Figure 4 Changes in decadal mean sea surface temperature (°C). **a**, Difference between 2PC run 1929–39 and control 1859–69; **b**, difference between GHG run 2089–99 and control 1859–69. In **a** are also shown the approximate paths of the sections used in Fig. 1 (the GIS ridge (MN), Cape Farewell (PQ), 24° N (XY)) and Fig. 3 (ABCD).

for the response of the ocean thermohaline circulation to CO_2 forcing. If this pattern is robust, a monitoring system based on repeated hydrographic sections in the Labrador Sea and at 24° N, and current-meter measurements of the GIS overflows and the Cape Farewell boundary current, could provide a means of detection of changes in thermohaline circulation resulting from increased greenhouse-gas forcing. Much of this would build on the existing historical database[11,21,22,29,30]. The extent to which such a signal could be detected at present depends on the natural variability in these elements of the circulation, which has not yet been fully quantified from observations. □

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Feature-based attention influences motion processing gain in macaque visual cortex

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Changes in neural responses based on spatial attention have been demonstrated in many areas of visual cortex[1–4], indicating that the neural correlate of attention is an enhanced response to stimuli at an attended location and reduced responses to stimuli elsewhere. Here we demonstrate non-spatial, feature-based attentional modulation of visual motion processing, and show that attention increases the gain of direction-selective neurons in visual cortical area MT without narrowing the direction-tuning curves. These findings place important constraints on the neural mechanisms of attention and we propose to unify the effects of spatial location, direction of motion and other features of the attended stimuli in a 'feature similarity gain model' of attention.

We studied the influence of attention on the sensory selectivity of neurons in visual cortex, namely direction-selective neurons in the middle temporal visual area (MT), which is important in the perception of visual motion and for motor planning[5,6]. MT neurons have been linked directly to psychophysical performance in motion tasks[7] and they characteristically show direction tuning curves (bell-shaped response profiles as a function of stimulus direction; Fig. 1b), which account well for psychophysical thresholds of motion perception[8].

We recorded from neurons in area MT of two macaque monkeys while using displays of coherently moving random dot patterns (RDP) to determine what effect attention might have on these direction tuning curves. Attention might enhance the sensory gain of the neuron, that is, increase the response to all attended stimuli by the same proportion ('multiplicative modulation'), leaving the

width of the tuning curve unchanged[9]. Alternatively, attention might increase the response of a neuron only for stimuli moving in the preferred direction, thus increasing the sharpness of the neuron's tuning curve ('sharpening modulation')[10].

Experiment 1 was designed to isolate the influence of spatial attention on tuning curves. One RDP was placed inside the receptive field of the neuron being recorded and the other one, moving in the same direction, was placed in the opposite visual hemifield (Fig. 1a). On a given trial, using a spatial cue, the animal's attention was directed to either one or the other stimulus, the 'target'. In both the 'attend-in' and the 'attend-out' conditions, we derived the neuron's tuning curve by randomly interleaving trials with one of 12 possible directions of movement (Fig. 1b).

Figure 1c shows a histogram of the changes in the height and width of the tuning curve between these two attentional conditions across all the cells we studied. On average, the height of the tuning curves was about 10% larger when the target was the stimulus inside the receptive field, but the tuning curves were not sharpened; instead, there was a slight, non-significant widening. The increase in the height of the tuning curve in the absence of narrowing indicates that attention has the same effect on all stimuli, that is it increases the responses by multiplicative modulation. This modulation reflects a purely spatial attentional mechanism, because the pairs of conditions compared in Fig. 1 differed only in the attended location, with the attended direction remaining the same.

