Some observations on asymmetrical correlated responses to selection

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Artificial selection applied to one character almost always leads to changes in others. The theory of such 'correlated responses' is well-known and has recently been reviewed by Falconer (1960a). In this, the genetic correlation between the two characters plays an important part and determines the predicted pattern of the correlated responses found in different experiments, e.g., the response in character 2 on selection for character 1 compared to that in 1 on selection for character 2 or the comparison of the responses in 2 on selection for 1 in opposite directions. Any discordance of the pattern of correlated responses from expectation will be termed an 'asymmetrical correlated response'. The same measurement made under two different environments will be considered as two separate 'characters'.

Falconer (1960b) selected mice for growth rate on high and low planes of nutrition and observed the correlated responses on the alternate nutritional level. The realized genetic correlations were equal for the first four generations of selection (0·67, 0·65) but were markedly different for generations 5 to 13 (1·25, −0·02). The asymmetry was attributed to changes in the basic parameters due to the selection applied, and large changes in the phenotypic standard deviations were observed. Asymmetry of the realized genetic correlations was also observed by Bell & McNary (1963) who selected *Tribolium castaneum* for increased pupal weight in both a wet and a dry environment, and by Yamada & Bell (1963) where selection was for increased and decreased 13-day larval weight in *Tribolium castaneum* under good and poor nutritional levels.

Similar results have been observed in poultry by Siegel (1962) and Nordskog & Festing (1962). The former selected for four generations for body weight and breast angle, and found a realized genetic correlation of about 0·55 when selection was for body weight and a value of about 0·45 when selection was for breast angle. The latter workers selected in both high and low directions for body weight and egg weight, and observed asymmetry of the realized genetic correlations between body and egg weights when either the direction of selection or the trait being selected was considered. In both of these papers, the asymmetry was attributed to differing genetic variances or heritabilities for the two traits.

Clayton, Knight, Morris & Robertson (1957) observed asymmetry in response of sternopleural bristle number in *Drosophila melanogaster* to selection for increased and decreased sternital bristle number. The results were somewhat erratic, which led the authors to conclude that gene drift may play an important part in the correlated response when the genetic correlation is low. In general, however, there was a positive correlated response when selection was for increased sternital bristle number and no correlated response when selection was for low sternital bristle number.

On the other hand, some selection experiments show a close fit of expected to observed correlated responses. For example, Reeve & Robertson (1953) selected for wing and thorax lengths in *Drosophila melanogaster* and found good agreement between estimates of the genetic correlation between the two characters in the base population and the realized genetic correlations in the populations selected for each trait separately.

The frequency with which asymmetrical correlated responses have been found suggests that some mechanism other than genetic sampling is affecting the correlated response in these populations. The purpose of this study was to re-examine the theory of correlated response and, if possible, to establish the conditions in which asymmetry of correlated response to selection was to be expected.

THE MODEL

It has been shown by Falconer (1960*a*) that the correlated response in trait 2 from selection for trait 1 would be,

$$\mathrm{CR}_{2 \cdot 1} = \bar{i}_1 h_1 h_2 r_G \sigma_2 \tag{1}$$

where $\bar{i}_1$ is the selection intensity for trait 1 in standard units, h_1 and h_2 are the square roots of the heritabilities for traits 1 and 2 respectively, r_G is the genetic correlation between the two traits, and σ_2 is the phenotypic standard deviation in trait 2. Dividing both sides by $\bar{i}_1 \sigma_2$ results in a standardized correlated response ($\mathrm{CR}'_{2 \cdot 1}$) or the correlated response in standard deviations in trait 2 for each standard deviation of selection in trait 1. Thus,

$$\frac{\mathrm{CR}_{2 \cdot 1}}{\bar{i}_1 \sigma_2} = \mathrm{CR}'_{2 \cdot 1} = h_1 h_2 r_G. \tag{2}$$

In a similar manner, $\mathrm{CR}_{1 \cdot 2} / \bar{i}_2 \sigma_1 = \mathrm{CR}'_{1 \cdot 2}$ can be obtained, and it is seen that

$$\mathrm{CR}'_{2 \cdot 1} = \mathrm{CR}'_{1 \cdot 2} = h_1 h_2 r_G = \operatorname{cov} G / \sigma_1 \sigma_2. \tag{3}$$

The standardized correlated response should be the same in the first generation whether selection is on trait 1 or on trait 2 or whether the selection is upwards or downwards.

