Genetic and environmental contributions to the acquisition of a motor skill

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PRACTICE, with feedback, is a fundamental variable that influences the aquisition of motor skills[1]: with it, everyone improves, but some improve more than others. This simple fact has led to frequent debate over the relative importance of genetic and environmental influences on motor learning. In principle these factors could influence subjects' initial level of proficiency, their rate of improvement or their final level of attainment. The problem has been investigated using the rotary pursuit (RP) task, in which subjects learn to track a rotating target with a stylus[2]; this is a factorially pure task which is relatively unaffected by cognitive or verbal factors[3,4]. Earlier studies of twins reared together[2,5] indicated that heredity was the primary factor responsible for individual differences in motor skill. Here we have studied learning in a sample of monozygotic (MZA) and dizygotic (DZA) twins who had been reared apart. Heritability of performance was high even in the initial phase, and increased with practice. The rate of learning was also significantly heritable. We propose that the effect of practice is to decrease the effect of environmental variation (previous learning) and increase the relative strength of genetic influences on motor performance.

Performance scores (time-on-target) for the RP task were calculated in blocks of five trials, with five blocks of five trials on each of the three days of the experiment. Reliability of each block of trial measures were calculated using Cronbach's alpha coefficient[6] and ranged from 0.92 for the first block of the first day to 0.97 for the last block of the last day. The mean time-on-target performance scores, expressed as a percentage of perfect scores (20.00 s), by trial block for MZA and DZA twin groups over all days of practice, are shown in the lower part of Fig. 1. Performance levels of the two groups are highly similar; both showing substantial improvement over the five trial blocks of the first day. Both groups also show considerable reminiscence (improvement) after the extended rest between days 1 and 2 (blocks 5–6) and days 2–3 (blocks 10–11). Patterns of variability for both groups are likewise quite similar, as shown in the upper part of Fig. 1. During the early stages of practice, levels of variability in performance are low. With practice, there is improvement for some subjects more than others, hence increases in the within-group variability with stability being found by day 3. The differences between the variances of the MZA and DZA twins were not statistically significant.

Using a repeated measures ANOVA on the RP performance scores, with day and practice-trial block as the within-subject variables, significant main effects were found for day of practice, $F_{2,174} = 628.84, P < 0.001$, and practice-trial block, $F_{4,172} = 36.83$, $P < 0.001$. An interaction between day and block, as shown by the differential degree of trial-block improvement as a function of day of practice (lower part of Fig. 1), was also significant, $F_{8,68} = 31.76$, $P < 0.001$.

Intraclass correlations, corrected for the effects of sex and age[7], for MZA and DZA twin pairs over the 15 blocks of practice trials, are shown in the lower part of Fig. 2. The MZA intraclass correlations are highly regular and show a slight increase over the three days of practice. The DZA correlations are much less stable and regular. This lack of stability in the DZA correlations may, in part, be due to the smaller number of DZA pairs. The slope of the regression line fitted to the DZA intraclass correlations for the last two days (not shown) is close to zero. These data suggest an asymptotically decreasing contribution of environmental factors as practice on the RP task continues. The consistently larger intraclass correlations for MZA compared with DZA twin sets also points to a significant genetic component of performance.

A purely environmental model was rejected for all of the 15 trial blocks, whereas a combined genetic and environmental model fitted the data at each of the 15 trial blocks. The upper curve in Fig. 2 gives the proportion of variance due to additive factors (the heritable components), together with their standard errors. The influence of heritable factors is high on the first block (0.66 ± 0.08), and remains high throughout the 15 trial blocks, ending on the last block with a value of 0.69 ± 0.08. The highest heritability (0.74 ± 0.08) was observed for the 14th block. The influence of heritability in the first trial block (0.66) is elevated relative to the other four blocks on the first day (0.53, 0.52, 0.55, 0.52, respectively, in all cases ±0.08). One reasonable hypothesis for this elevation is that, without previous experience, individuals rely largely on their current abilities; MZA twins share genetic influences on these abilities to a greater degree than DZA twins. With the exception of the first block of trials, there is a trend towards increased heritability across the 15 blocks. Moreover, the similarity between MZA twins across the 15 blocks of trials is indistinguishable from the block-to-block similarity of an individual's performance across time. If heritability is high, we would expect the matrix of MZA intraclass correlations among the 15 blocks not to differ significantly from the interblock correlation matrix. Whereas the MZA intrablock correlation matrix did not differ significantly from the sample interblock correlation matrix;

