WEEKLY EVENING MEETING,

Friday, February 9, 1877.

Sir W. Frederick Pollock, Bart. M.A. Vice-President, in the Chair.

Francis Galton, Esq. F.R.S. F.G.S. *M.R.I.*

Typical Laws of Heredity.

We are far too apt to regard common events as matters of course, and to accept many things as obvious truths which are not obvious truths at all, but present problems of much interest. The problem to which I am about to direct attention is one of these.

Why is it, when we compare two groups of persons selected at random from the same race, but belonging to different generations of it, we find them to be closely alike? Such statistical differences as there may be, are always to be ascribed to differences in the general conditions of their lives; with these I am not concerned at present; but so far as regards the processes of heredity alone, the resemblance of consecutive generations is a fact common to all forms of life.

In each generation there will be tall and short individuals, heavy and light, strong and weak, dark and pale; yet the proportions of the innumerable grades in which these several characteristics occur tend to be constant. The records of geological history afford striking evidences of this statistical similarity. Fossil remains ot plants and animals may be dug out of strata at such different levels, that thousands of generations must have intervened between the periods in which they lived; yet in large samples of such fossils we seek in vain for peculiarities that will distinguish one generation taken as a whole from another, the different sizes, marks, and variations of every kind, occurring with equal frequency in both. The processes of heredity are found to be so wonderfully balanced, and their equilibrium to be so stable, that they concur in maintaining a perfect statistical resemblance so long as the external conditions remain unaltered.

If there be any who are inclined to say there is no wonder in the matter, because each individual tends to leave his like behind him, and therefore each generation must resemble the one preceding, I can assure them that they utterly misunderstand the case. Individuals do *not* equally tend to leave their like behind them, as will be seen best from an extreme illustration.

Let us then consider the family history of widely different groups, say of 100 men, the most gigantic of their race and time, and the same number of medium men. Giants marry much more rarely than medium men, and when they do marry they have but few children. It is a matter of history that the more remarkable giants have left no issue at all. Consequently the offspring of the 100 giants would be much fewer in number than those of the medium men. Again, these few would, on the average, be of lower stature than their fathers, for two reasons. First, their breed is almost sure to be diluted by marriage. Secondly, the progeny of all exceptional individuals tends to "revert" towards mediocrity. Consequently the children of the giant group would not only be very few, but they would also be comparatively short. Even of these the taller ones would be the least likely to live. It is by no means the tallest men who best survive hardships; their circulation is apt to be languid and their constitution consumptive.

It is obvious from this that the 100 giants will not leave behind them their quota in the next generation. The 100 medium men, on the other hand, being more fertile, breeding more truly to their like, being better fitted to survive hardships, &c., will leave more than their proportionate share of progeny. This being so, it might be expected that there would be fewer giants and more medium-sized men in the second generation than in the first. Yet, as a matter of fact, the giants and medium-sized men will, in the second generation, be found in the same proportions as before. The question, then, is this: How is it, that although each individual does *not* as a rule leave his like behind him, yet successive generations resemble each other with great exactitude in all their general features?

It has, I believe, become more generally known than formerly, that although the characteristics of height, weight, strength, and fleetness are very different in themselves, and though different species of plants and animals exhibit every kind of diversity, yet the differences in height, weight, and every other characteristic, among members of the same species, are universally distributed in fair conformity with a single law.

The phenomena with which that law deals are like those perspectives spoken of by Shakespeare, which, when viewed awry, show nothing but confusion.

Our ordinary way of looking at individual differences is awry: thus we naturally, but wrongly, judge of differences in stature by differences in heights measured from the ground, whereas on changing our point of view to that whence the law of deviation regards them, by taking the average height of the race, and not the ground, as the point of reference, all confusion disappears, and uniformity prevails.

It was to Quetelet that we were first indebted for a knowledge of the fact, that the amount and frequency of deviation from the average among members of the same race, in respect to each and every characteristic, tends to conform to the mathematical law of deviation.

The diagram contains extracts from some of the tables by which he corroborates his assertion. Three of the series in them refer to the heights of Americans, French, and Belgians respectively, and the fourth to the strength of Belgians. In each series there are two parallel columns, one entitled "observed," and the other "calculated," and the close conformity between each of the pairs is very striking.

Scale of Heights.	American Soldiers (25,878 Observations).		France (Hargenvilliers).		Belgium, Quetelet. 20 years' Observations.	
	Observed.	Calculated.	Observed.	Calculated.	Observed.	Calculated.
mètres.						
1·90	1	3				
1·90	7	5	..	..		
·87	14	13	..	1	1	1
·84	25	28		3	2	3
·81	45	52	25	7	7	7
·79	99	84		16	14	14
·76	112	117	32	32	34	28
·73	138	142	55	55	48	53
·70	148	150	88	87	102	107
·68	137	137	114	118	138	136
·65	93	109	144	140	129	150
·62	109	75	140	145	162	150
·60	49	45	116	132	106	136
·57	14	24	..	105	110	107
·54	8	11		73		53
·51	1	4		44		28
·48	..	1		24	147	14
·45	..	..	286	11		7
·42	..	..		4		3
·39	..	..		2		1
·36	..	..		1		
	1000	1000	1000	1000	1000	1000