Psychophysical studies suggest that attention can also be selectively allocated to stimuli that match a particular feature, without shifts in the attended location (see for example refs 11–13). To test for such effects of non-spatial, feature-based attention, we intro-duced a variation into Experiment 1 (Fig. 2a). While the stimulus inside the receptive field now always moved in a given neuron's preferred direction, the other stimulus moved in either the same (as in the previous experiment, Fig. 2a, arrow B) or the opposite direction (Fig. 2a, arrow A). This allowed the attended direction to be switched without changing the attended location and without changing the stimulus inside the receptive field. We compared the responses when attention was directed to the stimulus outside the receptive field, moving either in the preferred or anti-preferred direction. Changing the stimulus direction outside the receptive field had no effect on the responses when that stimulus was behaviourally irrelevant, that is when the animal was attending inside the receptive field or simply fixating.

Figure 2b shows a histogram of the resulting attentional modulation across all neurons studied. Attending to the preferred motion outside the receptive field increased the response by, on average, about 13% above the response evoked when attending a null-direction stimulus outside the receptive field. This is not an effect of spatial attention, as the location of attention was unchanged between the two conditions. Rather, it represents a neural correlate of attention to stimulus feature. Comparing the responses against those evoked in trials in which none of the moving stimuli was behaviourally significant shows that this non-spatial attentional modulation is a combination of enhancement (preferred direction target, mean enhancement of ~5%) and suppression (anti-pre-ferred direction target, mean suppression of ~6%). Thus, attending to a given direction enhances the responses of neurons whose preferred direction aligns with the attended direction and reduces the responses of those neurons preferring the opposite direction.
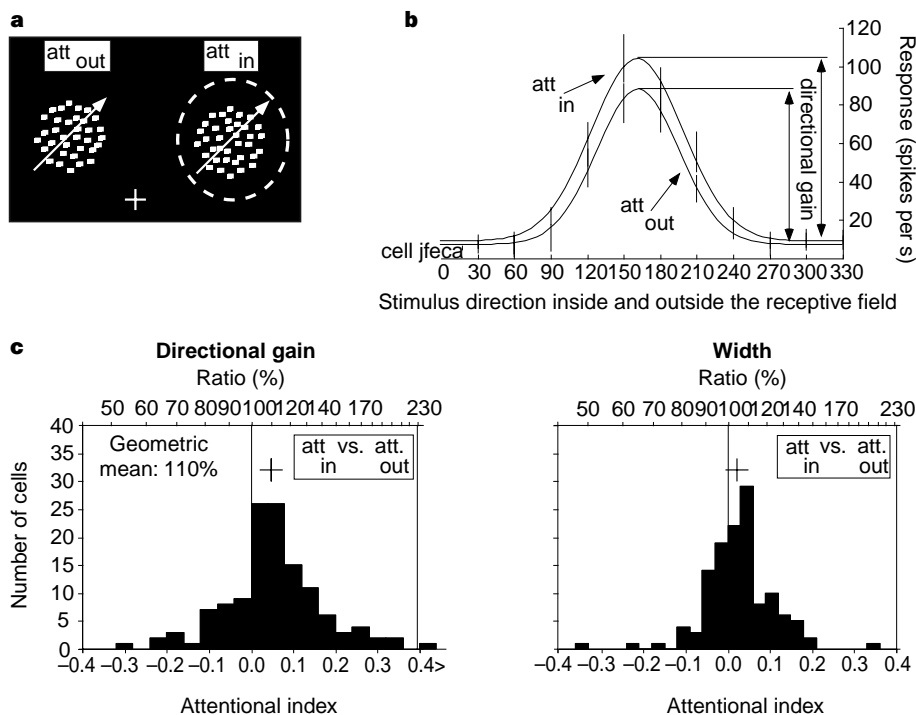
Figure 1 Experiment 1: Effect of directing attention inside versus outside the receptive field on the directional tuning curve. **a**, Sketch of the stimulus layout on the screen. One random dot pattern (RDP) was presented inside the classical receptive field (dashed circle) while the other was presented about the same distance from the fixation point in the opposite hemifield. In a given trial, both RDPs moved in the same of 12 possible directions. **b**, Examples of tuning curves. The upper curve shows the response when the monkey was attending to the stimulus inside the receptive field (marked att$_{in}$ in **a**), and the lower curve plots the responses when the monkey was attending to the stimulus outside the receptive field (marked att$_{out}$). These tuning curves show an increase in directional gain and width when attention is switched from outside to inside the receptive field.

