding have been described by O'Connor & Potts (1969).

The dogs were readily trained to run on a moving belt of non-slip rubber travelling over a rigid wood floor. The dimensions of the track were similar to that described by Rydin & Verney (1938). The belt was driven through a variable-speed gear box. The speed was shown on a speedometer driven by a wheel running on the belt and calibrated by timing revolutions of the belt of which the length had been measured. The dogs stood in Pavlov slings and soon learnt to walk and then trot as the speed increased. In preliminary trials a speed was found for each dog at which it could trot comfortably. Small dogs would trot comfortably at up to 10 km/hr (6 m.p.h.), taking about 150 steps per minute; in general the bigger dogs were not comfortable at speeds greater than 7 km/hr (4·5 m.p.h.), 110 steps/min, because at faster speeds their hind quarters tended to sway against the side-barriers of the track. A speed of 10 km/hr is for a dog only a gentle trot causing no distress. Immediately after a run the heart rate had risen by about 30/min and returned to the initial rate of about 70/min within 5–15 min after the end of an hour's run. Panting also ceased within 5–15 min. During an hour of running the vaginal temperature increased by 0·1–0·6° C.

In an hour of running the dog ran at the chosen speed for six periods of 8 min. During the 2 min pauses drinking could be tested by placing the water pot in front of the dog standing in the Pavlov slings. Where drinking was tested without running with the animal standing in the slings, water was similarly offered for 2 in every 10 min. All of the observations were made by the one observer, with no one else in the room. Drinking was measured by weighing the water pot before and after each drink; usually each drink was timed with a stopwatch and the number of laps counted by the observer.

For the estimation of loss of water by evaporation, the animal was weighed as described by O'Connor & Potts (1969) to the nearest 3 g before and after the test period. Allowing for the measured weight of any water drunk, loss of weight was produced by evaporative loss of water and by the greater weight of CO_2 expired over O_2 absorbed. Cerretelli, Piiper, Mangili & Ricci (1964) have measured the gas exchanges of dogs at rest and running on a treadmill. From their figures dogs at rest would lose about 0·1 g/kg.hr and dogs running at 7–10 km/hr, 0·4–0·6 g/kg.hr due to the gas exchange. The above values have been assumed to calculate the evaporative losses from the observed changes in weight.

The protocol of an individual experiment is shown in Fig. 2*a*. About 1 hr before each experiment began, the animal was brought from the animal house and rested in a cage in the laboratory or standing in the slings on the running track. During this preliminary period she was offered water and sometimes drank, sometimes not. The running experiments were then carried out in the next 1½ hr. In control experiments the animal continued to stand with water offered for 2 in every 10 min and rarely drank. Doses of NaCl by stomach tube were given after the preliminary period; the stated dose was given in 20–25 ml. 0·15 M-NaCl and so is the dose in excess of isotonicity. When NaCl was given by infusion, at the end of the preliminary period the animal was placed on its side on a table and an infusion given as described by Holgate & O'Connor (1958). An infusion of 0·15 M-NaCl at 0·24 or 0·43 ml./min was set up and changed to 2·84 M (i.e. 2·69 M-NaCl dissolved in normal saline) for 15–30 min during which the required dose was given. The infusion cannula was then removed and the animal again stood until drinking was tested 15–20 min after the end of the infusion.

RESULTS

Drinking produced by NaCl

Fig. 1*a* records the drinking by Betty 15 min after the end of an infusion of NaCl (filled circles) or 60 min after NaCl by stomach tube (open circles). With this dog and three others no difference was apparent between the effect of NaCl given intravenously or by stomach tube. The drinks were taken as a single draught when water was first offered after NaCl and there was negligible further drinking when water was again offered 10 min later. The minimum dose of NaCl to cause drinking in Betty (Fig. 1*a*) was 6 m-mole, 0·6 m-mole/kg body wt.; in four other dogs the minimum effective dose was 1·0, 0·5, 1·2, 1·0 m-mole/kg.

Substantial drinks were always produced by doses of 1·5 m-mole/kg. Di Salvo (1955) also found that about 1 m-mole/kg was the lowest dose of NaCl to cause dogs to drink and a similar sensitivity has been demonstrated in rats (Fitzsimons, 1963).