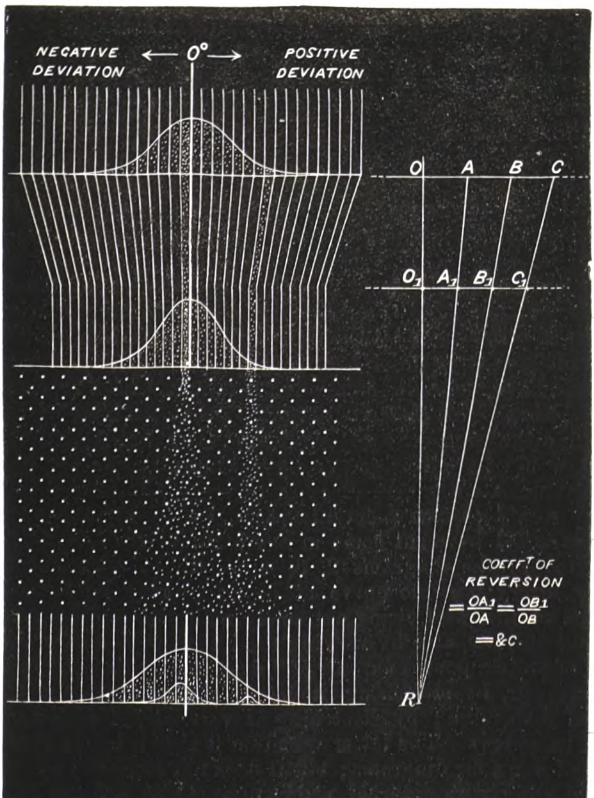
Degrees of Dynamometer.	Lifting Power of Belgian Men.	
	Observed.	Calculated.
200	1	1
190	9	10
180		
170	23	23
160		
150	32	32
140		
130	22	23
120		
110	12	10
100		
90	1	1
	100	100

These tables serve another purpose; they enable those who have not had experience of such statistics to appreciate the beautiful balance of the processes of heredity in ensuring the repetition of such finely graduated proportions as those that the tables record.

The outline of my problem of this evening is, that since the characteristics of all plants and animals tend to conform to the law of deviation, let us suppose a typical case, in which the conformity shall be exact, and which shall admit of discussion as a mathematical problem, and find what the laws of heredity must then be to enable successive generations to maintain statistical identity.

I shall have to speak so much about the law of deviation, that it is

FIG. 1.



absolutely necessary to tax your attention for a few minutes to explain the principle upon which it is based, what it is that it professes to show, and what the two numbers are, which enable long series to be calculated like those in the tables just referred to. The simplest way of explaining the law is to begin by showing it in action. For this purpose I will use an apparatus that I employed three years ago in this very theatre, to illustrate other points connected with the law of deviation. An extension of its performance will prove of great service to us to-night; but I will begin by working the instrument as I did on the previous occasion. The portion of it that then existed, and to which I desire now to confine your attention, is shown in the lower part of Fig. 1, where I wish to direct your notice to the stream issuing from either of the divisions just above the dots, to its dispersion among them, and to the little heap that it forms on the bottom line. This part of the apparatus is like a harrow with its spikes facing us; below these are vertical compartments; the whole is faced with a glass plate. I will pour pellets from either of these divisions or from any other point above the spikes; they will fall against the spikes, tumble about among them, and after pursuing devious paths, each will finally sink to rest in the compartment that lies beneath the place whence it emerges from its troubles.

The courses of the pellets are extremely irregular; it rarely happens that any two starting from the same point will pursue the same path from beginning to end; yet, notwithstanding this, you will observe the regularity of the outline of the heap formed by the accumulation of pellets.

This outline is the geometrical representation of the curve of deviation. If the rows of spikes had been few, the deviation would have been slight, almost all the pellets would have lodged in the compartment immediately below the point whence they were dropped, and would then have resembled a column; if they had been very numerous, they would have been scattered so widely that the part of the curve for a long distance to the right and left of the point whence they were dropped would have been of uniform width, like an horizontal bar. With intermediate numbers of rows of teeth, the curved contour of the heap would assume different shapes, all having a strong family resemblance. I have cut some of these out of cardboard; they are represented in the diagrams 2, 3, 4 and 5, below. Theoretically speaking, every possible curve of deviation may be formed by an apparatus of this sort, using extremely numerous and delicate spikes and minute pellets, and by varying the length of the harrow and the number of pellets poured in. Or if I draw a curve on an elastic sheet of indiarubber, by stretching it laterally I produce the effects of increased dispersion; by stretching it vertically I produce that of increased numbers. The latter variation is shown by the three curves in each of the four diagrams; but it does not concern us to-night, as we are dealing with internal proportions, which are not affected by the absolute number of the sample employed. To specify the variety of curve so far as dispersion is concerned, we must measure the amount of lateral stretch of the indiarubber sheet. The curve has no

FIG. 2.

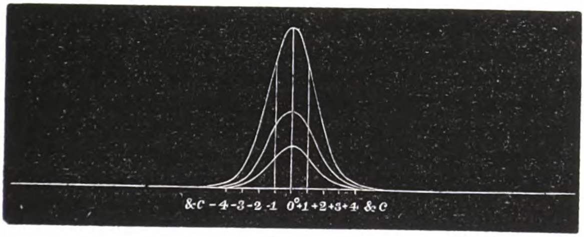


FIG. 3.