c, Histograms showing the influence of attention on the directional gain and width of the tuning curves for 131 cells. Binning is according to the attentional index $AI = (X_{in} - X_{out})/(X_{in} + X_{out})$, where X is the gain or width in the corresponding attentional condition. The top scale shows the corresponding ratios. The left histogram shows a shift to the right, with an average AI of 0.05 (marked by the cross, where the horizontal arms span the 95% confidence interval of the mean), indicating that attention increases the height of the tuning curves on average (geometric mean) by about 10%. The right histogram shows no shift to the left, demonstrating that attention does not sharpen the tuning curves. Rather we find a small, non-significant increase in the width of the tuning curves (average increase: 4%, $P > 0.05$ in paired t-test).

This influence is far reaching; our stimuli were as much as 20° apart and in opposite visual hemifields.

Having demonstrated attentional modulation of about equal size with shifts in the spatial location of attention and with feature-based effects in the absence of a shift of the attended location we plot the combined effect of the two modulations. Figure 2c compares responses when the animal was attending the anti-preferred stimulus outside the receptive field with those trials when attention was directed into the receptive field to the stimulus moving in the preferred direction (Fig. 2a, arrows A and C). The attentional modulation (25% on average) is the sum of the shifts shown in Figs 1c and 2b, emphasizing that feature-based attentional effects can be additively combined with modulations based on the spatial location of attention. Comparing the two attentional conditions against responses when neither of the stimuli was behaviourally significant shows that the attentional modulation is a combination of the suppressive effect of switching attention to the null direction outside the receptive field (~6% suppression) and the enhancing effect of directing attention into the receptive field onto the preferred direction (~15% enhancement).

Previous studies demonstrated a strong response modulation when attention was switched between stimuli that were both inside the receptive field[1–4]. In our third experiment we tested whether the absence of attentional sharpening of the tuning curves persists under these circumstances by placing two stimuli side-by-side inside the receptive field. Pattern A always moved in the anti-preferred direction of the cell. To generate a tuning curve, pattern B moved in one of twelve directions of motion. Again, in a given trial, either one of the patterns was designated as the target. By plotting the response of the neuron as a function of the direction of motion of pattern B, a tuning curve could be determined for each of the two attentional conditions. Figure 3 shows an example of these tuning curves for one cell together with the 'sensory' tuning curve, recorded when neither of the two patterns inside the receptive field was behaviourally relevant.

The lower panels of Fig. 3 show histograms of the attentional modulation of the directional gain and tuning width. As in Experiment 1, attention increases the directional gain of the neuron, although now with a mean effect of about 60%. Even with these very strong response modulations, no sharpening of the tuning was observed.

Our results demonstrate a physiological correlate of non-spatial, feature-based attention by showing response modulations in the absence of spatial shifts of attention. We further show that spatial and feature-based attention represent summable processes that have a multiplicative effect on the responses of neurons. Such attentional modulations resemble changes to a neuron's sensory gain and thus can be mimicked by sensory effects, such as reducing the luminance contrast of a stimulus, which similarly does not change the tuning width of direction-selective neurons[14,15], suggesting that response modulation based on attentional and sensory aspects employ common mechanisms.

Non-spatial, feature-based modulation of sensory responses has been observed in imaging studies[16,17] and using psychophysical paradigms[12–14]. However, previous studies did not show an unambiguous single-cell correlate of this effect, because they investigated attentional selection based on stimulus features, leaving open the possibility that the modulation itself is based on stimulus location[18,19], or confounded a change in the attended feature with a simultaneous change in attended location[9].

