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The presence of zalambdalestids argues that the superordinal clade including Glires had separated from other superordinal placental clades by this time. This is also applicable for zhelestids, thus suggesting that some ungulate clades had separated from other superordinal placental clades by this time. The dates of these fossil taxa are concordant with molecularly based estimates of 64–104 Myr ago (median 84 Myr ago) for the superordinal diversification of placentals⁵. No members of extant placental orders, however, are known from the Late Cretaceous (with the possible exception of some insectivores). Subsequent diversification of living placental orders within these Late Cretaceous placental superordinal groups did not begin until about 65 Myr ago, after dinosaur extinction^{7,8}. □

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Rapid responses of British butterflies to opposing forces of climate and habitat change

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Habitat degradation and climate change are thought to be altering the distributions and abundances of animals and plants throughout the world, but their combined impacts have not been assessed for any species assemblage^{1–4}. Here we evaluated changes in the distribution sizes and abundances of 46 species of butterflies that approach their northern climatic range margins in Britain—where changes in climate and habitat are opposing forces. These insects might be expected to have responded positively to climate warming over the past 30 years, yet three-quarters of them declined: negative responses to habitat loss have outweighed positive responses to climate warming. Half of the species that were mobile and habitat generalists increased their distribution sites over this period (consistent with a climate explanation), whereas the other generalists and 89% of the habitat specialists declined in distribution size (consistent with habitat limitation). Changes in population abundances closely matched changes in distributions. The dual forces of habitat modification and climate change are likely to cause specialists to decline, leaving biological communities with reduced numbers of species and dominated by mobile and widespread habitat generalists.

We studied all 46 non-migratory British butterfly species that reach their northern margins in Britain, where the summer–spring climate has warmed by approximately 1–1.5 °C in the past 25 years^{5,6}. Many of these butterflies are restricted to warm local environments in Britain and have faster larval growth rates, earlier flight periods and increased abundances at higher temperatures (within the British temperature range)^{1,7–9}. Range expansions have

also been observed at northern margins^{10–13}. Under the hypothesis that climate is limiting, most species should have benefited from climate warming. In contrast, intensification of agriculture in Britain has led to 70% (range 40–97%) losses of semi-natural habitats since 1940 (ref. 13). On the basis of habitat alone, most species should have declined¹³ (see Fig. 1). Here we report how butterflies differing in dispersal and habitat specialization^{14,15} have responded to an improving climate but continued habitat degradation.

For each species, distribution change was measured as the difference in the number of 10-km grid squares occupied between 1970–82 and 1995–99 (refs 13, 16; the 1995–99 data subsampled to equalize recorder effort; see Methods), divided by the 1970–82 distribution size. Three-quarters (34/46) of species declined in distribution area. Habitat specialists fared worse than wider-countryside generalists: 26/28 specialists declined compared to 9/18 wider-countryside species (Fig. 2; $t = 2.97$, degrees of freedom, d.f., 8, $P = 0.018$). Sedentary species fared worse than mobile species: 24/26 sedentary species declined compared to 11/20 mobile species ($t = 3.68$, d.f., 10, $P = 0.004$). The effects of mobility and habitat specificity cannot be separated, as these traits are highly correlated among butterflies (26/28 specialist species are sedentary, 18/18 wider-countryside species are mobile). In conjunction, low mobility and high habitat specialization restrict species in fragmented habitats, and limit expansion across patchy, human-modified landscapes^{17–21}. Even expanding species have expanded more slowly in areas where there is less suitable habitat for them to expand into^{2,18}.

Changes in abundance were measured from weekly counts of adults at around 120 fixed sites between 1976 and 2000 (ref. 14), and summarized as the slope of the regression between log of the abundance and the year. Mobile generalists tended to increase