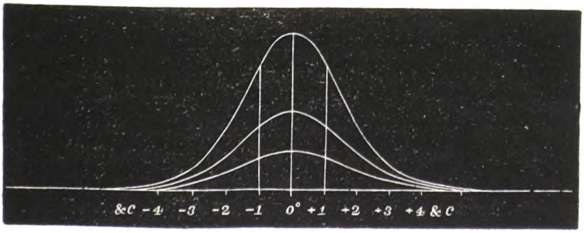


FIG. 4.

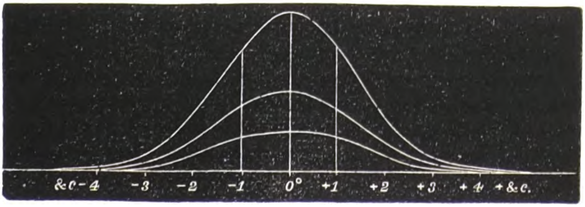
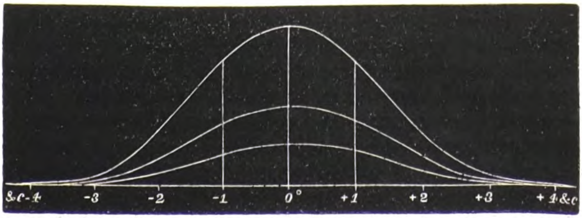
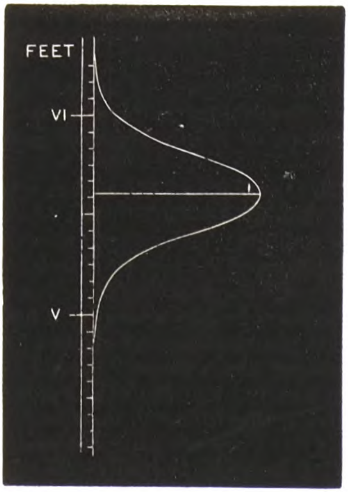


FIG. 5.



definite ends, so we have to select and define two points in its base, between which the stretch may be measured. One of these points is always taken directly below the place whence the pellets were poured in. This is the point of no deviation, and represents the mean position of all the pellets, or the average of a race. It is marked as 0°. The other point is conveniently taken at the foot of the vertical line that divides either half of the symmetrical figure into two equal areas. I take a half curve in cardboard that I have again divided into two portions along this line; the weight of the two portions is equal. This distance is the value of 1° of deviation, appropriate to each curve. We extend the scale on either side of 0° to as many degrees as we like, and we reckon deviation as positive, or to be added to the average, on one side of the centre, say to the right, and negative on the other, as shown on the diagrams. Owing to the construction, one-quarter or 25 per cent. of the pellets will lie between 0° and 1°, and the law shows that 16 per cent. will lie between + 1° and + 2°, 6 per cent. between + 2° and + 3° and so on. It is unnecessary to go more minutely into the figures, for it will be easily understood that a formula is capable of giving results to any minuteness and to any fraction of a degree.

Fig. 6.



Let us, for example, deal with the case of the American soldiers. I find, on referring to Gould's Book, that 1° of deviation was in their case 1·676 inches. The curve I hold in my hand, Fig. 6, has been drawn to that scale. I also find that their average height was 67·24 inches. I have here a standard marked with feet and inches. I apply the curve to the standard, and immediately we have a geometrical representation of the statistics of height of all those soldiers. The lengths of the ordinates show the proportion of men at and about their heights, and the area between any pairs of ordinates gives the proportionate number of men between those limits. It is indeed a strange fact, that any one of us sitting quietly at his table could, on being told the two numbers just mentioned, draw out a curve on ruled paper, from which thousands of vertical lines might be chalked side by side on a wall, at the distance apart that is taken up by each man in a rank of American soldiers, and know that if the same number of these American soldiers, taken indiscriminately, had been sorted according to their stature and marched up to the wall, each man of them would find the chalked line which he saw opposite to him to be of exactly his own height. So far as I can judge from the run of the figures in the table, the error would never exceed a quarter of an inch, except at either extremity of the series.

The principle of the law of deviation is very simple. The important influences that acted upon each pellet were the same; namely, the position of the point whence it was dropped, and the force of gravity. So far as these are concerned, every pellet would have pursued an identical path. But in addition to these, there were a host of petty disturbing influences, represented by the spikes among which the pellets tumbled in all sorts of ways. The theory of combination shows that the commonest case is that where a pellet falls equally often to the right of a spike as to the left of it, and therefore drops into the compartment vertically below the point where it entered the harrow. It also shows that the cases are very rare of runs of luck carrying the pellet much oftener to one side than the other of the successive spikes. The law of deviation is purely numerical; it does not regard the fact whether the objects treated of are pellets in an apparatus like this, or shots at a target, or games of chance, or any other of the numerous groups of occurrences to which it is or may be applied.*

I have now done with my description of the law. I know it has been tedious, but it is an extremely difficult topic to handle on an occasion like this. I trust the application of it will prove of more interest.