When the correlated response is measured over several generations, selection may change the value of the parameters themselves in such a way that the standardized responses, as measured in the two different populations, are asymmetrical and different from those predicted on the basis of the original parameters. This

follows the suggestion of Falconer (1960b) that the asymmetrical responses he observed were the consequence of changes in parameters due to selection. Large changes in the phenotypic standard deviations were observed, and the potential effect of these changes on the standardized correlated response is evident from equation (3).

The three parameters of interest in (3) are the genetic covariance and the phenotypic standard deviations, and consideration is centered on how these parameters can change during selection for each trait involved.

The genetic covariance between two traits, as calculated in any population by the usual analysis of covariance technique, can be caused either by linkage disequilibrium of genes affecting the two traits independently or by the pleiotropic effects of single genes. In the case of linkage, the population would tend toward equilibrium at variable rates depending upon the cross-over distance between the genes. The effect of linkage on the correlated response would be similar to that of pleiotropic genes, except that, as crossing-over occurred and the population approached equilibrium, the effect of linked genes on the asymmetry of correlated response over a number of generations would be less than that of pleiotropic genes. Therefore only pleiotropic genes are considered as the most extreme and constant case.

A genetic model for correlated responses was then constructed, and the expected values of the parameters and the correlated responses obtained from a Sirius computer for each of nine generations of selection. In the first series of selections, only additive gene effects were considered since these would appear to be least likely to yield asymmetrical correlated responses. Four types of loci are considered in the model, with the following effects of a gene substitution on the two traits:

	(A)	(B)	(C)	(D)
Trait 1	α	β_1	γ_1	0
Trait 2	0	β_2	$-\gamma_2$	δ

Loci A and D affect the two traits independently. Loci B and C affect both traits, the former making a positive and the latter a negative contribution to the covariance. The substitution effects shown refer to one-half the difference between the alternative homozygotes. Only one locus of each type with additive effects is assumed. The existence of more than one locus having the same type of correlated effects would not affect the occurrence of asymmetry, but only the rate and pattern of its development, as we shall see later. It is assumed that the frequencies of the genes at each locus are q_A, q_B, q_C and q_D respectively, the first three referring to the allele with positive effect on trait 1. For this model it is seen that

$$\operatorname{cov} G = 2q_B(1-q_B)\beta_1\beta_2 - 2q_C(1-q_C)\gamma_1\gamma_2,$$
$$V_1 = 2q_A(1-q_A)\alpha^2 + 2q_B(1-q_B)\beta_1^2 + 2q_C(1-q_C)\gamma_1^2 + V_{E1},$$
$$V_2 = 2q_B(1-q_B)\beta_2^2 + 2q_C(1-q_C)\gamma_2^2 + 2q_D(1-q_D)\delta^2 + V_{E2},$$

where V_{E1} and V_{E2} are the environmental variances of the two traits.

The computer was programmed to obtain the expected gene frequency at each locus for each generation. For example, the change in gene frequency at the A locus due to selection for trait 1 is $(\bar{i}_1\alpha/\sigma_1)q_A(1-q_A)$, $\bar{i}_1\alpha/\sigma_1$ being the selective advantage of the gene at the locus (Griffing, 1960). The new gene frequencies were used to calculate the genetic covariance, the genetic and phenotypic variances, the mean of each trait and the standardized correlated response for each generation when selection was on either trait 1 or trait 2. In all models $\bar{i}_1 = \bar{i}_2 = 1 \cdot 0$, corresponding to a retention of 40% of the individuals as parents, except for models (ii) and (iv), in which $\bar{i}_1 = \bar{i}_2 = 0 \cdot 5$, corresponding to 70% retention. In all runs the environmental variance was arbitrarily set equal to the genetic variance when all gene frequencies were one-half. The initial heritabilities of traits 1 and 2 were then close to one-half in all models.

Because the above formula for the change in gene frequency was used for selection on the two characters, the correlated response is always symmetrical in the first generation. This formula does not in fact hold for genes with large effects and such genes could well produce asymmetry in the very first generation of selection. This appears to be most important under conditions when the gene selected for is at frequencies greater than $0 \cdot 8$ and when $\bar{i}\alpha/\sigma_1$ or equivalent expressions are greater than unity.