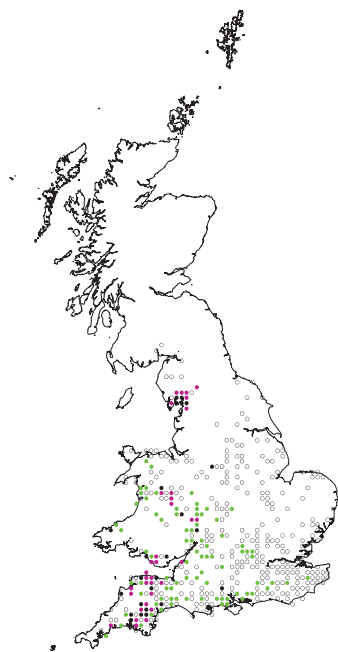


Figure 1 Reduced distribution of the high-brown fritillary. Distribution changes between 1970–82 and 1995–99 (full data set) of the high-brown fritillary *Argynnis adippe*, the habitat specialist that has shown the most rapid decline in distribution size. Black circles (10-km grid resolution) show butterfly records for populations in both 1970–82 (ref. 16) and 1995–99 (ref. 13); green shows apparent extinction (recorded 1970–82; not recorded 1995–99); pink shows new records (no record 1970–82; record in 1995–99); white circles show pre-1970 extinctions (data 1857–1969). Recording was incomplete in the past, so the real decline has been ever steeper.

relative to sedentary specialists (Fig. 3; specialists versus wider-countryside $t = 2.98$, d.f., 5, $P = 0.031$; sedentary versus mobile $t = 2.93$, d.f., 4, $P = 0.043$). Changes in abundance and changes in distribution size were correlated across all species for which abundance data were available (Fig. 3; $r^2 = 0.63$, $F_{1,24} = 41.55$ (1 and 24 d.f.), $P < 0.0001$). Many species face both declining abundance and declining distribution.

The negative intercept of the regression (Fig. 3; non-phylogenetic $c = -0.148$, standard error of the mean, s.e.m. = 0.032, $P < 0.001$) suggests that abundance changes have been more favourable than distribution changes: on average, a species that showed no abundance change on monitored sites over the past 25 years declined by 15% in distribution area. The effect was stronger for sedentary specialists (21–22% distribution decline for no change in local abundance) than for mobile generalists (9–9.5% decline). In an analysis of covariance (ANCOVA) for the mobility effect, $F_{1,24} = 5.16$, $P = 0.032$; for the specialization effect, $F_{1,24} = 3.95$, $P = 0.058$.

These analyses suggest that most sedentary and specialized species, and at least half of the other species, are limited by factors other than climate. We studied this by fitting climate response surface models^{12,22} at 50-km grid resolution to the distributions of British butterflies throughout Europe²³ to estimate the extent of climatically suitable areas potentially available for each species in Britain. Generally there were good fits between observed and

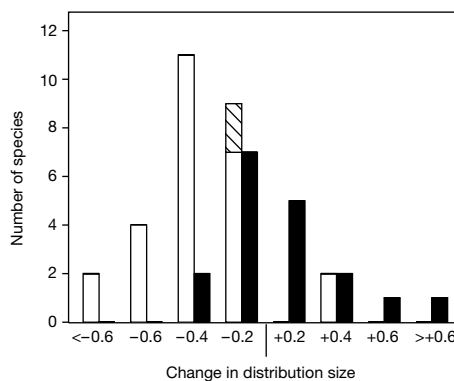


Figure 2 Proportional changes in distribution sizes of butterflies between 1970–82 and 1995–99. Sedentary specialists (white), mobile specialists (hatched) and mobile wider-countryside species (black) are shown.

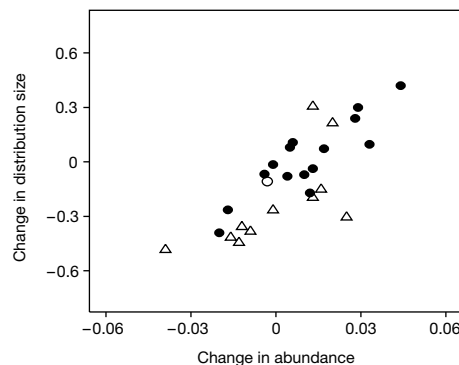


Figure 3 Correlation between changes in the abundance and distribution of butterflies. The data show the relationship between the trend in population abundance between 1976 and 2000 and the change in distribution size between 1970–82 and 1995–99, for sedentary specialists (open triangles), mobile wider-countryside species (filled circles), and one mobile specialist (open circle).