Authors who have attempted to determine drinking thresholds have usually expressed their results by calculating the increase in osmotic pressure to produce drinking. After doses of NaCl which caused drinking by rats, Fitzsimons (1963) calculated and Hatton & Almli (1969) measured increases of 1–3 % in osmotic pressure. During infusions of NaCl Wolf (1950) found that when men felt thirsty, the calculated osmotic pressure was increased by 1–2 % and when dogs drank, the calculated increase had reached about 3 %. The threshold dose of 1 m-mole/kg in these experiments would give an estimated increase of about 1 % in osmotic pressure.

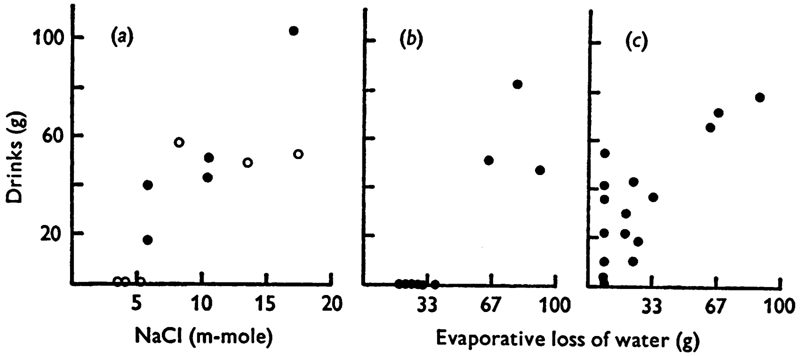

Fig. 1. The drinking by Betty, 10 kg. (*a*) After NaCl by stomach tube (○) or by intravenous infusion (●); abscissa, dose of NaCl in excess of isotonicity; (*b*) 10–30 min after the end of a period of running; (*c*) immediately after a period of running. In (*b*) and (*c*) abscissa is calculated evaporative loss of water at the time when drinking was tested.

Evaporation during running

With the dogs standing on the running track the range of mean evaporative loss of the six dogs was 0·8–1·2 g/kg.hr, which was a little more than the evaporative loss of dogs lying on a table (0·25–0·7 g/kg.hr; O'Connor & Potts, 1969). The dogs moved about in the slings but did not pant.

Soon after the dogs began running the mouth opened and the tongue protruded in the manner of panting. During the running it was not possible to recognize respiratory movements separate from the general movements presumably because the respirations were fast and shallow.

The mouth opened and the tongue protruded in some dogs as soon as running began, in others after about 5 min of running. The evaporative loss of the dogs while running increased to a range of mean values of 2–7 g/kg.hr. In absolute amounts the loss of water of the dogs standing on the track was 10–20 g/hr and in an hour of running 45–90 g (column 6, Table 1).

Drinking 10–30 min after running

To collect the data plotted in Fig. 1*b*, Betty ran at 8 km/hr (5 m.p.h.) for three or six periods of 8 min, and was then allowed to stand for 10–30 min before drinking was tested. The drinks were taken as a single draught immediately water was offered and there was no further drinking when water was again offered 10 or 20 min later. In three experiments where Betty had run for 1 hr (six periods) she drank 52, 49 and 83 g with evaporative loss at that time of 60–90 g water; in six experiments after running for 30 min (three periods) with evaporative loss of 15–35 g she did not drink.

The abscissa scales of Fig. 1*a*, *b* have been drawn to correspond in that the loss of 100 g of water by evaporation has been drawn as equal to the intake of 15 m-mole NaCl. When Betty ran for an hour the evaporative loss was about 80 g and this was associated with about the same drinking (about 60 g) as the intake of 12 m-mole NaCl. Running for 30 min caused the evaporation of about 25 g water, which should provide the same stimulus to drinking as the ingestion of 4 m-mole NaCl; neither produced drinking.

This comparison has been made with two other dogs with the same conclusion: when water was offered ½ hr after the end of a run, the drinking was similar to that produced by NaCl, on the theory that the evaporative loss of 100 g water provides a stimulus equal to the ingestion of 15 m-mole NaCl.

Drinking during running

Fig. 2*a* shows a typical experiment in which water was available during pauses in the running. Gina ran at 9·2 km/hr (5·7 m.p.h.) for six periods of 8 min; in the 2 min pauses between the runs water was offered and Gina drank 25–30 g at three of the opportunities. In consequence of the intake of 81 g water, the body weight did not fall during the run.