The asymmetry of the genetic covariances generated by the first generation of selection may be expressed algebraically as the difference between the genetic covariances after one generation of selection on trait 1 and trait 2 respectively. At the B locus, for instance, the genetic covariance is $2\beta_1\beta_2 q_B(1-q_B)$. If the gene frequency is increased by $\varDelta q_B$, then the covariance is increased by

$$2\beta_1\beta_2[(1-2q_B)\varDelta q_B - (\varDelta q_B)^2].$$

Inserting the expressions for the change in gene frequency on selection for the two characters into this, and including the C locus, we obtain for the difference in covariance,

$$\text{cov}\,G_1 - \text{cov}\,G_2 =$$
$$2\beta_1\beta_2 q_B(1-q_B)\left[(1-2q_B)\left(\frac{\bar{i}_1\beta_1}{\sigma_1} - \frac{\bar{i}_2\beta_2}{\sigma_2}\right) - q_B(1-q_B)\left(\frac{\bar{i}_1^2\beta_1^2}{V_1} - \frac{\bar{i}_2^2\beta_2^2}{V_2}\right)\right]$$
$$- 2\gamma_1\gamma_2 q_C(1-q_C)\left[(1-2q_C)\left(\frac{\bar{i}_1\gamma_1}{\sigma_1} + \frac{\bar{i}_2\gamma_2}{\sigma_2}\right) - q_C(1-q_C)\left(\frac{\bar{i}_1^2\gamma_1^2}{V_1} - \frac{\bar{i}_2^2\gamma_2^2}{V_2}\right)\right] \qquad (4)$$

This equation is generalized to n loci affecting the two traits as

$$\text{cov}\,G_1 - \text{cov}\,G_2 =$$
$$2\sum_{k=1}^{n}\lambda_k\mu_k q_k(1-q_k)\left[(1-2q_k)\left(\frac{\bar{i}_1\lambda_k}{\sigma_1} - \frac{\bar{i}_2\mu_k}{\sigma_2}\right) - q_k(1-q_k)\left(\frac{\bar{i}_1^2\lambda_k^2}{V_1} - \frac{\bar{i}_2^2\mu_k^2}{V_2}\right)\right] \qquad (5)$$

where q_k is the frequency of one allele at the kth locus and λ_k and μ_k are one-half the homozygote differences in traits 1 and 2 respectively, and can have either positive or negative values.

Expressions for the change in V_1 and V_2 on selection for the two characters can be obtained by substituting λ_k^2 and μ_k^2, respectively, for $\lambda_k \mu_k$ outside the square brackets in (5). It then follows that a symmetrical change in the covariance will also mean symmetry in the contributions of the B and C loci to the variance of the two characters.

Equation (4) consists of four terms in two pairs. Inside the square brackets two terms have linear gene effects in them and will both be zero when the gene frequency is 0·5. At usual selection intensities, and from what is known of gene effects, it is unlikely that expressions like $\bar{i}_1 \beta_1 / \sigma_1$ will be greater than 0·5. The second pair of terms contain such expressions squared and will therefore be smaller than the first pair. The gene frequency component in these will be at a maximum when the gene frequency is 0·5.

Of the components containing gene effects, it will be seen that three contain differences and only one contains a sum. From this, it is established that the simplest condition for asymmetry is the presence of C-type loci making a negative contribution to the genetic covariance, with frequencies other than 0·5. From the entire gene frequency expression entering into this term, $q(1-q)(1-2q)$, the greatest absolute contribution to the asymmetry in the covariance will occur at frequencies of 0·2 or 0·8.

It is hardly surprising that the effects of A- and D-type loci do not appear directly in (4). They are of course involved in σ_1 and σ_2. It then follows that changes in the frequency of alleles at these loci are not of great importance and are exactly equivalent to changes in the environmental variance of either of the characters or to changes in the gene effects of these loci. This was confirmed by the computer results.

The other three terms in (4) contain differences in gene effects. They are more accurately differences in the selective advantage of the genes under the two kinds of selection. The two containing square terms in gene effects will have maximum effects at gene frequencies around 0·5, while the other will have a maximum at 0·2 or 0·8. But, if gene effects are small, the term containing $(1-2q_B)$ will be dominating in the early generations.

Equation (4) gives the expected change in one generation. In t generations, the two linear terms will be multiplied approximately by t, but the squared terms approximately by t^2. In situations in which changes in the covariance in the first generation are entirely due to squared terms, the asymmetry in the covariance will then increase as the square of the number of generations. An example will be given among the computer results.

The computer results

The computer results shown in Tables 1 and 2 give the standardized direct and correlated responses accumulated over nine generations of selection of the same intensity for the two traits. Various combinations of gene effects and initial frequencies have been chosen to exemplify the conclusions drawn from (4). The essential features of the gene effects chosen in the different models are given below.

