was accessible, were entirely unable to form the green or brown ground-colour. The production of dark superficial cuticular pigment was, however, unchecked. One of the larvæ fed in this way was perfectly healthy, and had become nearly mature when it was accidentally killed. Many others died early, but resembled that last described in the inability to form a ground-colour.

The experiment seems to leave no doubt as to the validity of the conclusions previously reached. Interesting questions as to the changes passed through by the derived pigments are suggested by this inquiry.

V. "The Influence of Exercise on the Interchange of the Respiratory Gases." By W. Marcet, M.D., F.R.S. Received May 18, 1893.

I had the honour of communicating two papers to the Royal Society on the interchange of pulmonary gases—one in June, 1891,* and another in June, 1892.†

The methods adopted and instruments employed have been fully described, and as the present inquiry is a continuation of the former investigation, carried on by similar methods and with the same instruments, there will be no necessity to refer to either of these on the present occasion.

It might, however, be stated that the expired air was collected in a bell-jar of a capacity of 40 litres, and over salt water; the CO_2 was determined by Pettenkofer's method, and the O by means of an eudiometer of a special construction. A short historical sketch of the work done on the subject under consideration has been given in the previous papers.

I have been very ably assisted in the present inquiry by Mr. Bernard F. Davis, B.Sc., who kindly submitted to experiment, and carried out for me, with every care, many determinations of carbonic acid and oxygen.

The object of the present communication is to show the influence of exercise on the interchange of pulmonary gases, but I must beg leave to preface the subject with a few remarks.

It has occurred to me that the words "interchange of respiratory gases" might not at first sight carry with them a perfectly clear meaning. The word "interchange" obviously refers to the movement of two gases exchanging places, and this applies to the passage of the oxygen of the air into the blood through the substance of the lungs,

* 'Proceedings Roy. Soc.,' vol. 50.
† 'Proceedings Roy. Soc.,' vol. 52.

and of the carbonic acid of the blood into the air of the pulmonary cavity also through the pulmonary tissue. The word "interchange" might be thought to mean that a certain volume of oxygen is exchanged for an equal volume of CO_2, but such is not the case, as the volume of oxygen taken up by the blood, and said to be consumed, is larger than the corresponding volume of CO_2 emitted, the difference being due to the O absorbed, which may be considered as employed in the phenomena of "tissue-change."

During ordinary respiration in a perfect state of repose, and under similar circumstances relating to temperature and food, the formation of CO_2 and absorption of O in the same person alters within certain limits. Together with these changes there is a marked tendency for the oxygen consumed (CO_2 produced and O absorbed) to assume a constant figure in the same person, or it may be said that there is a marked tendency to a decrease of CO_2 expired being accompanied by an increase of oxygen absorbed, and *vice versâ.* Four different persons were experimented upon, and this tendency is very clearly shown on three in the accompanying table, in which every figure is the mean of the two readings most alike.

In the fourth case, that of my present assistant, Mr. B. F. Davis, the tendency is of a different kind.

On a close consideration, the phenomenon observed on the three first persons experimented upon admits, I think, of the following explanation:—

If the carbonic acid expired should suddenly increase, it does so at the expense of the oxygen absorbed, and there is less of it left for the purposes of tissue-change; hence it is observed to diminish at the same time as the CO_2 is increased.

Table showing the tendency of the Oxygen consumed to remain constant under similar circumstances.

The Author.

Under influence of food.			Fasting.		
CO_2 expired.	O absorbed.	O consumed.	CO_2 expired.	O absorbed.	O consumed.
228·0 c.c.	26·0 c.c.	254 c.c.	207·2 c.c.	31·0 c.c.	238 c.c.
220·0 „	29·0 „	249 „	202·6 „	32·2 „	335 „
206·7 „	35·8 „	242 „	192·9 „	42·5 „	235 „

Mr. Russell.