Table 1 shows the drinking of six dogs in a total of eighty-four experiments like that of Fig. 2*a*. One dog, Lassie, never drank in fourteen experiments. With the others, drinks were usually taken at two to five of the six opportunities in each experiment, giving the total drinking shown in column 5. In contrast in thirty-three control experiments

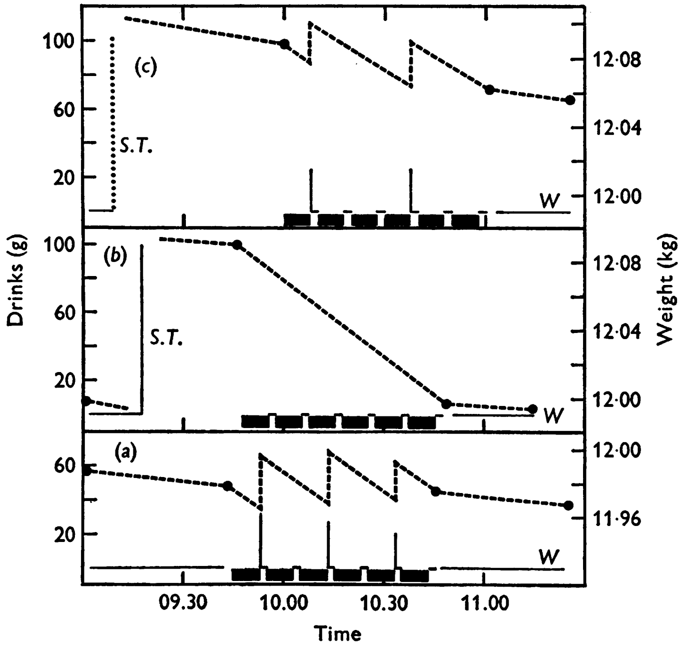

Fig. 2. The drinking by Gina (11 kg) offered water during the pauses in running at 9·2 km/hr. Water was offered during the times shown by the horizontal lines *W*; filled blocks indicate periods of running. Drinking is shown by the height of the vertical lines (scale on the left). Also plotted is the weight (kg, scale on the right). (*a*) No preliminary dose of water; (*b*) 100 ml. water by stomach tube at *S.T.* 30 min before running; (*c*) 100 ml. 0·145 M-NaCl by stomach tube at *S.T.*, 50 min before running.

where the dogs (other than Lassie) were just kept standing on the track there were only five drinks in a total of 177 opportunities.

With the exception of Lassie, the water drunk was usually about the same or rather more than the water lost by evaporation during the hour of running, so that the weight often increased during the run. In two sets of experiments, one with Blackie and one with Sandy, the drinking was much larger and exceeded by as much as 200 g the water lost by evaporation; these are shown as separate lines in Table 1.

The individual drinks were small, usually less than 3 g/kg of body weight, i.e. less than 50 g and consisted of 5–30 laps taken in less than 10 sec. The drink was taken usually within a few seconds of the water being placed in front of the dog and only very occasionally was there more than one drink in a single 2 min test period. In any experiment the first drink was nearly always at the first or second opportunity when the evaporative loss was only small and drinking continued through the six opportunities. In the average of all experiments 26 % of the total intake was in the first opportunity after 8 min running, 18 % at the second after 16 min running and 18, 11, 18 and 8 % after the third, fourth, fifth and sixth runs. In a few experiments where Gina ran for nine periods drinking continued in the further opportunities.

TABLE 1. Evaporative loss of water and drinking when water was offered six times during a run of 1 hr as in Fig. 2*a*. Drinking is shown as the average number of drinks in the six opportunities and as the total water intake (g) ± S.D. of an observation

Dog and wt. (kg)	Dates month/year	No. of experiments	Drinking /6	Drinking g	Evaporative loss (g)
Gina, 10–12	5, 7, 11/67, 9/69	15	3·1	76 ± 26	72 ± 9
Blackie					
19	8, 12/67	7	4·6	120 ± 32	72 ± 11
18	6–8/68, 10/69	9	4·1	234 ± 27	< 110*
Sandy					
20	8/67, 8/68	7	2·3	80 ± 43	58 ± 10
20	5/68	7	4·6	262 ± 78	48 ± 11
Titch, 10–11·5	5/68, 10/69, 5/70	19	2·5	61 ± 31	58 ± 12
Betty, 10·5	5, 7/70, 7/71	6	3·7	76 ± 22	54 ± 17
Lassie, 15–16·5	5, 7, 11/67, 6/68, 9/69	14	0	0	86 ± 8

* Some urine was lost during the runs.