E Table 1. *Standardized direct responses* (R) *and standardized correlated responses* (CR) *after nine generations of selection on trait 1* (T1) *and trait 2* (T2), *with* $h_1^2 \sim h_2^2$

Gene effects: T1 a, β_1, γ_1; T2 $\beta_2, \gamma_2, \delta$

Initial gene frequencies q_A, q_B, q_C, q_D		(i) 1,1,1 / 1,1,1		(ii) 0,1,1 / 1,1,0		(iii) 1,1,1 / 1,1,2		(iv) 0,1,0 / 1,0,1		(v) 1,2,1 / 2,1,1		(vi) 1,1,2 / 1,2,1		(vii) 1,2,1 / 1,2,1	
		T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2
(a) 0·5, 0·5, 0·5, 0·5	R	1·87	1·87	2·99	2·99	1·87	1·79	2·17	2·99	1·79	1·79	1·79	1·79	1·79	1·79
	CR	0·00	0·00	0·00	0·00	0·00	0·00	1·47	2·11	−0·61	−0·61	−0·39	−0·39	−0·46	0·46
(b) 0·5, 0·2, 0·5, 0·5	R	2·28	2·28	3·61	3·61	2·28	2·10	3·37	3·61	2·29	2·29	2·10	2·10	2·29	2·10
	CR	0·39	0·39	0·72	0·72	0·26	0·36	2·30	2·93	0·93	0·93	−0·11	−0·11	−0·19	0·94
(c) 0·5, 0·5, 0·2, 0·5	R	2·28	1·55	3·61	2·23	2·28	1·54	2·17	2·99	2·10	1·54	2·29	1·35	2·10	1·35
	CR	−0·39	0·38	−0·71	0·97	−0·26	0·38	1·46	2·11	0·11	0·69	−0·93	0·13	−0·94	0·72
(d) 0·5, 0·5, 0·5, 0·2	R	1·87	2·28	2·99	2·99	1·87	2·29	2·17	3·61	1·79	2·10	1·79	2·10	1·79	2·10
	CR	0·00	0·00	0·00	0·00	0·00	0·00	1·54	2·09	0·40	0·39	−0·40	−0·39	−0·47	0·46
(e) 0·5, 0·2, 0·2, 0·5	R	2·64	1·97	4·04	2·97	2·64	1·86	3·37	3·61	2·56	2·06	2·56	1·66	2·56	1·66
	CR	0·00	0·77	0·00	1·72	0·00	0·74	2·30	2·93	0·66	1·22	−0·66	0·41	−0·67	1·21
(f) 0·5, 0·8, 0·3, 0·5	R	1·81	1·31	2·77	1·65	1·81	1·26	0·95	2·23	1·55	1·16	1·87	1·23	1·55	1·23
	CR	−0·64	−0·13	−1·54	−0·33	−0·43	−0·13	0·61	0·95	−0·32	0·07	−1·04	−0·35	−1·06	0·11
(g) 0·5, 0·3, 0·8, 0·5	R	1·81	2·51	2·77	3·95	1·81	2·28	2·98	3·45	1·87	2·40	1·55	2·46	1·87	2·46
	CR	0·64	−0·13	1·54	−0·15	0·43	−0·11	2·03	2·75	1·04	0·47	0·32	−0·74	0·27	0·53

The comparison of standard deviations have been calculated for all gene frequencies
at 0·5.