Although the absence of a sharpening of the tuning curves is in contrast to one report from areas in the ventral visual pathway[10], it closely matches another[9], indicating that attention may work in similar ways in the dorsal and ventral visual pathways. A recent study attempting to model psychophysical orientation discrimination performance in dual-task attentional paradigms has indicated that the observed performance can only be accounted for by models that implement sharpening of tuning curves with attention[20]. As we have found no indication for such sharpening, further studies will be necessary to understand the reasons for this discrepancy. The
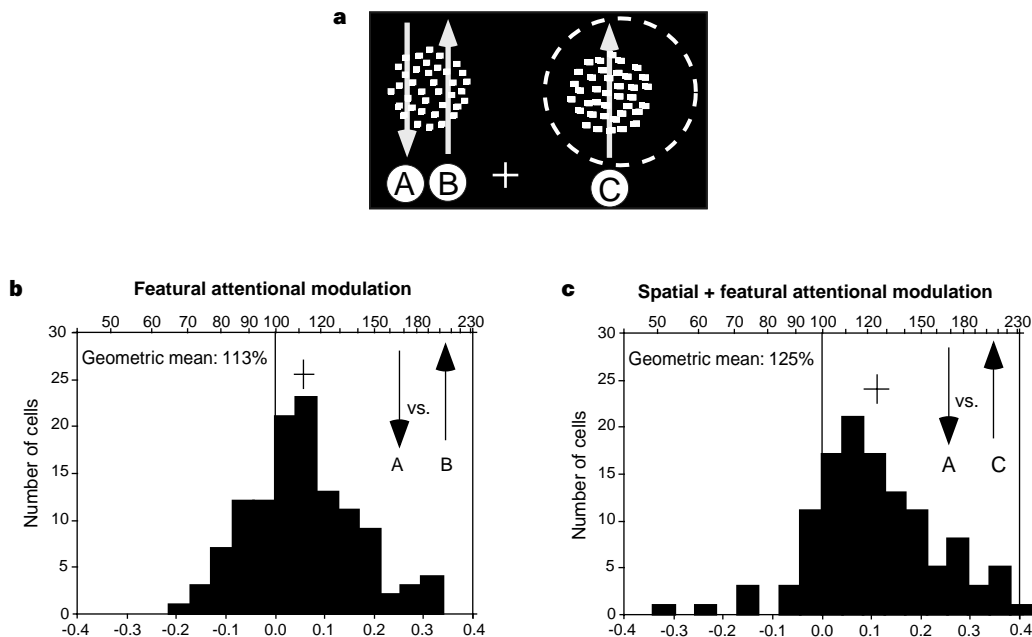
Figure 2 Experiment 2: Non-spatial effects of attention and the summing of spatial and featural attentional modulation. **a**, Stimulus conditions used. The stimulus inside the receptive field always moved in the cell's preferred direction (upward pointing arrow); the stimulus outside moved in either the same (B) or the opposite direction (A). Trials in which the animal was instructed to attend to A, B and C were presented in an interleaved fashion. **b**, Histogram comparing responses of 131 cells when attention was on the preferred (B) or anti-preferred (A) direction outside the receptive field. The histogram is shifted to the right (mean shift 13%) indicating an increased response when the stimulus moved in the cell's preferred direction. **c**, Histogram comparing responses when attention was on anti-preferred motion outside (A) or the stimulus inside the receptive field (C). The histogram is shifted to the right, indicating an increased response when the target was inside the receptive field.
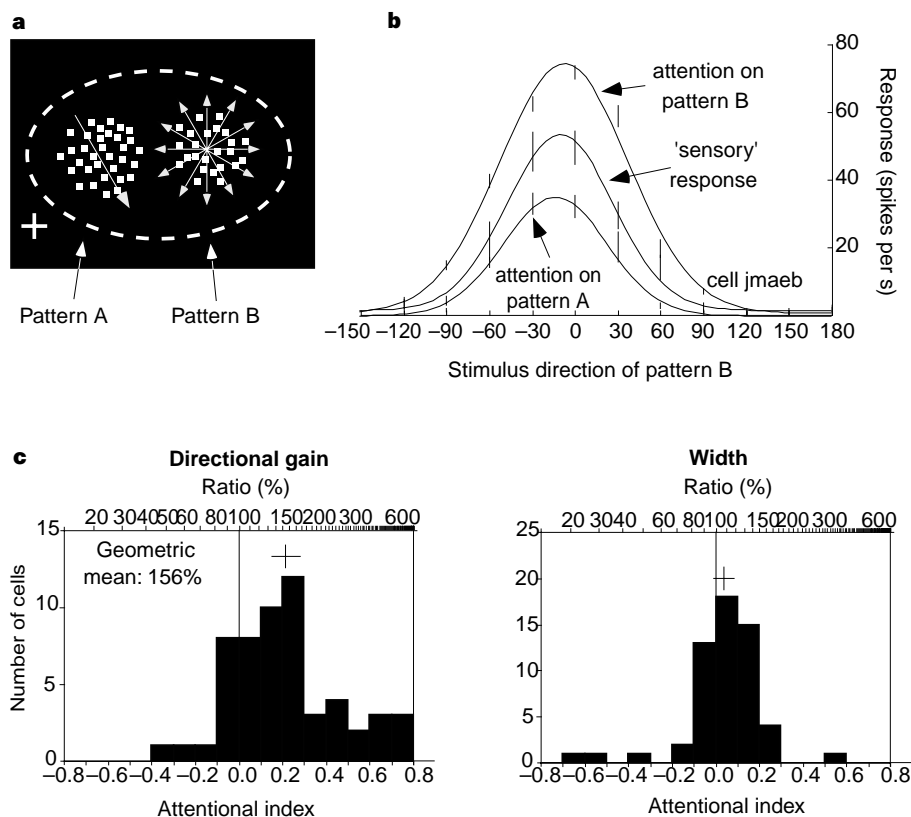
Figure 3 Experiment 3: Effect of directing attention to one of two stimuli inside the receptive field. **a**, Stimulus configurations. Both patterns were presented inside the receptive field. Pattern A always moved in the cell's anti-preferred direction, pattern B in one of 12 possible directions. **b**, Tuning curves when pattern B was the target (upper curve), when pattern A was the target (lower curve) and when neither pattern was behaviourally relevant (central curve) because the animal was instructed to respond to a luminance change at the fixation point. **c**,