Under food.			Fasting.		
CO_2 expired.	O absorbed.	O consumed.	CO_2 expired.	O absorbed.	O consumed.
305·1 c.c.	27·4 c.c.	332 c.c.	255·1 c.c.	25·5 c.c.	281 c.c.
292·7 „	42·3 „	335 „	241·3 „	38·4 „	280 „
282·0 „	49·6 „	332 „	226·2 „	36·2 „	262* „

Mr. D. Smith.

Under food.			Fasting.		
CO_2 expired.	O absorbed.	O consumed.	CO_2 expired.	O absorbed.	O consumed.
236 c.c.	45·1 c.c.	282 c.c.	225 c.c.	32·2 c.c.	257 c.c.
229 „	59·8 „	289 „	212 „	34·2 „	246 „
222 „	46·8 „	269* „	211 „	35·8 „	247 „

We now have to account for the fourth person under experiment giving results at variance with the others. In this case, instead of the CO_2 produced and O absorbed varying in opposite directions as they do with the three other persons experimented upon, they rise and fall together, their ratios being somewhat similar. This will be seen in the following table, in which each figure is the mean of two determinations nearest to each other.

B. F. Davis under Experiment. Under the Influence of Food.

	Winter.			Summer.		
	CO_2 expired.	O absorbed.	Ratio.	CO_2 expired.	O absorbed.	Ratio.
	c.c.	c.c.		c.c.	c.c.	
	264·1	59·9	0·227	252·5	44·3	0·175
	255·5	59·9	0·234	247·0	50·1	0·203
	236·0	50·5	0·214	235·3	44·8	0·190
	219·8	49·6	0·226	210·6	37·4	0·177
Means..	234·8	55·0	0·225	236·3	44·1	0·186

* The figures marked with an asterisk show the only exceptions.

These experiments show a remarkable uniformity of results in winter and summer respectively.

As to the experiments fasting, not tabulated in this paper, while in summer they agree with those of the three other persons under experiment, no uniform relation can be traced in winter between the CO_2 expired and O absorbed.

In this case, in the winter and summer experiments referred to, the CO_2 expired and O absorbed may be said to rise and fall together, which means that, instead of a tendency to a constant figure for O consumed, there is, at all events between 1 and 2 hrs. after a full meal, the reverse tendency, and the figure for O consumed is observed either to rise or fall. Consequently there must be in the case of Mr. Davis a function of the body different from the corresponding function in the three other persons. Now this gentleman is just twenty-one years of age and is still growing; indeed, there has been a marked appearance in him of physical development within the last few months, and I fully believe that this is the cause of the present result. While with the three other persons as the carbonic acid increased the oxygen absorbed diminished, in this particular case as the CO_2 increases the O absorbed also becomes larger, this excess being due, it may be concluded, to the requirements of new tissue.

Influence of Exercise.

The method of investigation was as follows:—In order to adopt a kind of muscular exercise similar, as near as possible, to one in common use, I selected the very simple act of stepping, within a small area, which imitated walking. This was done by raising the feet alternately sixty-eight times a minute, according to the striking of a metronome. I raised the feet by nearly 10 cm., and Mr. Davis by nearly 18 cm., measured at the heel; consequently the degree of exercise was not the same in each case. Moreover, the exercise may not have been strictly regular in every experiment, although sufficiently so for the purpose in view. In most cases, before exercise was taken, a preliminary experiment was made on the person *in repose;* with that object he rested for half an hour, reclining in a deck chair, then the air expired in a recorded time (in absolutely natural breathing) was collected in the two bell-jars, measured, and then transferred to an india-rubber bag faced with oil silk, in order to liberate the bell-jars for further use. The next part of the experiment was stepping and breathing the air expired into a bell-jar during exercise. It must be understood that this air was not collected during the whole time the exercise lasted, but only at the end of that time, and during about "3 mins."