(i), (ii), (iii) The B and C locus effects are the same:
$\sigma_1 = \sigma_2$ for (i) and (ii) but $\sigma_1 < \sigma_2$ for (iii).
(iv) No variation at the C locus, $\beta_1 = \beta_2$ but $\sigma_1 < \sigma_2$.
(v) B locus effects twice those at C, and $\sigma_1 = \sigma_2$.
(vi) B locus effects one-half those at C, and $\sigma_1 = \sigma_2$.
(vii) The B locus has the greater effect on trait 1 but the C locus on trait 2, and
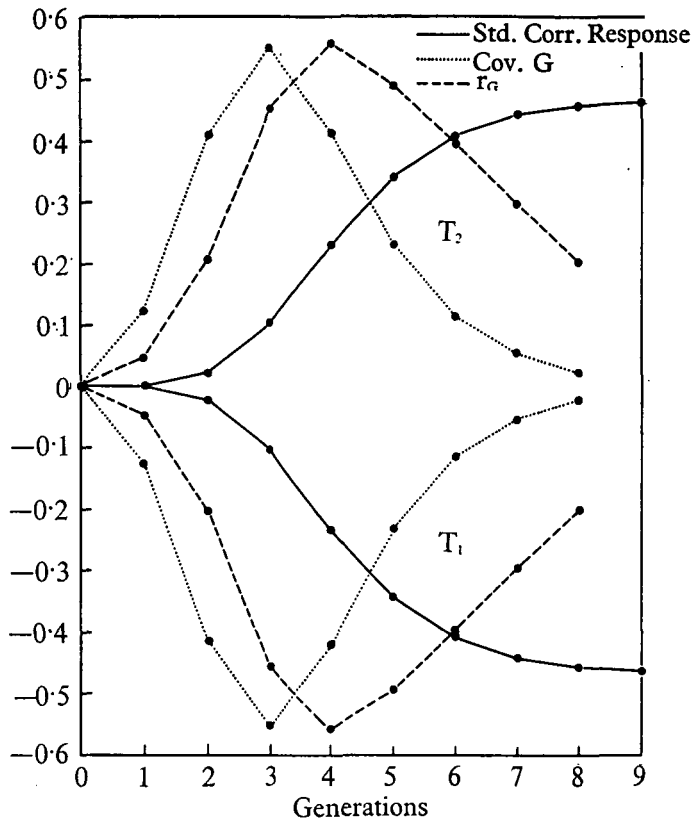$\sigma_1 = \sigma_2$.

Fig. 1. Standardized correlated responses, genetic covariances (cov G) and genetic
correlations (r_G) for selection on trait 1 (T1) or trait 2 (T2). Model (vii) (a). All
gene frequencies 0·5. Selection for trait 1 rapidly fixes a locus making a positive
contribution to cov G, that for trait 2 fixes one making a negative contribution.

In all models, the environmental variance for both characters was set equal to
the genetic variance when all gene frequencies were 0·5.

The main points of interest in the correlated responses are as follows, classified
according to the gene frequency combinations:

(a) All gene frequencies equal to 0·5. Only the squared terms in (4) can then
contribute to the change in covariance. There is symmetry for all effect models

except (iv) $(\beta_1/\sigma_1 \neq \beta_2/\sigma_2)$ and (vii). In the latter, the selection for trait 1 causes most change in gene frequency away from 0·5 in a B locus and therefore reduces the genetic covariance. But selection for trait 2 changes most the frequency at a C locus and therefore increases the covariance. The asymmetry in the covariance increases as t^2 in the early generations (Fig. 1). In (iii) the two squared terms are not zero but cancel out.

(b) $q_B \neq 0·5$. There is now slight asymmetry in (iii), arising from the linear term since, though $\beta_1 = \beta_2$, $\sigma_1 \neq \sigma_2$.
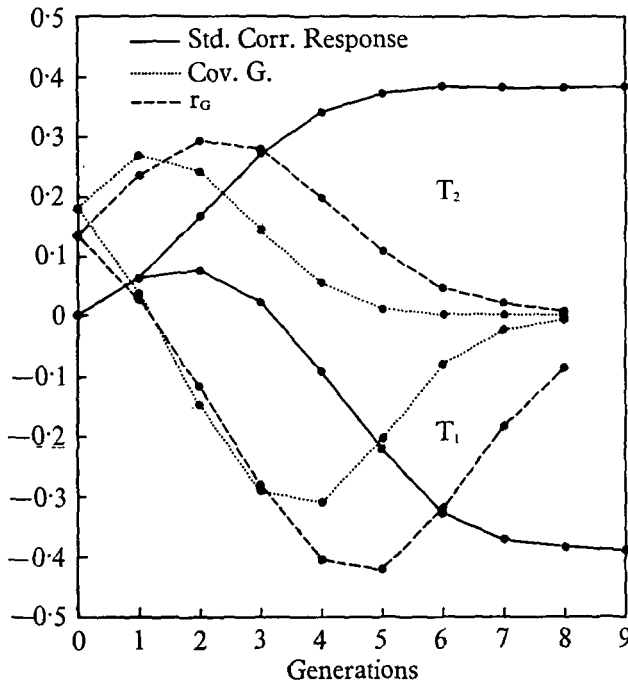

Fig. 2. See caption to Fig. 1. Model (i) (c). All gene effects equal. All frequencies 0·5 except that at a locus making a negative contribution to cov G. Perhaps the most frequent cause of asymmetry in practice?