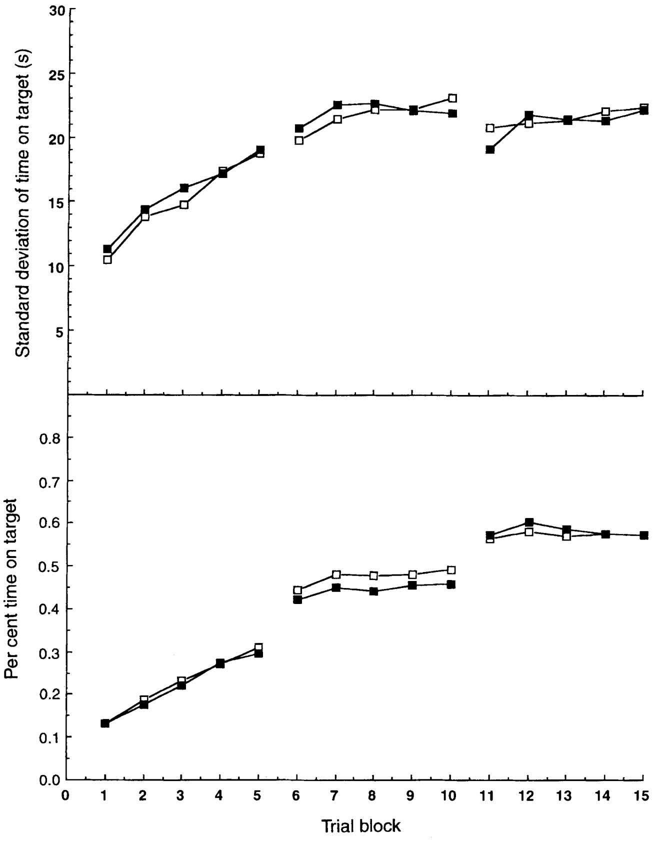

FIG. 1 Standard deviations of time-on-target (upper figure) and percentage of time on target (lower figure) for the rotary pursuit task for MZA (open squares) and DZA (filled squares) twins for each of 15 trial blocks.

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$\chi^2(120), N = 160) = 92.58, P = 0.97$, the DZA intrablock correlation matrix did differ significantly; $\chi^2(120, N = 128) = 1,064.20$, $P = 0.0001$. Thus, MZAs perform as similarly to each other across blocks as any one individual to him or herself.

Performance on the rotary pursuit task may be examined in other ways. Table 1 shows the twin intraclass correlations, corrected for age and sex, for the slope of rotary pursuit performance on each day, and the reminiscence effect observed between days 1 and 2, and days 2 and 3. Model-fitting revealed that heritable (H) and environmental (E) factors had significant effects on performance, and the hypothesis of common parameter estimates for the three slopes ($H^2 = 0.66 \pm 0.05$; $E^2 = 0.34 \pm 0.03$) could not be rejected. A model including genetic and environmental effects was also necessary to explain the two reminiscence effects and again the hypothesis of common parameter estimates ($H^2 = 0.40 \pm 0.07$; $E^2 = 0.60 \pm 0.04$) could not be rejected.