First, let me point out a fact which Quetelet and all writers who have followed in his path have unaccountably overlooked, and which has an intimate bearing on our work to-night. It is that, although characteristics of plants and animals conform to the law, the reason of their doing so is as yet totally unexplained. The essence of the law is that differences should be wholly due to the collective actions of a host of independent *petty* influences in various combinations, which were represented by the teeth of the harrow, among which the pellets tumbled in various ways. Now the processes of heredity that limit the number of the children of one class, such as giants, that diminish their resemblance to their fathers, and kill many of them, are not petty influences, but very important ones. Any selective tendency is ruin to the law of deviation, yet among the processes of heredity there is the large influence of natural selection. The conclusion is of the greatest importance to our problem. It is, that the processes of heredity must work harmoniously with the law of deviation, and be themselves in some sense conformable to it. Each of the processes must show this conformity separately, quite irrespectively of the rest. It is not an

* Quetelet, apparently from habit rather than theory, always adopted the binomial law of error, basing his tables on a binomial of high power. It is absolutely necessary to the theory of the present paper to get rid of binomial limitations and to consider the law of deviation or error in its exponential form.

admissible hypothesis that any two or more of them, such as reversion and natural selection, should follow laws so exactly inverse to one another that the one should reform what the other had deformed; because characteristics, in which the relative importance of the various processes is very different, are none the less capable of conforming closely to the typical condition.

When the idea first occurred to me, it became evident that the problem might be solved by the aid of a very moderate amount of experiment. The properties of the law of deviation are not numerous, and they are very peculiar. All, therefore, that was needed from experiment was suggestion. I did not want proof, because the theoretical exigencies of the problem would afford that. What I wanted was to be started in the right direction.

I will now allude to my experiments. I cast about for some time to find a population possessed of some measurable characteristic that conformed fairly well to the law, and that was suitable for investigation. I determined to take seeds and their weights, and after many preparatory inquiries, fixed upon those of sweet-peas. They were particularly well suited to my purposes; they do not cross-fertilise, which is a very exceptional condition; they are hardy, prolific, of a convenient size to handle, and their weight does not alter when the air is damp or dry. The little pea at the end of the pod, so characteristic of ordinary peas, is absent in sweet-peas. I weighed seeds individually, by thousands, and treated them as a census officer would treat a large population. Then I selected with great pains several sets for planting. Each set contained seven little packets, and in each packet were ten seeds, precisely of the same weight. Number one of the packets contained giant seeds, all as nearly as might be of $+3°$ of deviation. Number seven contained very small seeds, all of $-3°$ of deviation. The intermediate packets corresponded severally to the intermediate degrees $\pm 2°$ $\pm 1°$ and $0°$. As the seeds are too small to exhibit, I have cut out discs of paper in strict proportion to their sizes, and strips in strict proportion to their weights, and have hung below them the foliage produced by one complete set. Many friends and acquaintances each undertook the planting and culture of a complete set, so that I had simultaneous experiments going on in various parts of the United Kingdom. Two proved failures, but the final result was this: that I obtained the more or less complete produce of seven sets, that is, of $7 \times 7 \times 10$, or 490 carefully weighed seeds.

It would be wholly out of place if I were to enter into the details of the experiments themselves, the numerous little difficulties and imperfections in them, or how I balanced doubtful cases, how I divided returns into groups, to see if they confirmed one another, or how I conducted any other of the well-known statistical operations. Suffice it to say that I took immense pains, which, if I had understood the general conditions of the problem as clearly as I do now, I should not perhaps have cared to bestow. The results were most satisfactory. They gave me two data, which were all that I required in order to understand the simplest form of descent, and so I got at the heart of the problem at once.

Simple descent means this. The parentage must be single, as in the case of the sweet-peas which are not cross-fertilised, and the rate of production and the incidence of natural selection must both be independent of the characteristic. The only processes concerned in simple descent that can affect the characteristics of a sample of a population are those of Family Variability and Reversion. It is well to define these words clearly. By family variability is meant the departure of the children of the same or similarly descended families, from the ideal mean type of all of them. Reversion is the tendency of that ideal mean filial type to depart from the parent type, "reverting" towards what may be roughly and perhaps fairly described as the average ancestral type. If family variability had been the only process in simple descent that affected the characteristics of a sample, the dispersion of the race from its mean ideal type would indefinitely increase with the number of the generations; but reversion checks this increase, and brings it to a standstill, under conditions which will now be explained.

On weighing and sorting large samples of the produce of each of the seven different classes of the peas, I found in every case the law of deviation to prevail, and in every case the value of 1° of deviation to be the same. I was certainly astonished to find the family variability of the produce of the little seeds to be equal to that of the big ones; but so it was, and I thankfully accept the fact; for if it had been otherwise, I cannot imagine, from theoretical considerations, how the typical problem could be solved.

The next great fact was that reversion followed the simplest possible law; the proportion being constant between the deviation of the mean weight of the produce generally and the deviation of the parent seed, reckoning in every case from one standard point. In a typical case, that standard must be the mean of the race, otherwise the deviation would become unsymmetrical, and cease to conform to the law.