(c) $q_C \neq 0·5$. This is the situation to which attention was drawn earlier of a C locus with a frequency away from 0·5, which will lead to an asymmetry of covariance increasing linearly with time in all situations. The actual response when all gene effects are equal is shown in Fig. 2.

(d) $q_D \neq 0·5$. In addition to models (iv) and (vii) a trivial asymmetry in correlated response is now found in models (v) and (vi) because asymmetry has developed in σ_2.

(e) $q_B = q_C \neq 0·5$. Asymmetry in all models. Note that in (i), (ii) and (iii) there is no correlated response on selection for trait 1 though there is on selection for trait 2 (Fig. 3).

(f) and (g) Deviations from 0·5 in opposite directions in B and C loci. Asymmetry in all models.

The critical point is simply that asymmetry of the correlated responses occurs whenever the *relative rate* of response of the B and C loci is different when selection is for trait 1, than it is when selection is for trait 2. The combination of factors which can account for differing relative rates of change at these two types of loci when selection is for different traits are shown in equation (4). This equation is very powerful in the analysis of these correlated responses, and remarkably so considering that it is strictly valid for only a single generation of selection. The occurrence of symmetry was predictable from equation (4) in all models.
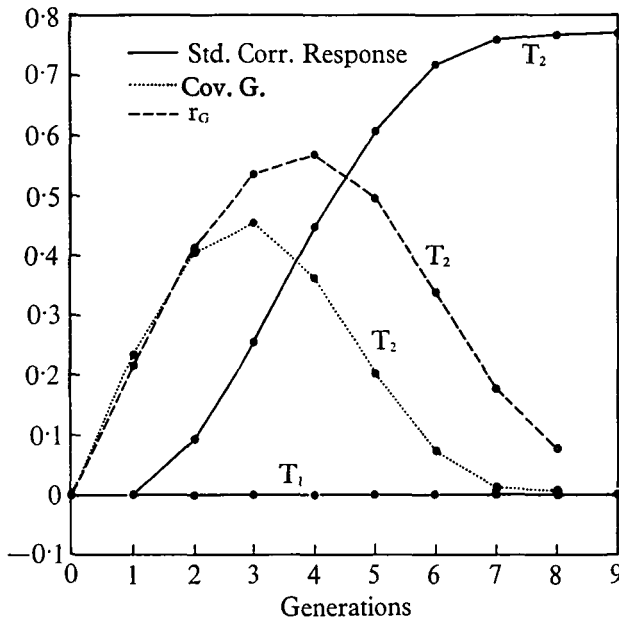

Fig. 3. See caption to Fig. 1. Model (i) (e). All gene effects equal. All frequencies 0.5 except at two loci, one with a positive and one with a negative contribution to cov G. Note the absence of any correlated response on selection for trait 1.

The table shows that quite remarkable degrees of asymmetry can be found in some of the models and differences in sign in the realized genetic correlation are frequently found, particularly in gene effect model (vii). Even with all gene frequencies at 0.5, the realized genetic correlation is about 0.25 for selection on trait 2 and -0.25 for trait 1.

Several computer runs were done with different heritabilities for the two characters ($h_1^2 \sim 2h_2^2$) and the results are given in Table 2. Gene effect model (i) still shows symmetry with all frequencies at 0.5. When the heritabilities were equal all four terms in (4) were zero, but now the linear terms are zero and the two square terms are equal but of opposite sign. But, with gene effect model (v), the change in heritability leads to asymmetry because the square terms in (4) are no longer zero. When both B and C loci have gene frequencies of 0.2 the change in heritability alters the existing asymmetry only a little.

In addition, one model with non-additive gene effects was studied. The model

assumed complete dominance, equal gene effects at all loci and all gene frequencies at 0·25. This frequency was chosen because the absolute change in the mean in the first generation of selection would be the same whether the selection is up or down. This condition would be the most likely to yield symmetry. Even so, asymmetry after nine generations was 0·21 standard deviations. Symmetry in the case of non-additive genetic effects could occur only if no negatively correlated loci were involved and the selective advantages of the positively correlated loci in the two traits were equal.