Drinking immediately after running

Fig. 1*c* collects the data from experiments in which Betty was offered water immediately after running for different periods and so with different evaporative loss of water. The points with evaporative loss about 8 g were from seven experiments like Fig. 2*a* and show the drinking and estimated evaporative loss after one period of running. They are characteristic of the findings with four other animals.

Points with evaporative loss 20–25 g were from six experiments where drinking was tested immediately after three periods of running and the drinking in each contrasts with the failure to drink in six experiments where drinking was tested 10–30 min after the end of a similar run (Fig. 1*b*). A similar contrast was found in six pairs of experiments with Titch, the only other animal tested immediately after 30 min running.

Finally, Fig. 1*c* also shows three experiments in which Betty was offered water immediately after running for 1 hr (six periods) with evaporative loss of 60–90 g; the drinks were not obviously larger than in Fig. 1*b* when drinking was tested with a delay of 30 min after the run. In all, comparisons have been made in three dogs with a total of nine pairs of experiments in which drinking immediately after 1 hr of running could be compared with an experiment within a few days where access to water was delayed for 30 min. The drinking with immediate access to water exceeded the drinking with delayed access by an average of 12 %, a difference which is not significant.

In both Betty and Titch it was found that the immediate stimulus to drinking was brief. In a total of seven experiments on the two animals, there was no drinking when water was offered 5–10 min after the end of a 30 min running, whereas there were drinks of 10–26 g in all of twelve experiments on the two animals when water was offered immediately. The brief immediate stimulus to drinking can be compared with the observation that panting stopped within 5–10 min after the run and that the heart rate which increased from 60–80 to about 95 beats/min immediately after the run had fallen again within the same time.

TABLE 2. The effect on drinking of giving water or saline by stomach tube before a run: Gina. The total drinking (g ± S.E. of mean) when water was offered during a run of 1 hr as in Fig. 2*a*; in similar experiments where doses of water were given by stomach tube 20–30 min before the run, as in Fig. 2*b*; and where doses 0·145 M-NaCl were given 30–50 min before the run as in Fig. 2*c*

Dose (ml.)	Drinking (g)
0	76 ± 7 (15)
50 water	18, 32, 87
80 water	15, 36
100 water	0, 0, 18
80 saline	35
100 saline	51 ± 9 (7)

Inhibition by water of drinking during running

In the experiment of Fig. 2*b*, Gina was offered water in the six pauses during a run of 1 hr, but had been given 100 ml. water by stomach tube 30 min before the run began. In comparison with Fig. 2*a*, when no water was given there was no drinking in Fig. 2*b*. Table 2 lists the experiments with Gina in which drinking during running was tested after doses of water. In experiments like Fig. 2*a*, with no water given, Gina drank in two to four of the six opportunities and the mean intake was 76 g. Given 50, 80 or 100 ml. water beforehand in the manner of Fig. 2*b* the drinking during running was reduced, and practically abolished by 100 ml.

The effect of water was tested within each of seven groups of experiments shown in Table 1. When with Gina, Blackie, Sandy, Titch and Betty the mean drinking during a run of 1 hr was normally 60–120 g;

a dose of 80–120 ml. water was given on seventeen occasions; in twelve of these experiments there was no drinking during the subsequent run and in the remaining five a drink of 4–36 g was taken at only one of the six opportunities. Merely passing the stomach tube and introducing a token dose of 10 ml. water had no effect on the subsequent drinking. Also in Table 1 two groups are shown where the drinking during the run averaged 234 g (Blackie) and 262 g (Sandy). Within these groups 120 ml. water was given on three occasions and the drinking during the running was 90–150 g; on six occasions when 200–250 ml. water was given before the runs, drinking was 36–116, mean 65 g.

After doses of water insufficient to produce complete cessation of drinking, the drinking occurred at any of the six opportunities. The drinking did not occur particularly in the later tests of each run when water had been lost by evaporation.