simulated distributions at a European scale (kappa goodness-of-fit^{12,24}, mean is 0.79, s.e.m., 0.007, range 0.67–0.87), showing that continental range limits of all the British study species could be described by three bioclimate variables (see Methods). Goodness-of-fit was not affected by mobility ($P = 0.2$) or specificity ($P = 0.3$). We then calculated the difference between the extent of land in Britain ($\sqrt{\text{area}}$, 10-km grid resolution) deemed climatically suitable and the area occupied by each species in 1995–99. Specialists lagged behind climate more than did species of the wider countryside (specialists' mean lag is -104.55 , s.e.m., 13.40, $n = 28$; wider-countryside mean lag is -37.03 , s.e.m., 8.48, $n = 18$; $t = 2.50$, d.f., 8, $P = 0.037$), and sedentary species tended to lag behind climate

more than mobile species ($t = 2.21$, d.f., 10, $P = 0.052$). Climatically suitable areas are apparently available for colonization, but most species (especially sedentary specialists) have failed to exploit them either because they do not contain suitable breeding habitats, or because breeding habitats are out of reach.

Three thermally limited species¹³ illustrate the patterns typical of most other species. *Plebejus argus* has low mobility, principally inhabits lowland heathland, and declined in area of occupancy by 28% (Fig. 4a). It is restricted within apparently suitable climatic areas (Fig. 4d), and is limited by habitat and dispersal more than by climate. Most declining species show comparable patterns. *Pararge aegeria* is a more mobile, wider-countryside species, capable of