Table 2. *Standardized direct responses* (R) *and standardized correlated responses* (CR) *after nine generations of selection on trait* 1 (T1) *and trait* 2 (T2), *with* $h_1^2 \sim 2h_2^2$

		Gene effects	T1 $\alpha, \beta_1, \gamma_1$			
			T2 $\beta_2, \gamma_2, \delta$			
			(i) 1, 1, 1 1, 1, 1		(v) 1, 2, 1 2, 1, 1	
Initial gene frequencies q_A, q_B, q_C, q_D			T1	T2	T1	T2
(a) 0·5, 0·5, 0·5, 0·5	R		1·87	1·25	1·79	1·15
	CR		0·00	0·00	0·29	0·44
(e) 0·5, 0·2, 0·2, 0·5	R		2·64	1·24	2·56	1·35
	CR		0·00	0·69	0·47	1·23

Selection in opposite directions for the same trait

A similar method of analysis can be used to explain asymmetry of response in trait 2 when both up and down selection is practised for trait 1, and vice versa. With symmetry, the correlated responses in trait 2 should be of the same magnitude but of opposite sign, and asymmetry will be observed after the first generation only if there are parameter changes. From one generation of selection for trait 1, the difference between the genetic covariances after up selection $(\text{cov}\,G_U)$ and down selection $(\text{cov}\,G_D)$ turns out to be

$$\text{cov}\,G_U - \text{cov}\,G_D = \frac{2}{\sigma_1} \sum_{k=1}^{n} \lambda_k^2 \mu_k q_k (1-q_k) \left[(1-2q_k)(\bar{i}_U + \bar{i}_D) - q_k(1-q_k)\frac{\lambda_k}{\sigma_1}(\bar{i}_U^2 - \bar{i}_D^2) \right] \quad (6)$$

where the notation is the same as in equation (5), and $\bar{i}_U$ and $\bar{i}_D$ are the absolute values of the standardized selection differentials for up and down selection respectively. If $\bar{i}_U = \bar{i}_D = \bar{i}$, equation (6) reduces to

$$\text{cov}\,G_U - \text{cov}\,G_D = 4\frac{\bar{i}}{\sigma_1} \sum_{k=1}^{n} \lambda_k^2 \mu_k q_k (1-q_k)(1-2q_k). \quad (7)$$

Equivalent formulae can be obtained when selection is practised on trait 2.

From formula (7), it can be seen that asymmetry is to be anticipated unless all gene frequencies are one-half, or in the situation where the changes in covariance due to genes with frequencies below 0·5 just balances that from genes at high

frequencies. The result of Clayton *et al.* (1957) in which there was a positive corre-
lated response to up selection, but none to down selection, could be explained by
the presence of positively correlated genes at low initial frequency, with few or no
negatively correlated genes.

It is quite possible for the correlated responses to be symmetrical on divergent
selection for one trait but asymmetrical on selection for the other. Equal gene
effects at the four types of loci and gene frequencies 0·5, 0·2, 0·2 and 0·5 would be an
example of this.

Hazel (see Lerner, 1950, p. 238) has pointed out that the eventual effect of
simultaneous selection for two characters must be to reduce the genetic correlation
by fixing first those loci contributing positively to the covariance. Some experi-
mental support of this prediction has been presented by Friars, Bohren & McKean
(1962) in poultry. Selection giving equal weight to one standard deviation in the
two characters would give an expression for the change in genetic covariance after
one generation of upward selection of

$$\Delta(\text{cov}\,G) = \bar{i} \sum_{k=1}^{n} \lambda_k \mu_k q_k(1-q_k) \left[(1-2q_k)\left(\frac{\lambda_k}{\sigma_1}+\frac{\mu_k}{\sigma_2}\right) - \tfrac{1}{2} q_k(1-q_k)\left(\frac{\lambda_k}{\sigma_1}+\frac{\mu_k}{\sigma_2}\right)^2 \right].$$

Obviously the loci with λ and μ both of the same sign will contribute most to this
change. But in early generations, the first term within the square brackets may
predominate and if such loci have low values of q_k, the genetic covariance may well
increase for a while.

DISCUSSION

Both from the algebraic treatment and from the computer results it is clear that
asymmetry of correlated response is likely to be found fairly frequently. The models
are, of course, rather simplified and it should be asked what relevance these results
have to real situations. The most obvious simplification is in the small number of
loci in the models. The next degree of complexity would be to deal with n genes of
each kind, but with the condition that the total additive genetic variance and the
heritability of the two characters should remain the same. Then the scale of
operations is altered by a factor $\sqrt{n}$, though the initial rate of response to selection
will not be changed. The linear effects of the genes will be reduced by this factor,
and the total advance under selection and the time scale of changes in the genetic
parameters will be increased. If time is measured as a proportion of the total period
of selection advance, the descriptions of asymmetry will become almost independent
of the number of genes concerned. From the computer results it would seem that
the greatest asymmetry (as measured by the difference between the genetic
covariance in the two lines) will occur when the lines are about half-way to the final
limit. The greater the number of genes concerned, the more likely it is that the
terms linear in gene effects in equation (4) will be greater than those in which the
effects are squared and the former will predominate in the early generations.