To test whether the inhibitory effect was specifically due to water, experiments such as that in Fig. 2*c* were performed. Here Gina was given 100 ml. 0·145 M-NaCl (isotonic saline) and the usual running procedure begun 50 min later, with in this instance two drinks of 25 and 27 g at the first and fourth opportunities. Table 2 shows the mean drinking on seven occasions when Gina was given 100 ml. saline; the mean of 51 ± 9 g (S.E. of mean) compares with 76 g ± 7 when no dose was given and 0, 0, 18 g in three experiments when 100 ml. water was given. In all, 80–120 ml. saline was given in seventeen experiments on four dogs and the mean drinking was 71 ± 9 % (S.E. of mean) of the drinking in corresponding control experiments when the dog ran without a preliminary dose. Intermingled were thirteen experiments in which 80–120 ml. water was given, when the drinking during the running was reduced to 0–40 % mean 9 % of the controls. Isotonic saline was less effective than water in inhibiting drinking during running but the evidence indicates that it did have some effect.

Diuretic effect of water

O'Connor & Potts (1969) found that doses of water which stopped drinking did not produce any large increase in urine flow. A direct comparison of the effect of water in producing water diuresis and in inhibiting drinking was made in a series of experiments on Betty, listed in Table 3. The dog was catheterized while standing on the treadmill and the urine flow recorded for 90 min after doses of water given by stomach tube. The results are shown in columns 2 and 3, where 120 or 150 ml. of water caused no increase in urine flow and 200 or 250 ml. caused a small diuresis in which urine flow increased to about 1 ml./min with a total urine volume in 90 min of about 50 ml. After the test for

TABLE 3. Betty. The production of water diuresis and the inhibition of drinking by water given by stomach tube. Doses of water are shown in column 1; columns 2, 3 show the maximum rate of urine flow and the total urine volume during 90 min after the dose of water; column 4 shows the total drinking at three opportunities in a run of 30 min consisting of three runs of 8 min

	Urine flow		
Dose of water (ml.)	Maximum (ml./min)	Total in 90 min (ml.)	Drinking in 3 opportunities (g)
0	—	—	53
20	0·07	6·5	36
30	—	—	100
120	0·13	9·2	0
150	0·09	6·9	11
150	—	—	4
200	1·0	47	0
250	1·3	63	0

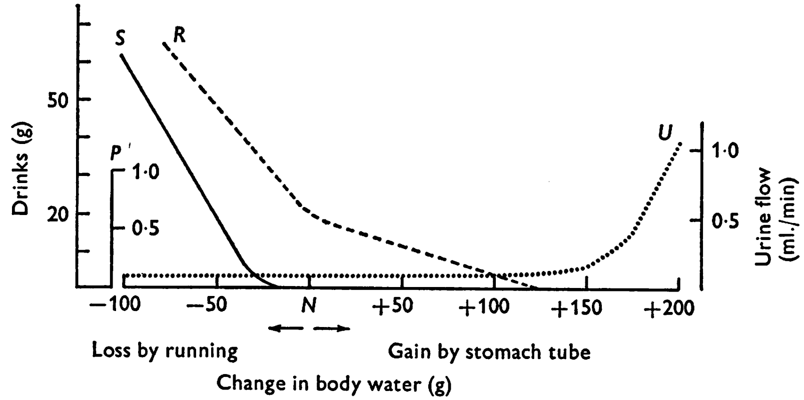

Fig. 3. A diagram showing the effect of changes in water load in determining drinking or water diuresis in a dog weighing 10 kg. For explanation and discussion see text.

water diuresis drinking was tested in three pauses in 30 min running, the total intake being shown in column 4 of Table 3. 120 ml. water, although insufficient to cause water diuresis, prevented the drinking during running. In a similar series of experiments with Titch 100 ml. water by stomach tube stopped drinking during running but neither 100 nor 200 ml. caused the urine flow to increase above 0·2 ml./min. O'Connor & Potts (1969) have already reported that doses of water adequate to prevent drinking by a dog in its cage produced little increase in the volume of the urine.