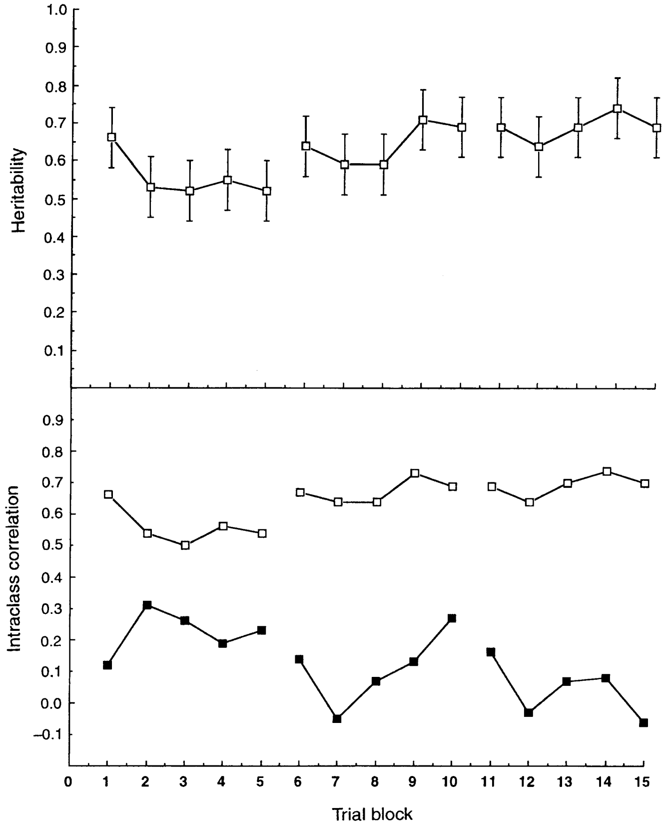

FIG. 2 Heritabiities estimated from model-fitting the twin data for each of 15 trial blocks (upper figure) (± s.e.) and intraclass correlations for MZA and DZA twins for percentage of time-on-target for the rotary pursuit task (lower figure) MZA twins, open squares; DZA twins, filled squares.

TABLE 1 Rotary pursuit task performance

Day	Measure	MZA ($N = 64$)	DZA ($N = 32$)
1	Slope	0.56 (0.37–0.71)	0.24 (−0.11–0.54)
2		0.69 (0.54–0.80)	0.17 (−0.18–0.48)
3		0.72 (0.58–0.82)	0.11 (−0.24–0.43)
1–2	Reminiscence	0.19 (−0.06–0.41)	0.22 (−0.13–0.52)
2–3		0.55 (0.35–0.70)	0.51 (0.20–0.72)

Intraclass correlations and 95% confidence intervals for slopes and reminiscence measures on the rotary pursuit task for monozygotic and dizygotic twins that were reared apart. Because day 3 of testing was added after the study began, a smaller number of MZA twin pairs (58) participated on Day 3.

Our results demonstrate the significance of genetic effects for individual differences in motor skill as measured by rotary pursuit performance. Significant genetic effects were found whether performance was defined simply as per cent time-on-target, defined in terms of changes in performance over time (slope of performance), or defined as improvement after a period of rest (reminiscence effects). Our conclusions are based on a greater MZA than DZA twin resemblance for performance on each trial of practice. The simplest and most reasonable explanation for the greater MZA twin resemblance is that motor performance reflects genetic influence. With practice, increases in environmental similarity reduce twin differences more for MZA twins (who are already genetically identical) than for DZA twins, and reveal stable or increasing heritabilities. The pattern of twin correlations found here also indicate that there might be an influence of nonadditive genetic effects. If these effects were significant, they would contribute even more to a decreased DZA twin similarity[8]. Our data also indicate that within the range of practice studied here, these differences are based to a considerable degree on differences in genotypes. This conclusion does not diminish the importance of practice with feedback for the acquisition of skill. Even the least gifted of our twins attained levels of skill after practice that were superior to those achieved in initial trials by the most gifted. Nevertheless, the main findings of our study unequivocably show the important contribution of genotypic factors underlying individual differences in skill acquisition on the rotary pursuit task. ☐