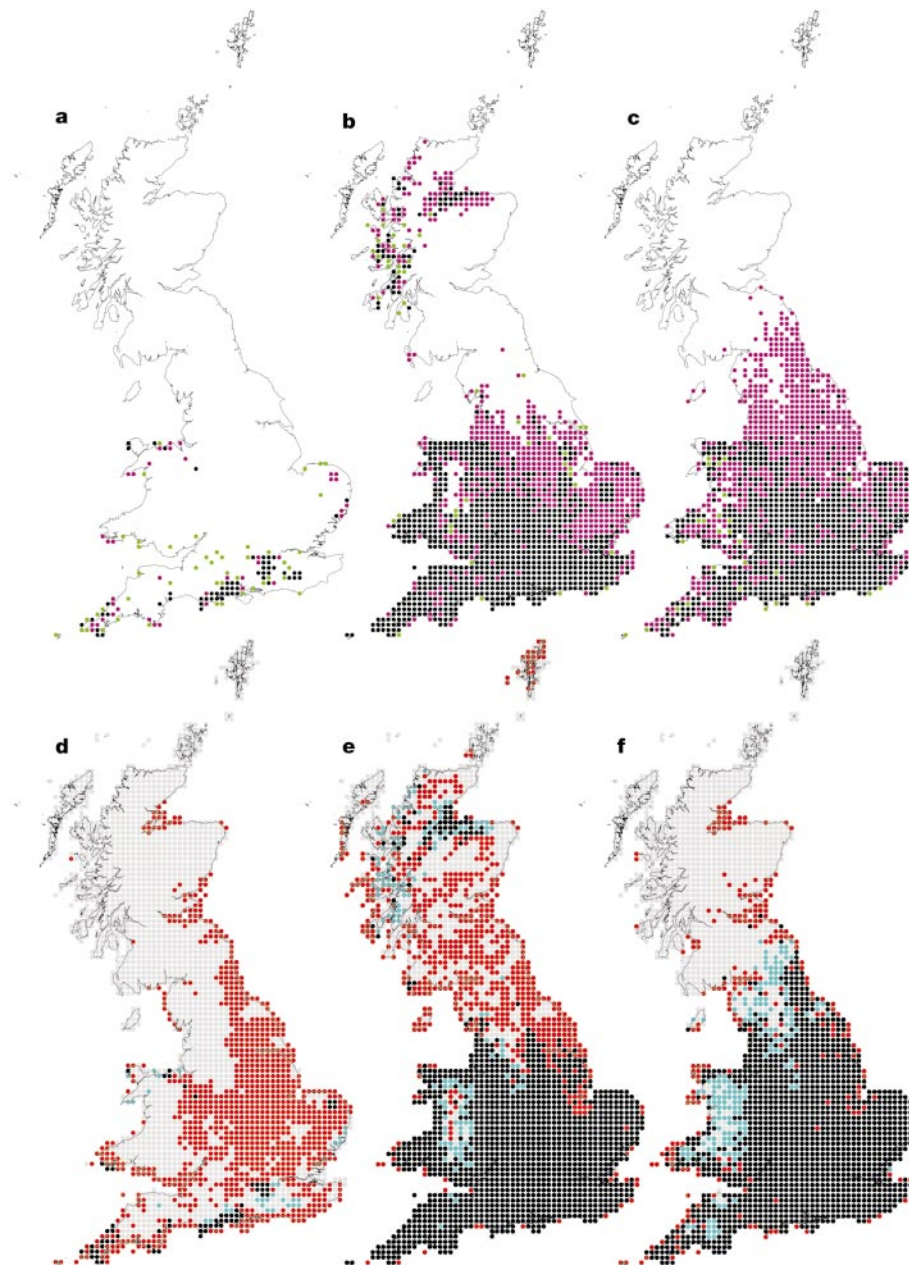


Figure 4 Climate and species ranges. The degree to which three species have changed their ranges (**a–c**, without subsampling) and are lagging behind current climates in Britain (**d–f**; 10-km grid resolution). **a, d**, Silver-studded blue, *Plebejus argus*; **b, e**, speckled wood, *Pararge aegeria*; **c, f**, comma, *Polygonia c-album*. For maps **a–c**, black circles show butterfly records for both 1970–82 (ref. 16) and 1995–99 (ref. 13); green circles show apparent extinction (recorded 1970–82; not 1995–99); pink circles show apparent

colonization (no record 1970–82; record 1995–99). For maps **d–f**, black circles (climate suitable, butterfly present) and grey circles (climate unsuitable, butterfly absent) show where observed 1995–99 and simulated distributions agree; red circles (climate predicted suitable, butterfly not recorded) and blue circles (butterfly recorded, climate deemed unsuitable) show mismatches.

inhabiting woodlands, scrub, hedgerows and shady gardens. Its distribution has expanded by 24%, but still lags behind climate¹² (Fig. 4b, e), with regional differences in its rate of expansion accurately predicted by differences in woodland cover²: both habitat and climate restrict its distribution. Most other expanding species show comparable patterns. *Polygonia c-album* is a very mobile butterfly of the wider countryside whose distribution has expanded by 30%, and shows little or no lag behind its climate (Fig. 4c, f). This species is mainly limited by climate.

Most species of non-migratory butterflies that reach the northern margins of their geographic ranges in Britain have declined over the last 30 years (as they have elsewhere in northern Europe^{21,25}) even though the climate has warmed. This is surprising because climate warming is expected to increase the range of habitats these species can inhabit^{1,19}. However, most sedentary specialists have not expanded because habitat patches are too isolated to colonize. Thus, quaternary expansions of species into areas where the climate 'improved' over the past 15,000 years³ are unlikely to be replicated for many sedentary and specialized species in heavily modified, modern landscapes⁴. In contrast, quaternary rates of decline are likely to be exceeded in regions where climate-change and habitat are both acting as agents of decline, potentially leading to serious losses of biodiversity in areas such as Mediterranean Europe^{10,25}, where most species already approach their climatic maxima. Large-scale protection and management of habitat networks are required to minimize habitat-related declines and to maximize the ability of species to track the distribution of suitable climate. If sedentary specialists continue to decline, biological communities will increasingly become dominated by mobile generalists. □

Methods

Distributions

65,826 and 437,690 separate record cards, listing all species observed on one field visit, were collated for England, Wales and Scotland for 1970–82 (ref. 16) and 1995–99 (ref. 13), respectively. To equalize recorder effort, we subsampled the 1995–99 data by randomly selecting the 1970–82 number of record cards from the 1995–99 data, subsampling separately for each 100-km Ordnance Survey grid square to retain the broad geographical distribution of 1970–82 records. Results are based on subsampling, except Figs 1 and 4 (all records) and measures of the lag between climate space and observed distributions (full 1995–99 distribution is appropriate). Statistical differences among species (according to mobility and habitat specialization) were robust when re-analysed (1) using the entire 1995–99 data set (rather than the subsample), and (2) measuring distribution change as the square root of area (in square kilometres), rather than proportional change.