I have adjusted an apparatus (Fig. 1) to exhibit the action of these two processes. We may consider them to act not simultaneously, but in succession, and it is purely a matter of convenience which of the two we suppose to act the first. I suppose first Reversion, then Family Variability. That is to say, I suppose the parent first to revert, and then to *tend* to breed his like. So there are three stages: (1) the population of parents, (2) that of reverted parents, (3) that of their offspring; or, what comes to the same thing, (1) the population of parents, (2) that of the *mean* produce of each parent, (3) that of their actual produce. In arranging the apparatus I have supposed the population to continue uniform in numbers. This is a matter of no theoretical concern, as the whole of this memoir relates to the distinguishing peculiarities of samples irrespectively of the absolute number of individuals in those samples. The apparatus consists of a row of vertical compartments, with trap-doors below them, to hold pellets which serve as representatives of a population of seeds. I will begin with showing how it expresses Reversion. In the upper stage of the apparatus the number of pellets in each compartment represents the relative number in a population of seeds, whose weight deviates from the average, within the limits expressed by the distances of the sides of that compartment from the middle point. The correct shape of the heap has been ensured by a slit of the proper curvature in the board that forms the back of the apparatus. As the apparatus is glazed in front, I have only to pour pellets from above until they reach the level of the slit. Such overplus as may have been poured in will run through the slit, to waste, at the back. The pellets to the right of the heap represent the heaviest seeds, those to the left the lightest. I shall shortly open the trap-door on which the few representatives of the giant seeds rest. They will run downwards through an inclined shoot, and fall into another compartment nearer the centre than before. I shall repeat the process on a second compartment in the upper stage, and successively on all the others. Every shoot converges towards one standard point in the middle vertical line; therefore the present shape of the heap of pellets is more contracted in width than it was before, and is of course more humped up in the middle. We need not regard the humping up; what we have to observe is, that each degree of deviation is simultaneously lessened. The effect is as though the curve of the first heap had been copied on a stretched sheet of indiarubber that was subsequently released. It is obvious from this that the process of reversion co-operates with the general law of deviation. The diagram that I annexed to Fig. 1, shows the principle of the process of reversion in a way that will be readily understood by many of those who are present.

I have now to exhibit the effects of variability among members of the same family. It will be recollected that the produce of peas of the same class deviated normally on either side of their own mean weight; consequently, I must cause the pellets which were in each of the upper compartments to deviate on either side of the compartment in which they now lie, which corresponds to that of the medium weight of their produce. I open the trap-door below one of the compartments in the second stage, the pellets run downwards through the harrow, dispersing as they run, and form a little heap in the lowest compartments, the centre of which heap lies vertically below the trap-door through which they fell. This is the contribution to the succeeding generation of all the individuals belonging to the compartment in the upper stage from which they came. They first reverted and then dispersed. I open another trap-door, and a similar process is gone through; a few extreme pellets in this case add themselves to the first formed heap. Again I continue the process; heap adds itself to heap, and when all the pellets have fallen through, we see that the aggregate contributions bear an exact resemblance to the heap from which we originally started. A formula (see Appendix) expresses the conditions of equilibrium. I attended to these conditions, when I cut out the slit in the backboard of the upper compartment, by which the shape of the original heap was regulated. As an example of the results that follow from the formula, I may mention that if deviation after reversion is to deviation before reversion as 4 to 5, and if 1° of family variability is six units, then the value of 1° in the population must be ten units.

It is easy to prove that the bottom heap is strictly a curve of deviation, and that its scale tends invariably to become the same as that of the upper one. It will be recollected that I showed that every variety of curve of deviation was producible by variations in the length of the harrow, and that if the pellets were intercepted at successive stages of their descent they would form a succession of curves of increasing scales of deviation. The curve in the second stage may therefore be looked upon as one of these intercepts; all that it receives in sinking to the third stage being an additional dose of dispersion.

As regards the precise scale of deviation that characterises each population, let us trace, in imagination, the history of the descendants of a single medium-sized seed. In the first generation the differences are merely those due to family variability; in the second generation the tendency to wider dispersion is somewhat restrained by the effect of reversion; in the third, the dispersion again increases, but is more largely restrained, and the same process continues in successive generations, until the step-by-step progress of dispersion has been overtaken and exactly checked by the growing antagonism of reversion. Reversion acts precisely after the law of an elastic spring, as was well shown by the illustration of the indiarubber sheet. Its tendency to recoil increases the more it is stretched, hence equilibrium must at length ensue between reversion and family variability, and therefore the scale of deviation of the lower heap must after many generations always become identical with that of the upper one.

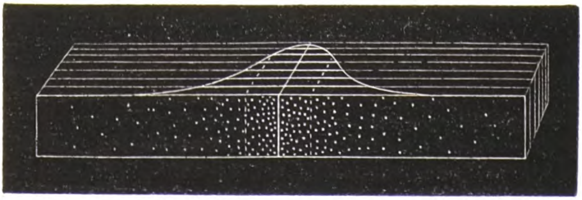
We have now surmounted the greatest difficulty of our problem; what remains will be shortly disposed of. This refers to sexual selection, productiveness, and natural selection. Let us henceforth suppose the heights and every other characteristic of all members of a population to be reduced to a uniform adult male standard so that we may treat it as a single group. Suppose, for example, a female whose height was equal to the average female height + 3° of female deviation, the equivalent in terms of male stature is the average male height + 3° of male deviation. Hence the female in question must be registered not in the feet and inches of her actual height, but in those of the equivalent male stature.