Methods

Subjects. The participants were 64 pairs of identical twins reared apart (MZA) and 32 pairs of same-sex fraternal twins reared apart (DZA) who participated in the Minnesota study of twins reared apart between 1979 and 1994 (ref. 9). Of the MZAs, 42% were male (age, 44.2 years; s.d., 15.51), 58% female (age, 40.97; s.d., 12.39). Of the DZAs, 31% were male (age, 44.20; s.d., 13.52), 69% female (age, 43.73; s.d., 11.54).

Apparatus and procedures. Participants were tested individually during three successive morning sessions, of roughly 30 min each, on the pursuit rotor task. We used a pursuit rotor apparatus (Lafayette Instrument Co.) that rotated at a constant speed of 60 r.p.m. in a clockwise direction. A standard hinged stylus and standard instructions were used. A timing mechanism calibrated in 0.01-s units was used. The task was to keep the stylus tip in contact with the moving target using the preferred hand. Trial duration was 20 s, with a 10 s intertrial interval. Twenty-five trials were conducted per daily session. Each trial began with the stylus tip in contact with the target. Participants were given information feedback in units rounded to 0.1 sec, and were occasionally encouraged to 'keep trying as hard as possible'.

Data analysis. An efficient approach to estimating the significance of genetic and environmental (non-familial) effects in these data involved specifying and evaluating various biometric models[10]. This was accomplished by comparing the covariances of MZA and DZA twins. Maximum likelihood procedures were used to estimate genetic (H^2) and environmental (E^2) parameters of the various biometric models that have been specified[11]. The maximum likelihood procedure also provides a χ^2 test of the fit of each particular model, as well as a χ^2 difference test for comparing the relative explanatory power of different models. Two models were examined here. One model assumed only non-shared environmental influences (in the absence of twins reared together, it is not possible to estimate shared familial components). A second model included genetic and environmental parameters. This combined model assumed that all genetic effects are additive, and that there is no assortative mating. Nonadditive genetic effects were not estimated owing to the difficulty of distinguishing additivity from nonadditivity reliably with small samples[12].

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Orthogonal motion after-effect illusion predicted by a model of cortical motion processing

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THE motion after-effect occurs after prolonged viewing of motion; a subsequent stationary scene is perceived as moving in the opposite direction[1,2]. This illusion is thought to arise because motion is represented by the differential activities of populations of cortical neurons tuned to opposite directions; fatigue in one population leads to an imbalance that favours the opposite direction once the stimulus ceases[3]. Following adaptation to multiple directions of motion, the after-effect is unidirectional[4–6], indicating that motion signals are integrated across all directions. Yet humans can perceive several directions of motion simultaneously[7–10]. The question therefore arises as to how the visual system can perform both sharp segregation and global integration of motion signals. Here we show in computer simulations that this can occur if excitatory interactions between different directions are sharply tuned while inhibitory interactions are broadly tuned. Our model predicts that adaptation to simultaneous motion in opposite directions will lead to an orthogonal motion after-effect. This prediction was confirmed in psychophysical experiments. Thus, broadly tuned inhibitory interactions are likely to be important in the integration and segregation of motion signals. These interactions may occur in the cortical area MT, which contains motion-sensitive neurons with properties similar to those required by our model[11–14].