After the air expired, under exercise, had been collected in a bell-jar, the person experimented upon sat down in the deck chair without

breathing, and then the air he expired was collected as usual for a period of 13 or 14 mins. In this way the whole phenomenon of respiration under exercise could be closely followed. The CO_2 alone, or CO_2 and O, were determined in the air expired in the state of repose, the CO_2 and O were determined in the air expired under exercise, and the CO_2 alone in the air expired while resting after the period of exercise. It had been found, experimentally, that the time taken to fill the two bell-jars (13 to 14 mins.) was sufficient for the CO_2 expired to return to its normal amount.

The object of the experiment was as follows:—The first stage in repose afforded data towards the comparison of the effects of exercise on the respiratory functions with those functions in the state of rest. The second stage had for its object to determine the CO_2 and O expired in a given time while under the exercise. The third stage showed the amount of CO_2 given out, while quite still, after the exercise had been concluded; and the excess of CO_2 thus obtained over the amount of CO_2 which would have been expired in the same lapse of time in perfect repose was looked upon as CO_2 which had accumulated in the blood during exercise, and this was proved by subsequent experiment.

[18*th August.*—Without entering at present into a discussion of this subject, a number of experiments, which I regret space does not allow me to describe, have shown most distinctly that respiration while in repose following exercise cannot be compared to forced respiration, inasmuch as in forced respiration the excess of CO_2 expired is much less than after exercise; and, moreover, immediately after a return to natural breathing after forced respiration the CO_2 expired is diminished nearly, although not quite, to the same amount as it had been increased under forced breathing, and this is not observed as a sequel to exercise.

I feel called upon to make this remark in due consideration to C. Speck's interesting paper on the consumption of oxygen and production of carbonic acid ('Schriften der Gesellschaft zur Beförderung der Gesammten Naturwissenschaften zu Marburg,' vol. 10, 1871.)]

The experiments on myself will be considered first: They were undertaken in December, January, and February last, and, with two exceptions, all between 1 and 2 hrs. after a full luncheon. The duration of the exercise was from about 17 to 19 mins., this period being selected, because after 19 or 20 mins. the phenomena were found to lose their regularity. The respiratory changes were also observed to be more regular in winter than in summer, and especially under the direct influence of digestion; or under circumstances producing most carbonic acid in the state of repose.

These experiments show that, in my case, under the kind of exercise taken, the amount of CO_2 expired per minute was very

Table showing Results of Experiments under Exercise.

The Author.

Perfect state of repose. CO_2 expired.	Winter experiments, 1—2 hours after meal.					Resting after exercise.		
	Duration of exercise.		CO_2 expired per minute.	O absorbed per minute.	Excess CO_2 expired in exercise over CO_2 in repose.	Total CO_2 retained.	CO_2 absorbed per minute.	Ratio of excess CO_2 expired under exercise to CO_2 absorbed.
c.c.	mins.	secs.	c.c.	c.c.	c.c.	c.c.	c.c.	
242·0	19	4	450·9	—	208·9	519	27·2	0·130
193·7	17	42	484·4	—	290·7	719	40·6	0·140
234·3	18	11	402·0	—	167·7	334	18·4	0·110
227·2	19	12	421·7	—	198·5	479	24·9	0·126
235·8	18	56	436·8	—	201·0	430	22·7	0·113
Fasting { 190·1	18	34	402·6	60·9	212·5	501	27·0	0·127
Fasting { 192·3	18	36	482·0	60·6	289·7	606	36·5	0·126
Fasting { 165·6	18	23	352·0	72·5	186·4	418	22·8	0·122
Fasting { 232·3	17	40	472·1	67·5	240·0	500	28·3	0·118
220·0	18	43	436·8	—	216·8	490	25·9	0·119
213·3	18	31	434·1	65·4	221·2	500	27·4	0·123