DISCUSSION

Control of water balance

The observations on one dog, Betty, are collected in Fig. 3. On the abscissa scale, *N* represents the state of the animal standing on the track during control experiments; to the left the abscissa shows loss of water by evaporation during running and to the right gain of water given by stomach tube. Drinking is shown on the double ordinate scale on the left giving the probability that a drink would be taken and the size of the drink. Drinking is represented by two lines: the continuous line *S* is drinking with the animal standing on the track with more than 10 min elapsed after running and is derived from Fig. 1*b*; the dashed line *R* shows the drinking immediately after a period of running and is drawn from Fig. 1*c*. The extension of the line *R* to the right of *N* shows the diminished drinking immediately after running when water had been given by stomach tube; a dose of 100–150 ml. completely stopped drinking as in Fig. 2*b* and Tables 2 and 3. The third line, *U*, dotted, shows the rate of urine flow (scale on the right) after doses of water by stomach tube indicated by the abscissa and is based on Table 3. A similar plot is shown by Adolph (1943, fig. 14), based on unpublished experiments by Kingsley & Adolph describing the diuresis after water loads or drinking after long periods of water deprivation. Adolph's figure shows progressively increasing drinking with increasing dehydration beyond the range studied in this paper, but does not distinguish between drinking due to dehydration and drinking immediately associated with activity.

Fig. 3 places in order four mechanisms which, by determining water intake or loss of water, are necessarily factors in maintaining water balance. At the extremes are two well established mechanisms – loss of water causes drinking (line *S*) and excess of water causes diuresis (line *U*). Fig. 3 shows these separated by 200 ml. water load, within which range the dog at rest does not drink and does not suffer water diuresis. However, within this range the line *R* shows two further mechanisms described by this paper. The third mechanism is that running causes drinking and because running also causes evaporative loss the amount of water drunk can approximate to the concurrent rate of water loss. The fourth mechanism is that drinking is inhibited by a water load insufficient to cause water diuresis. Other circumstances may also cause drinking at the state of hydration indicated by *N*. Experiments now in progress on these dogs indicate that exposure to heat (W. J. O'Connor, unpublished) and also intake of food (O'Connor & Potts, 1969) can cause drinking; both can bestopped by doses of water by stomach tube.

Fig. 3 composed from the results with Betty, with adjustment of the scales for different body weights, also applies to Gina and Titch and to half of the experiments on Blackie and Sandy. For the relationships of Fig. 3 to be all displayed on one dog requires that the drinking by the animal in the hours before the experiment shall leave her at the state of hydration *N*, between a dehydration which would cause the animal to drink when standing (curve *S*) and an over-hydration which would stop all drinking or cause diuresis. Those experiments in Table 1 where Blackie and Sandy drank larger amounts during running would be explained if the state of the animals in control experiments was to the left of *N* just insufficient to cause drinking while standing but increasing the drinking immediately after running. The failure of Lassie to drink would be explained if she were in the state to the right of *N*, sufficiently hydrated to prevent drinking during running but not to cause water diuresis. Two animals were not studied in detail because they often drank when standing in control experiments; presumably after the preliminary period they remained further to the left of *N*. Additional drinking due to running could not then be satisfactorily investigated but it was found that all drinking could be abolished with water by stomach tube. The mechanisms set out in Fig. 3 provide no means by which water balance is accurately controlled within the range of about 200 ml. between drinking on standing and water diuresis. This was not apparent in experiments such as those considered by Adolph (1943), where large water losses and loads were studied. However, in this paper where the object is to study the normal small drinks of dogs near normal states of hydration, variations such as those considered above must be expected between individual animals.

The mechanisms depicted in sequence in Fig. 3 explain how water balance in laboratory dogs can be maintained by drinking, as described by O'Connor & Potts (1969). At times of activity in their cages, evaporative loss of water is produced by panting; water however is available and by many small drinks due to the mechanism of line *R*, dehydration is avoided and the mechanism of line *S* is rarely evoked. Water contained in the food and post-prandial drinking also add to the water intake but there is rarely a water diuresis because drinking stops before the ingestion of enough water to increase the urine volume.

The environment of laboratory dogs is unusual in that water is always available. To free-living animals with intermittent access to water, the mechanism of line *S* becomes important. Activity without immediate access to water causes dehydration and according to line *S* the animal then drinks according to its state of water balance when water becomes available. Again it would be unusual for the dog to drink enough to produce water diuresis. O'Connor & Potts (1969) produced this kind of drinking by leaving active dogs for a few hours without access to water and much larger dehydrations studied by Adolph (1943) produced much larger drinks.

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