Two populations of dots moving in different directions are readily perceived as two transparently moving sheets[15]. After adaptation to such ‘transparent motion’, observers never perceive a transparent motion after-effect (MAE), but rather a unidirectional MAE, opposite to the vector sum of the adaptation directions[4–6]. This non-transparent MAE cannot be explained by the standard ratio model proposed by Sutherland[16], in which motion is perceived as an imbalance of activities in a pair of oppositely tuned motion detectors. Following adaptation, one of the members of such a pair will respond below baseline. Through opponency between the two members this results in temporary activation of the previously inactive member, thus causing the percept of an MAE. The non-transparent MAE suggests that motion information is integrated across all directions, and not just across opponent pairs of directions. The distribution-shift model[4] accounts for this MAE by a global shift in activities across a population of motion-encoding neurons, due to adaptation. However, it does not explain why multiple motion vectors are perceived during the adaptation phase, while only a single motion vector is perceived during the test phase. To address this paradox, we added broadly tuned inhibition between motion directions to the distribution-shift model. The expanded model is aimed at understanding motion integration and segregation, in particular how transparent motion can cause a non-transparent MAE[17].

The model has two stages, based on the physiology of motion perception in primates. A motion-detection stage, corresponding to directionally selective cells in area V1[18], feeds into a global motion integration stage, corresponding to area MT. Motion detectors have a bandwidth of about 70°, which is typical of V1 neurons[11]. Motion detectors excite second-stage units of similar preferred direction with a directional divergence from stage 1 to stage 2 of 30°. As a result, stage 2 units have a bandwidth of about 90°, similar to the bandwidth of MT neurons[11]. Moreover, inhibitory inputs to stage 2 are driven by the output from stage 1 with a bandwidth of 180°, thus normalizing responses at stage 2[19,20]. These interactions between different motion directions are similar to those observed in area MT[12]. Perceived motion corresponds to supra-threshold peak(s) in the distribution of motion-sensitive cells in the second stage, analogous to the findings in area MT of macaques[13] and humans[14]. The strength of the motion percept is related to the response amplitude, while the width of the response distribution relates to the sharpness of the perceived motion direction. The MAE can be explained by adaptation of motion detectors when they are activated. This has been implemented in our model through weights for the output of stage 1 that decay when motion detectors are activated, and recover after stimulus offset[21]. The time constant for this process is about 10 seconds (refs 22, 23). During the test phase (following adaptation) all stage 1 detectors are weakly active, especially when a dynamic test stimulus is used that consists of incoherent motion. Adapted units are temporarily suppressed, which causes disinhibition of oppositely tuned units at stage 2, thus causing an MAE. The model accounts for segregation of transparently moving patterns during adaptation, as well as global integration during the test phase as previously shown[4–6]. The broad tuning of inhibition causes a broad MAE, agreeing with the finding that the MAE is indistinguishable from directionally biased noise[2].

The model simulations (Fig. 1*a*) show that transparent motion induces a unidirectional MAE. Adaptation to opposite directions causes no MAE parallel to the adaptation directions, in agreement with psychophysical results[4]. The model, however, suggests that adaptation to opposite motion directions can cause an MAE, provided that disinhibition is sufficiently strong and broad. In particular, motion during adaptation causes broadly tuned disinhibition in the test phase, leading to maximal combined disinhibition in directions orthogonal to the adaptation vectors. The model thus predicts an orthogonal MAE for oppositely directed motion. Simulation results show that the same model can account for both a vector average MAE (Fig. 1*a*) and an orthogonal MAE (Fig. 1*b*). The orthogonal MAE is a surprising prediction that runs counter to recent research showing vector addition in MAEs[4–6].

We tested this prediction in a psychophysical experiment. We adapted subjects to motion, and asked them to report the motion they perceived when viewing randomly moving dots. During the adaptation phase two populations of dots moving in opposite directions were displayed on the screen (Fig. 2*a*). There were four adaptation conditions: the two populations could move along the vertical, the horizontal or the two diagonals. During the test phase displacements for all dots were drawn from a distribution spanning all 360 degrees, thus creating incoherent motion (Fig. 2*b*). The motion displacements in the test phase were globally balanced to ensure that no directional biases were present. Subjects had to report whether they saw motion during the test phase, and if so, to indicate the axis along which they saw motion. The axis was not directed; for example, subjects could report motion along the vertical, but no distinction was made between up

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