Abundance

Weekly count data were collected along about 120 fixed transect routes¹⁴ and summarized as one collated index of abundance for each species in each year²⁶ (for sites where present, excluding sites after two successive zeros were recorded, including colonized sites after two successive presences). Species were included only if the abundance trend was based on data from more than 10 sites per year (mean is 36 sites per year per species, $n = 27$ species). We excluded *Polyommatus icarus* (number of generations varies regionally), *Thymelicus sylvestris* and *T. lineola* (not identified separately on transects).

Species and their characteristics

We included all southerly distributed species, except *Colias croceus*, *Pieris brassicae*, *P. rapae*, *Vanessa atalanta*, and *V. cardui*, which migrate between the UK and continental Europe, and *Papilio machaon*, which has many British records of vagrants from continental Europe.

We used a mobility ranking¹⁵ (other rankings are in close agreement), and scored species as relatively sedentary (ranks 0–2 (ref. 15), $n = 26$ species) or mobile (ranks 3–6, $n = 20$ species; ranks recalculated to exclude expansion data). On the basis of mark–release–recapture studies¹⁶, *Argynnis aglaja*, *A. paphia* and *Hipparchia semele* were re-classified as sedentary, and *Aphantopus hyperantus* as mobile. Statistical conclusions are unaffected by these changes. We scored species as wider-countryside species ($n = 18$ species) or specialists restricted to specific habitats ($n = 28$) species¹⁴.

Analyses were controlled for phylogeny²⁷ using independent phylogenetic contrasts (CAIC program²⁸). Mobility and habitat specificity were scored as binary variables. Unless stated, all analyses were phylogenetically controlled: non-phylogenetic analyses (not shown) supported all conclusions. Non-phylogenetic methods were used for analysing the regression intercepts of abundance–distribution relationships because regressions based on phylogenetic contrasts must pass through the origin²⁸.

Climate response surface models

Butterfly distributions^{23,13} were converted to presence/absence on a 50-km Universal Transverse Mercator grid (Azores to longitude 30° E; Mediterranean coast to Svalbard; 2,648 cells). We used mean monthly temperature, precipitation and cloudiness relating to the climate normal period 1931–60 (ref. 29) to interpolate values for the midpoint and mean elevation of each 50-km cell²². For each cell, we computed (1) mean temperature of the coldest month (related to overwintering survival); (2) annual temperature sum over 5 °C (development potential for immature stages); (3) an index of moisture availability (ratio of actual to potential evapotranspiration). We fitted climate response surfaces describing each species' European distribution using these variables^{12,22}.

Climate response surfaces generated at 50-km grid resolution were applied to finer-scale (10-km grid) climate data to simulate the 1961–90 extent of climatically suitable areas for each species in Britain. Bioclimate values were derived for the midpoint and mean elevation of each 10-km cell (2,805 cells) in Britain using the same techniques and data sets. For each species, we computed the difference between the area of suitable climate (black plus red circles in Fig. 4d–f) and the area currently occupied (black plus blue circles in Fig. 4d–f). Most blue circles (butterfly recorded, climate deemed unsuitable) in Fig. 4d–f are from areas of high relief where the species occurs in warm habitats (for example, south-facing slopes) below the mean elevation of the grid cell.

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Perceptual basis of bimanual coordination

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Periodic bimanual movements are often the focus of studies of the basic organizational principles of human actions^{1–25}. In such movements there is a typical spontaneous tendency towards mirror symmetry. Even involuntary slips from asymmetrical movement patterns into symmetry occur, but not vice versa. Traditionally, this phenomenon has been interpreted as a tendency towards co-activation of homologous muscles, probably originating in motoric neuronal structures. Here we provide evidence contrary to this widespread assumption. We show for two prominent experimental models—bimanual finger oscillation¹ and bimanual four-finger tapping²—that the symmetry bias is actually towards spatial, perceptual symmetry, without regard to the muscles involved. We suggest that spontaneous coordination phenomena of this kind are purely perceptual in nature. In the case of a bimanual circling model, our findings reveal that highly complex, even ‘impossible’ movements can easily be performed with only simple visual feedback. A ‘motoric’ representation of the performed perceptual oscillation patterns is not necessary. Thus there is no need to translate such a ‘motoric’ into a ‘perceptual’ representation or vice versa, using ‘internal models’ (ref. 29). We suggest that voluntary movements are organized by way of a representation of the perceptual goals, whereas the corresponding motor activity, of sometimes high complexity, is spontaneously and flexibly tuned in.