nearly twice the amount expired in a perfect state of repose (213·3 c.c. and 434·1 c.c.); the mean excess, 221·7, may be looked upon as due to the production of heat to be converted into motion, but it will be seen presently that there is really more heat developed from carbon burnt to the extent of about 12 per cent. of the above excess. The oxygen absorbed, 65·4 c.c., looks much too high, as the mean amount obtained under the influence of food in my last experiments is 35·7, and at first it occurred to me that more oxygen was really absorbed under exercise than in repose. But on inquiring closely into the present result, it became obvious that this figure for oxygen absorbed included some oxygen retained in the body as CO_2. The next point was to determine, if possible, how much oxygen was absorbed for tissue-change, and how much was retained as CO_2. This result was obtained by a consideration of the third stage of the experiment which concerned resting after exercise. In this third stage the mean excess of CO_2 found to have been expired under exercise over the CO_2 expired in repose is equal to 500 c.c. for a mean exercise of 18 mins. 31 secs.; or, in other words, in 18 mins. 31 secs. an amount of CO_2 had accumulated in the body equal to 500 c.c. Assuming that this accumulation took place regularly, it would have amounted to a mean of 27·6 c.c. per minute. We are now in a position to find out the volume of CO_2 present, together with the amount of O absorbed per minute; this is done by subtracting the volume of CO_2 absorbed per minute, or 27·4 from the volume of O entered as absorbed, or 65·4; this gives 38 c.c. for the actual volume of oxygen absorbed, which is very near to the figure 35·7, the mean volume of oxygen absorbed in my case under food and in the state of repose.

It then occurred to me that the total CO_2 retained in the blood under exercise might bear some proportion to the excess of CO_2 expired under exercise over the CO_2 expired sitting. On calculating these relations I found that there certainly was such a ratio. Of course the ratio varied somewhat in each experiment, but the means of the ten experiments gave the figure 0·123, while the extremes were 0·110 and 0·140. Therefore, by multiplying the mean ratio 0·123 by the excess of the CO_2 under exercise over the CO_2 in repose, the result will give, with a certain degree of approximation, the figure for the CO_2 absorbed per minute during the exercise without being at the trouble of determining this figure experimentally.

We now turn to the corresponding experiments made on Mr. Davis. There are five of them; the sixth was discarded from some irregularity which could not be accounted for.

In the first experiment the air expired was collected on beginning the exercise; in the second it was collected six minutes after exercise was begun; in the third 9 mins. after; in the fourth 12 mins.; and in the fifth 15 mins. after.

Results of Experiments under Exercise.

B. F. Davis, in Winter, 1—2 hrs. after a Meal.

Duration of exercise before collecting air....	0 min.	6 mins.	9 mins.	12 mins.	15 mins.
	c.c.	c.c.	c.c.	c.c.	c.c.
O consumed...........	719·0	770·0	834·0	799·0	775·0
CO_2 produced	634·0	659·7	743·0	682·6	660·0
O and CO_2 absorbed	84·8	110·3	90·0	116·3	115·1

The figures obtained under the heading "O and CO_2 absorbed," were, with the exception perhaps of the first, fairly close to each other, with a mean of 103 c.c. By multiplying the factor 0·123 found in my experiment by the mean excess of CO_2 under exercise over CO_2 in repose (the data in repose being obtained from other experiments), and subtracting the result from the O and CO_2 found as absorbed, as was done in the other case, the figure for carbonic acid absorbed is 50, and for O absorbed 53; the latter being very near "55," which is, for Mr. Davis, the mean volume of oxygen absorbed after a meal in the state of repose. Therefore, again, in the present case in the winter experiments, between 1 and 2 hrs. after a full meal, by applying the factor 0·123, we find the same volume of oxygen absorbed under exercise as when in a perfect state of repose. In the experiments on Mr. Davis, the third stage had been omitted, as the experiments were done before any attempt to judge experimentally of the CO_2 absorbed in the blood had been thought of.

