

Figure 1 The stimuli used and the after-effect. **a, b**, Two different sequences of images that were used to test for the after-effect. The stimuli were produced with a VSG series 3 stimulus generator (Cambridge Research System, Rochester, UK). The radial patterns rotate clockwise or anticlockwise and the concentric rings move either inwards or outwards. The grey image is the blank screen of the same average luminance (31.3 cd m^{-2}) as the patterns. The screen was placed at a distance of 85 cm. **c**, A simulated enlarged image of the windmill after-effect that most observers see (lower left blank in **a** and **b**). The contrast approximates to the strength of the percept. The Supplementary Information includes a demonstration of the illusions as in **a** and **b**, as well as the script for viewing them on the VSG system.

The after-effect in Fig. 1a resembles the windmill pattern and is not related to the spatial frequency of the rings. If the angular frequency of the windmill changes, so does that of the after-effect. An essential requirement for the after-effect we describe is that the windmill pattern should be moving slowly, at 1 Hz or less, indicating that the stimulation of sustained pattern channels⁷ is crucial to the illusion.

The version shown in Fig. 1b demonstrates the effect more vividly. If the windmill and concentric patterns are both presented at a slow and then at a faster rate (for example, 0.2 Hz and then 2 Hz) with intervening blank screens, and the routine is cycled, after-effects can be seen in each blank period. In the period after the windmill (Fig. 1b, top right), a concentric ring after-effect can be seen; in the period after the concentric rings (bottom left), a windmill after-effect is seen. We presented these patterns to 13 naive subjects, who all reported seeing the illusions. Figure 1c approximates the windmill after-effect that most subjects perceive. It is unlikely that a retinal after-image could produce the illusion because the inducing patterns were not stationary and the after-effects seen were not of the immediately preceding patterns.

Even though the effects could be obtained with simple sine-wave gratings, we

recommend radial patterns to avoid retinal after-images from pursuit eye movements. The after-effect is also stronger with radial patterns, which might be related to the meridional bias reported at many levels of the visual system^{4,8,9}.

If, after the windmill pattern, a moving grating is presented instead of concentric rings, the after-effect is seen in an hourglass fashion, with the radial lines only at orientations orthogonal to the grating. This orientation selectivity, together with our finding that the effects are seen better binocularly than monocularly, suggests that a cortical locus is involved.

We propose the occurrence of two neuronal processes to explain the illusion. First, the stimulation of pattern channels not only leads to a decrease in sensitivity for that pattern¹, but also causes the deposition of a trace lasting for about half a minute, possibly at the synaptic level, akin to some form of short-term plasticity¹⁰. Second, this trace is brought to perceptual threshold by a rebound from inhibition caused by orthogonal orientations.

Georgeson⁶ explained McKay's rays by proposing that there is mutual antagonism between pattern and movement channels within the same orientation column. We suggest that this antagonism between pattern and movement channels also exists between orthogonal orientation columns.

The phenomenon that we have observed might serve as a strategy of the visual system for preventing the spurious excitation of contour detectors. Visual cortical cells, although best stimulated by bars moving perpendicular to the long axis of their receptive fields, often respond to small stimuli moving along this axis¹¹. During eye movements, texture elements in the scene could therefore inappropriately stimulate cells whose optimum orientation is the same as the direction of movement. We propose that this excitation is prevented by inhibition from cells tuned to orthogonal orientations when the latter are activated by moving stimuli.

The transient existence of a stimulus trace is hard to explain. It might be an inevitable consequence of synaptic processes underlying short-term or long-term potentiation. It might also be a way of rapidly facilitating the perception of pre-existing contours after an eye movement.

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Climate change related to egg-laying trends

Analysis of 20 species of UK breeding birds over a 25-year period found a long-term trend towards earlier egg-laying¹. Further studies have correlated such trends with spring temperatures (one species)² or the North Atlantic Oscillation (three species)³. We have studied a data set spanning 57 years and find that laying date is related to temperature or rainfall for 31 of 36 species (86%), and that 53% of species show long-term trends in laying date over time, of which 37% can be statistically accounted

for by changes in climate. These data provide evidence for the large-scale impact of rising temperatures on wildlife. Our analysis of a UKCIP98 national-level climate scenario⁴ predicts that average laying dates will be even earlier for 75% of species by the year 2080.

We analysed 92,828 records gathered from throughout the United Kingdom between 1939 and 1995 by the British Trust for Ornithology's Nest Record Scheme (see Supplementary Information). Annual median laying dates for 36 species, for which we had at least 1,000 records each, were used to measure shifts in the timing of whole nesting seasons. In most cases, the upper and lower tails of the distributions shifted in parallel to the medians, but the latter were less subject to random variation when annual samples were relatively small. Of these 36 species, 19 (53%) exhibited significant long-term trends, most of which were curvilinear, with laying dates becoming later in the 1960s and 1970s, and then earlier through the 1980s and 1990s (Fig. 1). Trends towards earlier laying in recent years are due to increased numbers of early nests and were never due solely to fewer records of late nests.