On this supposition we may take the numerical mean of the stature of each couple as the equivalent of a single hermaphrodite parent, so that a male parent plant having 1° deviation, and of a female parent plant having 2° of deviation, would together rank as a single self-fertilised plant of + 1½°.

In order that the law of sexual selection should co-operate with the conditions of a typical population, it is necessary that selection should be *nil;* that is, that there should not be the least tendency for tall men to marry tall women rather than short ones. Each strictly typical quality taken by itself must go for nothing in sexual selection. Under these circumstances, one of the best known properties of the law of deviation (technically called that of "two fallible measures") shows that the population of sums of couples would conform truly to the law, and the value of 1° would be that of the original population multiplied by $\sqrt{2}$. Consequently the population of *means of couples* would equally conform to the law; but in this case, as the deviations of means of couples are half those of sums of couples, the 1° of original deviation would have to be divided by $\sqrt{2}$.

The two remaining processes are Productiveness and Survival. Physiologically they are alike, and it is reasonable to expect the same general law to govern both. Natural selection is measured by the percentage of survival among individuals born with like characteristics. Productiveness is measured by the average number of children from all parents who have like characteristics, but it may physiologically be looked upon as the percentage of survival of a vast and unknown number of possible embryos, producible by such parents. The number being unknown creates no difficulty, if there may be considered to be, on an average, the same in every class. Experiment could tell me little about either natural selection or productiveness. What I have to say is based on plain theory. I can explain this best by the process of natural selection. In each species, the height, &c., the most favoured by natural selection, is the one in which the demerits of excess or deficiency are the most frequently balanced. It is therefore not unreasonable to look at nature as a marksman, her aim being subject to the same law of deviation as that which causes the shot on a target to be dispersed on either side of the point aimed at. It would not be difficult, but it would be tedious, to justify the analogy; however, it is unnecessary to do so, as I propose to base the analogy on the exigencies of the typical formula, no other supposition being capable of fulfilling its requirements. Suppose for a

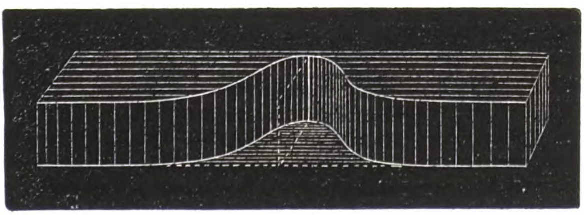
FIG. 7.



moment that nature aims, as a marksman, at the medium class, on purpose to destroy and not to save it. Let a block of stone, as is Fig. 7, represent a rampart, and let a gun be directed at a vertical line on its side on purpose to breach it, the shots would fall with the greatest frequency in the neighbourhood of the vertical line, and their marks would diminish in frequency as the distance increased, in conformity with the law of deviation. Each shot would batter away a bit of stone, and the shape of the breach would be such that its horizontal outline will be the well-known curve. This would be the action of nature were she to aim at the destruction of medium sizes. Her action as preserver of them is the exact converse, and would be represented by a cast that filled the gap and exactly replaced the material that had been battered away. The percentage of thickness of wall that had been destroyed at each degree of deviation is represented by the ordinate of the curve, therefore the percentage of survival is also an ordinate of the same curve of deviation. Its scale has a special value in each instance, subject to the general condition in every typical case, that its 0° shall correspond to the 0° of deviation of height, or whatever the characteristic may be.

In Fig. 8, the thickness of wall that has been destroyed at each

FIG. 8.



degree of deviation is represented by the corresponding ordinate of the horizontal outline of the portion which remains. Similarly, in the case of an imaginary population, in which each class was *equally* numerous, the amount of survivors at each degree of deviation will be represented by the corresponding ordinate of this or a similar curve.

But in the original population at which we are supposing nature to aim, the representatives of each class are not equally numerous, but are arranged according to the law of deviation; the middle class being most numerous, while the extreme classes are but scantily represented. The ordinate of the above-mentioned outline will in this case represent, not the *absolute number*, but the *percentage* of survivors at each degree of deviation.

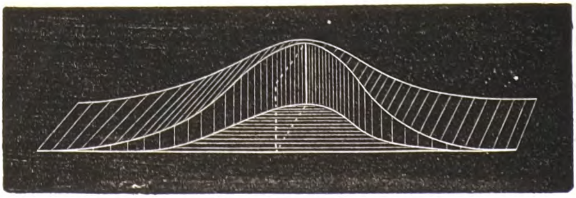
If a graphic representation is desired, that shall give the absolute number of survivors at each degree, we must shape the rampart which forms nature's target so as to be highest in the middle and to slope away at each side according to the law of deviation. Thus Fig. 9 represents the curved rampart before the battered part has been removed; Fig. 10, afterwards.

I have taken a block of wood similar to Fig. 7, to represent the rampart; it is of equal height throughout. A cut has been made at right angles to its base with a fret-saw, to divide it into two portions —that which would remain after it had been breached, Fig. 8, and the

FIG. 9.

cast of the breach. Then a second cut with the fret-saw has been made at right angles to its face, to cut out of the rampart an equivalent to the heap of pellets that represents the original population. The gap that would be made in the heap and the cast that would fill the gap are curved on two faces, as in the model. This is sufficiently represented in Fig. 10.