So far the results of these experiments must be considered as depending to a great extent on the season of the year—winter—on the time which has elapsed since food has been partaken of—1—2 hrs.—and on the period during which exercise has been taken—a period not exceeding 18 or 19 mins. It stands to reason that after exercise has lasted a certain time the blood cannot take up any more CO_2, and this time does not appear to exceed 19 or 20 mins. It was found, experimentally, that after that period the volume of CO_2 accumulated in the blood varies greatly.

The exercise was continued in other experiments for 33 mins., 42 mins., and 1½ hrs., when the volume of CO_2 stored up in the blood was found to range from 0 c.c. to 353 c.c. In the warm summer weather the CO_2 formed under exercise appears to leave the blood at the lungs more rapidly than in winter. So far I have not succeeded in finding any uniform volume absorbed during any given time in spring and summer, although a number of experiments were carefully made with that object in view.

Therefore, so far, the accumulation of CO_2 in the body may only be considered as regular under certain fixed conditions; but there is invariably a tendency towards CO_2 being retained in the blood the first few minutes exercise is taken after a period of repose.

A certain number of minutes after exercise has been commenced the CO_2 stored up in the blood is given out. In C. Bernard's experiment, where a solution of sulphuretted hydrogen is injected into the circulation of a dog, the gas comes out at the mouth in large volumes in a few successive expirations following deep inspirations. I should be inclined to think that a similar phenomenon takes place with reference to CO_2 in respiration under exercise, the gas accumulates in the blood up to a certain stage, and is then given out in the form of a wave, after which the accumulation goes on afresh, but the phenomenon is not regular, and depends on many causes which would be very difficult to determine. My experiments are certainly opposed to the idea that under exercise the CO_2 is eliminated as fast as it is produced, leaving a uniform balance of CO_2 in the blood. With prolonged exercise and training the intermittence would probably become less and less.

One of the questions for investigation which occurred to me in the course of this enquiry was the time required for the carbonic acid expired and oxygen absorbed to return to their normal condition of rest after the stepping exercise. This portion of work was done in the season 1891–92, when Mr. Darnell Smith, B.Sc., acted as my assistant. We both submitted to experiment. The first stage was the determination of CO_2 expired and O absorbed after resting for half an hour perfectly still in the deck chair.* Then the person under experiment took the stepping exercise for a quarter of an hour, and sat down, remaining quite still, for 10 mins. After that lapse of time the CO_2 expired and O absorbed were again determined. The results are shown in the following table (p. 51).

It will be seen in this table that, with both of us, after 10 mins.' rest the CO_2 expired had returned to the normal, or very nearly so. In my case the CO_2 had quite recovered its mean in repose; in Mr. Smith's it was only by 2 per cent. in excess. The oxygen absorbed was, however, quite altered from its original figures. Instead of 31·7 c.c. I absorbed per minute in repose, the figure had fallen to 24·8 c.c., and with Mr. Smith it had been reduced from 25·8 c.c. in repose to 14 c.c. The reason of this phenomenon appears to me very obvious. While the respiratory phenomena are all excited under exercise, the blood becomes charged with more oxygen than it can

* In three of these experiments, on the assumption that 30 mins.' rest after exercise were sufficient for a return of normal breathing in repose, the CO_2 and O were determined 30 mins. after the exercise was over instead of before the exercise was begun.

Time for Return of Normal Respiration after Exercise.

The Author under experiment.