If time is measured in generations, then the greater the number of genes con-
cerned, the longer the time for the asymmetry to develop. The amount of asymmetry

expected in the early generations of selection would be between $1/\sqrt{n}$ and $1/n$ times that in the original model with one locus of each type, depending on whether the linear or square terms in equation (4) contribute most to the asymmetry. The expression for the change in covariance on divergent selection for a single character has only linear terms in it and the effect would therefore be $1/\sqrt{n}$ times as large. The number of loci involved does not affect the eventual presence or absence of asymmetry. Unequal numbers of loci contributing positively or negatively to the covariance would have a similar effect on asymmetry as would unequal effects at the two loci in the model.

Nordskog & Festing (1962) have proposed a differential control of the genetic variance in the two characters (similar to model iv) and Siegel (1962) has proposed different heritabilities for the two characters as explanations of asymmetry of correlated response. From the results of this study, it appears that these causes will in some combinations lead to asymmetry, but that neither of these causes are, in themselves, either necessary or sufficient to produce asymmetry. The same is true of the gene frequencies at any one type of locus, the gene effects on the two traits at one locus, the ratio of the selection intensities in the two traits, and the ratio of the environmental variances in the two traits as used in the model studied. While there are many combinations of these factors which will lead to asymmetrical correlated responses (i.e., equation $(4) \neq 0$), only a few specific combinations of these factors will result in symmetrical correlated responses (equation $(4) = 0$). In our view, the most frequent combination of factors giving asymmetry will be loci contributing negatively to the covariance and having gene frequencies other than $0\cdot5$.

Perhaps the most important consequence of these results is not directly concerned with the asymmetry itself. If asymmetry exists, any *a priori* prediction of correlated response must have been incorrect. It has been accepted in quantitative genetic theory that predictions of direct response have only short-term validity because of the necessary changes that selection would bring about in the genetic variance. It appears from the results that the genetic covariance between two characters may be even more sensitive to changes in gene frequency brought about by selection, and presumably also to changes due to random sampling when the population size is small. The additive genetic variance of any character will be made up of contributions from the separate loci. These contributions will change as the gene frequencies are altered by selection or by random drift and they will not all change in the same way, depending on the gene frequencies at the loci concerned. But the genetic covariance (if the genetic correlation is not close to 1) will either be made up of a much smaller number of terms, if all loci contribute to the covariance with the same sign, or will be made up of positive and negative contributions from different loci. In either case the *proportional* change in the genetic covariance is likely to be greater than in the genetic variances themselves. It must therefore be expected that the static description of a population in terms of additive genetic variances and covariances will be valid in prediction over a much shorter period for correlated responses than it will be for direct responses.

If the patterns of correlated responses in any situation are to be fully understood, it will be necessary to analyse the basic causes of the genetic correlations between characters. Our results point clearly to the need for the development of new experimental techniques for this purpose.

SUMMARY

The pattern of changes of the genetic covariance between two characters on selection was examined in an effort to explain the asymmetry of correlated responses in two traits, or of the same trait in two environments, frequently observed in experimental results.

The algebraic conclusions were further examined by model selection experiments using a computer. The computer was programmed to calculate the change in gene frequency from generation to generation and to calculate from it the expected changes in genetic variances and covariance as selection proceeded. This procedure was carried out with several models of gene effects and gene frequencies.

Asymmetry of the genetic covariance, and consequently of the correlated responses, resulted when the relative change in gene frequency at the loci contributing positively and negatively to the covariance depended on the trait selected. The conditions necessary for the development of asymmetry were examined and the results suggest that any symmetry found in an experiment is perhaps more surprising than asymmetry. Probably the most frequent contribution to asymmetry in practice will be from loci contributing negatively to the covariance and having frequencies other than 0·5.

Accurate prediction of correlated response over many generations is therefore not possible without prior knowledge of the composition of the genetic covariance, as well as its magnitude. The validity of existing theory for the prediction of correlated responses is likely to be much poorer than for the prediction of direct responses. Predictions would then have to be based on the genetic parameters estimated in each generation.

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