This data set does not allow us to distinguish first clutches from subsequent ones, or from re-nests after failure, and species might extend their nesting seasons as a consequence of earlier nesting opportunities. Although this study is therefore statistically conservative, and so might underestimate trends towards earliness (and the effect of weather on laying dates), only the robin *Erithacus rubecula* (which has several broods a year) showed evidence of significant increases in the incidence of early and late nests, using a measure of the width of the two tails of the distribution.

We investigated relationships of median laying date with temperature and rainfall using the Central England Temperature (CET)⁵ and the England and Wales Precipitation (EWP)⁶ records, which are broadly representative of UK weather⁷. We used forward stepwise regression to identify the mean monthly temperature and precipitation variables that accounted for variation in median laying date, weighted by sample size. Weather variables were entered only for months in which laying had been recorded and for the previous month. Significant CET or EWP effects were found for 31 species (86% of the total); the five species without effects were among those with relatively small average annual sample sizes, which may have limited the statistical power. Given the number of associations between month and weather that were tested for significance, some results might be due to chance effects, although more than half the species exhibited weather relationships at $P < 0.001$ and only six species were solely

dependent upon effects at $P > 0.01$ (see Supplementary Information).

Of 19 species with long-term trends in laying date, 17 species (89%) exhibited significant weather effects (Fig. 1). The key weather variables were the temperatures in March and April, which show a strong curvilinear trend since the 1940s, having cooled in the 1960s and 1970s (Fig. 1). When trend variables (year, year² or year³, as appropriate) were included in the weather models for 7 (41%) of these 17 species, trend variables were no longer significant. Thus, variation in CET and EWP was sufficient to account for these long-term trends, describing, on average, 29% more of the variation in laying date than the trend models alone. These seven species (winter wren, *Troglodytes troglodytes*; dun-nock, *Prunella modularis*; blackcap, *Sylvia atricapilla*; willow warbler, *Phylloscopus trochilus*; spotted flycatcher, *Muscicapa striata*; long-tailed tit, *Aegithalos caudatus*; and greenfinch, *Carduelis chloris*) are all widespread in Britain, and it is likely that their records provide the best match with the weather data. For a further ten species, trend variables had additional effects to weather variables, accounting for, on average, 16% more than the weather models alone.

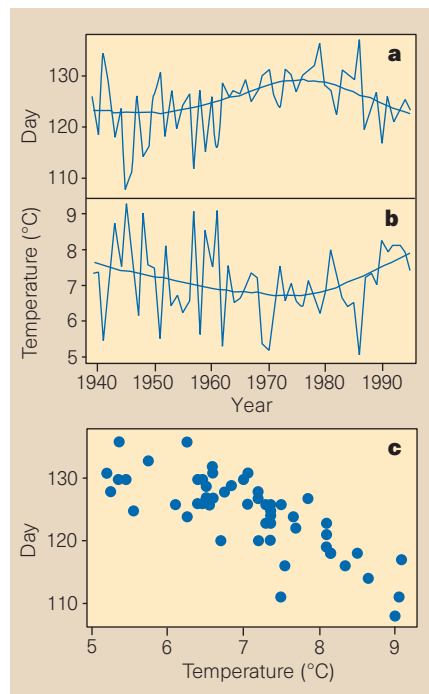


Figure 1 Weather and laying dates of the chaffinch, *Fringilla coelebs*. **a**, Temporal changes in annual median laying date. **b**, Temporal changes in the mean of March and April monthly mean Central England Temperatures (CETs). **c**, Relation between annual median laying date and mean of March and April CETs ($r = -0.76$, $P < 0.001$). Laying date is numbered such that day 110 is 20 April and day 121 is 1 May. The smoothed lines are calculated using a LOWESS (locally weighted scatterplot smoother) method.

These residual trends (and those of the two species without any CET or EWP effects) could be due to the choice of weather variables (for example, the temperature of the soil, rather than the air, might have been more appropriate for some species), or because birds may respond to environmental factors (such as food supply) for which CET and EWP are to some extent surrogates; in addition, the residual trends may be unrelated to climate (for example, large-scale changes in land use might have affected some farmland birds, and magpies may nest earlier because of their rapid expansion into urban areas).

There appear to be no obvious taxonomic, ecological or life-history correlates of the species that are more or less affected by weather. Within each of the groups identified in the Supplementary Information there are, allowing for the size of the groups, mixtures of both residents and migrants, insectivores and granivores, and single- and multibrooded species. The only possible correlate might be body size, as the small number of larger-bodied species (corvids and water birds) appear to show little response to temperature.

We have used the 'medium-high' UKCIP98 climate scenario⁴ for Britain to predict how laying dates for each species may change by 2080, based on the (linear) coefficients of temperature and precipitation. For the 27 species that are predicted to lay earlier, the average advancement is 8 days, ranging up to 18 days (see Supplementary Information). The significance of these findings for nesting success and the subsequent survival of young needs now to be investigated, especially with respect to the possibility of mistimed reproduction in relation to food supplies^{2,8}.

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