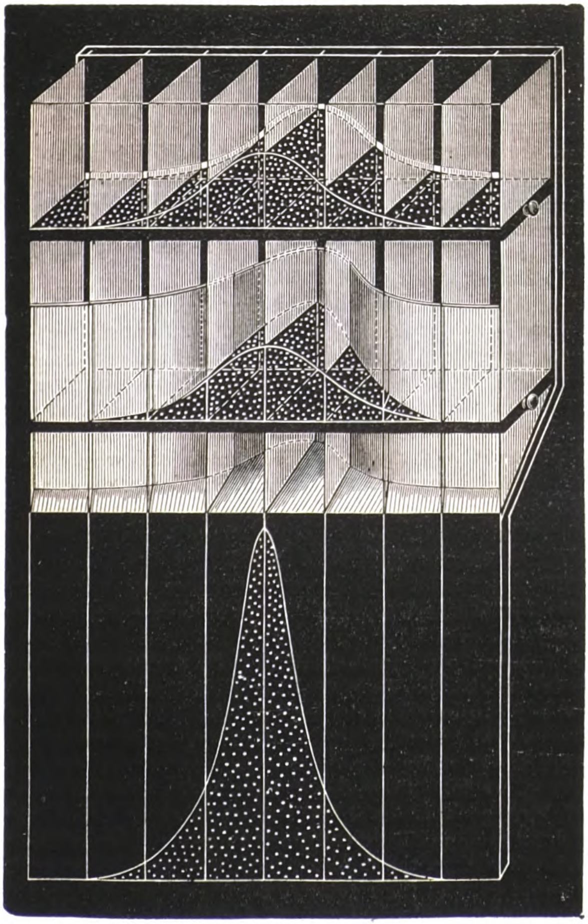
FIG. 10.



The operation of natural selection on a population already arranged according to the law of deviation is represented more completely in an apparatus, Fig. 11, which I will set to work immediately.

It is faced with a sheet of glass. The heap, as shown in the upper compartment of the apparatus, is 3 inches in thickness, and the pellets rest on slides. Directly below the slides, and running from side to side of the apparatus, is a curved partition, which will separate the pellets as they fall upon it, into two portions, one that runs to waste at the back, and another that falls to the front, and forms a new heap. The curve of the partition is a curve of deviation. The shape of this heap is identical with the cast of the gap in Fig. 10. It is highest and thickest in the middle, and it fines away towards either extremity. When the slide upon which it rests is removed, the pellets run down an inclined plane that directs them into a frame of uniform and shallow depth. The pellets from the deep central compartments (it has been impossible to represent in the diagram as many of these as there were in the apparatus) will stand very high from the bottom of the shallow frame, while those that came from the distant compartments will stand even lower than they did before. It follows that the selected pellets form, in the lower compartment, a heap of which the

Fig. 11.



scale of deviation is much more contracted than that of the heap from which it was derived. It is perfectly normal in shape, owing to an interesting theoretical property of the law of deviation (see formula at end of this memoir).

Productiveness follows the same general law as survival, being a percentage of possible production, though it is usual to look on it as a simple multiple, without first multiplying and then dividing by the 100. Looking upon it as a simple multiple, the front face of each compartment in the upper heap represents the number of the parents of the same class, and the depth of the partition below compartment represents the average number that each individual of that class produces.

To sum up. We now see clearly the way in which the resemblance of a population is maintained. In the purely typical case, all the processes of heredity and selection are subject to well-defined and simple laws, which I have formulated in the appendix. Family variability, productiveness, and survival are all subject to the law of deviation, and reversion is expressed by a simple fractional coefficient. It follows that when we know in respect to any characteristic, the values of 1° in the several curves of family variability, productiveness and survival, and when we know the coefficient of reversion, we know absolutely all about the ways in which the characteristic in question will be distributed among the population at large.

I have confined myself in this explanation to purely typical cases, but it is easy to understand how the actions of the processes would be modified in those that were not typical. Reversion might not be directed towards the mean of the race; neither productiveness nor survival might be greatest in the medium classes, and none of their laws may be strictly of the typical character. However, in all cases the general principles would be the same, and the same actions that restrain variability are capable of restraining the departure of average values beyond certain limits in cases where any of the above-mentioned processes are unsymmetrical in their actions. The typical laws are those which most nearly express what takes place in nature generally; they may never be exactly correct in any one case, but at the same time they will always be approximately true and always serviceable for explanation. We estimate through their means the effects of the laws of sexual selection, of productiveness, and of survival, in aiding that of reversion in bridling the dispersive effect of family variability. They show us that natural selection does not act by carving out each new generation according to a definite pattern on a Procrustean bed, irrespective of waste. They also explain how small a contribution is made to future generations by those who deviate widely from the mean, either in excess or deficiency, and they enable us to discover the precise sources whence the deficiencies in the produce of exceptional types are supplied, and their relative contributions. We see by them that the ordinary genealogical course of a race consists in a constant outgrowth from its centre, a constant dying away at its margins, and a tendency of the scanty remnants of all exceptional stock to revert to that mediocrity, whence the majority of their ancestors originally sprang.

APPENDIX.