	CO_2 produced per minute.		O absorbed per minute.	
	After a rest of 30 min.	After 10 mins.' rest following exercise.	After 30 mins.' rest.	After 10 mins.' rest following exercise.
1........	222 c.c.	234 c.c.	37·1 c.c.	31·0 c.c.
2........	218 „	211 „	27·8 „	14·0 „
3........	195 „	185 „	34·6 „	22·0 „
4........	190 „	188 „	27·5 „	22·3 „
Means...	206 c.c.	204 c.c.	31·7 c.c.	24·8 c.c.
		D. Smith under experiment.		
1........	241 c.c.	232 c.c.	23·1 c.c.	7·3 c.c.
2........	271 „	239 „	29·0 „	10·7 „
3........	233 „	266 „	24·1 „	8·1 „
4........	249 „	222 „	35·1 „	32·1 „
5........	223 „	225 „	19·7 „	16·7 „
6........	208 „	213 „	23·5 „	9·1 „
Means...	228 c.c.	233 c.c.	25·8 c.c.	14·0 c.c.

hold in the state of rest; therefore under the state of repose following exercise, the blood is sufficiently rich in oxygen to supply the tissue-change without drawing upon atmospheric air for a further amount of the gas.

In the experiments related above, 10 mins.' rest after exercise sufficed for the carbonic acid expired to return to its normal amount in the state in repose; possibly with some other persons a little longer, say, 15 mins., may be necessary. As for the period of rest required for the O absorbed to return to its normal figure in repose, after stepping exercise, half an hour appeared perhaps barely sufficient. I have considered, however, half an hour's rest as long enough when active exercise had not been previously taken; and half an hour's repose was adopted, as a rule, to bring the body into the physiological state of rest.

The following is a summary of the contents of this paper:—

1st. I have shown that in three persons out of four there was a great tendency to an uniformity of figure for the oxygen *consumed* under similar physical circumstances (food, temperature, &c.), so that, if the CO_2 expired fell, the oxygen absorbed rose, and *vice versâ;* this was accounted for by assuming that an increase of CO_2

in the blood in the state of repose is produced at the expense of the O absorbed. The fourth person experimented upon exhibited no such tendency, the CO_2 expired and O absorbed rose and fell together, which was ascribed to the fact that he was still growing.

2nd. Experiments were made on the influence of exercise on respiration which showed that if stepping exercise is taken after a period of rest, there occurs for a few minutes an accumulation of CO_2 in the blood; of course the degree of this storage of CO_2 must be controlled by the normal amount of CO_2 produced in repose, and the kind of exercise taken; this storage would in the cold winter weather, and between 1 and 2 hrs. after food continue for about 18 or 20 mins. In my case the volume of CO_2 retained in the blood amounted to a mean of 500 c.c. while stepping sixty-eight times per minute about 10 cm. high. The CO_2 in store is next given out in the form of a wave, which is renewed after a certain lapse of time, so that there does not appear to be in respiration under exercise a fixed relation between the CO_2 expired and the CO_2 left in the blood. With practice and training this relation would probably become more and more uniform.

The storage of CO_2 in winter and after food was found to exhibit a certain relation to the excess of CO_2 expired under exercise over the CO_2 expired in repose; but 18 or 20 mins. after exercise had been commenced this relation failed to show itself any longer.

The ratio in question was the same with two different persons; but further experiment is required to determine whether it can be looked upon as general; the mean ratio found is shown by the figure 0·123; therefore, so far as the present enquiry goes, and under the conditions expressed in this paper, by multiplying this figure 0·123 by the excess of CO_2 given out per minute under exercise over the CO_2 expired in repose during the same lapse of time, the result will show the volume of CO_2 absorbed in the blood per minute.

After the exercise had lasted 18 to 20 mins., the volume of CO_2 stored up in the blood after exercise was found to vary.

3rd. After the exercise adopted in this enquiry had been followed by a complete repose of 10 mins., the CO_2 expired had returned to the normal in repose, but the volume of O absorbed per minute had considerably fallen, clearly owing to the blood having charged itself with oxygen during exercise, so that the first few minutes after rest was taken the blood was in a condition to supply oxygen for tissue-changes without taking it from the air breathed. After half an hour's perfect rest following exercise the respiratory changes had returned to their normal state of repose, or nearly so, the oxygen absorbed still occasionally showing signs of being a little lower than before exercise had been taken.