How do coordinative processes in the motor system and in the domain of perception and imagery contribute to the organization of voluntary movement? Spontaneous coordination phenomena such as the symmetry tendency in bimanual movements are of particular interest here. The traditional view is that the symmetry tendency is due to a bias towards co-activation of homologous muscles^{1,3}, probably originating in motoric neuronal structures. Recently, the possible influence of perception and perceptual imagery on spontaneous coordination phenomena has been stressed^{4–8,26}. However, many of these studies tend to assume that motoric, or efferent, constraints are also of central importance. Clear experimental evidence is lacking.

In our first experiment we addressed the symmetry tendency in a classical bimanual finger oscillation model^{1,2,9,10}: a person stretches out both index fingers and oscillates them in mirror symmetry or in parallel (Fig. 1a, b). The symmetrical mode is much more stable than the parallel mode. With increasing oscillation frequencies, a parallel pattern often involuntarily switches into a mirror-symmetrical movement pattern. In contrast, symmetrical movements never switch into asymmetry. Is this symmetry bias

towards co-activation of homologous muscles or towards perceptual, spatial symmetry?

Participants ($n = 8$) performed bimanual index-finger oscillations, either in symmetry or in parallel, with both movement instructions (symmetry or parallelity) defined in visual, perceptual space. To register trajectory, both fingers were inserted in cuffs of 50-g weight, with a graphics tablet stylus attached to each finger. The hands were individually put either palm up or palm down. Thus, there were four bimanual hand positions (Fig. 1c–f). If both palms are either up or down, the hand position is congruous. If one palm is up and the other is down the hand position is incongruous. In a session, each combination of movement instruction and hand position was performed four times, in a total of 32 randomized trials. In a trial, a metronome pulse paced the oscillation frequency from 1.4 Hz up to 3.6 Hz, in a time interval of 24 s. Participants were requested to execute one full movement cycle on each beat. Should the movement pattern change, participants were instructed to give in and perform the more comfortable pattern¹¹.

The experimental rationale, as adopted from designs in the literature^{7,12–14}, was as follows. With a congruous hand position, perceptual movement symmetry goes along with periodic co-activation of homologous muscles. Thus, a bias towards symmetrical oscillation is to be expected, as it is a replication of results reported previously. The critical condition is with incongruous hand position, because perceptual parallelity goes along with co-activation of homologous muscles. Thus, if there is a dominant tendency towards co-activation of homologous muscles, a bias towards parallel oscillation is to be expected. If there is a dominant tendency towards perceptual symmetry, there should be a bias towards symmetrical oscillation.

The results were clear: independent of hand position, an instructed symmetrical oscillation pattern is always stable, whereas instructed parallel oscillations tend to disintegrate and to switch into symmetry. Figure 2 demonstrates this by showing histograms of the relative phase of the fingertips, as defined in a position versus velocity coordinate system^{11,15}. Zero degrees relative phase means symmetry, whereas 180° relative phase means parallelity, in perceptual space. Relative phase was calculated on every right reversal of the left finger.

We define a relative phase of $0 \pm 60^\circ$ as symmetry, of $180 \pm 60^\circ$ as

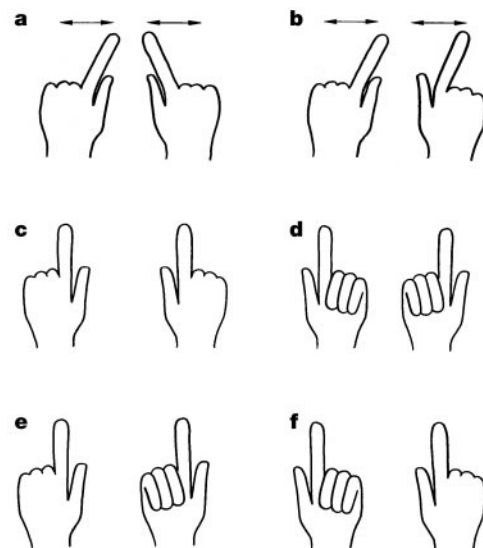


Figure 1 Instructed, synchronous finger oscillation patterns and hand positions. **a**, Symmetrical movement. **b**, Parallel movement. **c**, **d**, Congruous positions with both palms up or both palms down. **e**, **f**, Incongruous positions with one palm up and the other palm down.