I will now proceed to formulate the typical laws. In what has been said, 1° of deviation has been taken equal to the "probable error" = $C \times 0 \cdot 4769$ in the well-known formula

$$y = \frac{1}{c\sqrt{\pi}} \cdot e^{-\frac{x^2}{c^2}}.$$

According to this, if x = amount of deviation in feet, inches, or any other external unit of measurement, then the number of individuals in any sample who deviate between x and $x + \delta x$ will vary as $e^{-\frac{x^2}{c^2}} \delta x$ (it will be borne in mind that we are for the most part not concerned with the coefficient in the above formula).

Let the modulus of deviation (c) in the original population, after the process has been gone through, of converting the measurements of all its members (in respect to the characteristic in question) to the adult male standard, be written c_0.

1. Sexual selection has been taken as *nil*, therefore the population of "parentages" is a population of which each unit consists of the mean of a couple taken indiscriminately. This, as well known, will conform to the law of deviation, and its modulus, which we will write c_1, has already been shown to be equal to $\frac{1}{\sqrt{2}} \cdot c_0$.

2. Reversion is expressed by a simple fractional coefficient of the deviation, which we will write r. In the "reverted" parentages (a phrase whose meaning and purport have already been explained),

$$y = \frac{1}{rc\sqrt{\pi}} \cdot e^{-\frac{x^2}{r^2c^2}}.$$

In short, the population of which each unit is a reverted parentage follows the law of deviation, and has its modulus, which we will write c_2, equal to $r c_1$.

3. Productiveness. We saw that it followed the law of deviation; let its modulus be written f. Then the number of children to each parentage that differs by the amount of x from the mean of the parentages generally (i.e. from the mean of the race) will vary as $e^{-\frac{x^2}{f^2}}$; but the number of such parentages varies as $e^{-\frac{x^2}{c_2^2}}$, therefore if each child absolutely resembled his parent, the number of children who deviated x would vary as $e^{-\frac{x^2}{f^2}} \times e^{-\frac{x^2}{c_2^2}}$, or as $e^{-x^2\left\{\frac{1}{f^2}+\frac{1}{c_2^2}\right\}}$. Hence the deviations of such children in their amount and frequency would conform to the law, and the modulus of the population of

children in the supposed case of absolute resemblance to their parents, which we will write c_3, is such that

$$\frac{1}{c_3} = \sqrt{\left(\frac{1}{f^2} + \frac{1}{c^2}\right)}.$$

We may, however, consider the parents to be multiplied, and the productivity of each of them to be uniform; it is more convenient than the converse supposition, and it comes to the same thing. So we will suppose the reverted parentages to be more numerous but equally prolific, in which case their modulus will be c_3, as above.

4. Family variability was shown by experiment to follow the law of deviation, its modulus, which we will write v, being the same for all classes. Therefore the amount of deviation of any one of the offspring from the mean of his race is due to the combination of two influences—the deviation of his "reverted" parentage and his own family variability; both of which follow the law of deviation. This is obviously an instance of the well-known law of the "sum of two fallible measures." * Therefore the modulus of the population in the present stage, which we will write c_4, is equal to $\sqrt{(v^2 + c_3^2)}$.

5. Natural selection follows, as has been explained, the same general law as productiveness. Let its modulus be written s, then the percentage of survivals among children, who deviate x from the mean, varies as $e^{-\frac{x^2}{s^2}}$; and for the same reasons as those already given, its effect will be to leave the population still in conformity with the law of deviation, but with an altered modulus, which we will write c_5, and

$$\frac{1}{c^5} = \sqrt{\left(\frac{1}{s^2} + \frac{1}{c_4^2}\right)}.$$

Putting these together, we have, starting with the original population having a modulus $= c_0$,

$$1.\quad c_1 = \frac{1}{\sqrt{2}} c_0.$$

$$2.\quad c_2 = r c_1.$$

$$3.\quad c_3 = \sqrt{\left\{\frac{f^2 c_2^2}{f^2 + c_2^2}\right\}}.$$

$$4.\quad c_4 = \sqrt{\{v^2 + c_3^2\}}.$$

$$5.\quad c_5 = \sqrt{\left\{\frac{s^2 c_4^2}{s^2 + c_4^2}\right\}}.$$

And lastly, as the condition of maintenance of statistical resemblance in consecutive generations,

$$6.\quad c_5 = c_0.$$

* Airy, 'Theory of Errors,' § 43.

Hence, given the coefficient r and the moduli v, f, s, the value of c_0 (or c_5) can be easily calculated.

In the case of simple descent, which was the one first considered, we have nothing to do with c_0, but begin from c_1. Again, as both fertility and natural selection are in this case uniform, the values of f and s are infinite. Consequently our equations are reduced to

$$c_2 = r\,c_1\,; \quad c_4 = \sqrt{\{v^2 + c_2^2\}}\,; \quad c_4 = c_1,$$

whence

$$c_1^2 = \frac{v^2}{1 - r^2}.$$

Suppose, for example, that $r = \frac{4}{5}$ and $v = 6$, then

$$c_1^2 = \frac{36}{1 - \frac{16}{25}} = \frac{36 \times 25}{9} = 100,$$

or

$$c_1 = 10,$$

as was mentioned in the course of the foregoing remarks.

[F. G.]