Histograms of the attentional modulation of the tuning curve across 56 cells. The mean increase in directional gain is about 60% (which is a combination of response enhancement when switching attention from the 'sensory' condition to pattern B and of suppression when switching to pattern A). Again there is no narrowing of the tuning width. On average, width is increased by 8% (non-significant, $P > 0.1$).

attentional enhancement we observe does support better stimulus discriminability even without tuning sharpening, by increasing the slope of the tuning curve[21,22].

A 'biased competition model' has been proposed[23], which supposes that attention influences the competition between two stimuli for access to a given cell in favour of the attended stimulus. This is achieved by increasing the strength of the signal coming from the population of input cells activated by the attended stimulus[24]. The attentional modulation we observed when attention was switched between two stimuli inside the receptive field (Experiment 3) conforms to the predictions of this model. Given the model's emphasis on competition within the receptive field, our findings in Experiment 2 (attentional effects outside the receptive field and the additivity of spatial and non-spatial effects when attention is switched into the receptive field) do not seem to be predicted by the model. We propose that spatial and non-spatial attentional effects can be unified in a 'feature similarity gain model', in which the up- or downregulation of the gain of a sensory neuron reflects the similarity of the features of the currently behaviourally relevant target and the sensory selectivity of the neuron along all target dimensions. Thus this up- or downregulation will also affect neurons whose receptive fields do not include the attended stimulus location. The relevant target features include the spatial location, direction of motion and presumably others. Correspondingly, the sensory selectivity of the neuron includes the location of its receptive field (or of the smaller receptive fields of its input neurons), its preferred direction of motion and presumably other preferred features. This model not only provides a good account of

other physiological studies of attention that included conditions without competing stimuli inside the receptive field[2,9], but also incorporates the idea, from psychophysical and imaging studies as well as other modelling attempts, that non-spatial stimulus features can be the basis of attentional effects. □

Methods

Cells and recording. Our recording methods have been described elsewhere[3,25]. All animal procedures complied with the NIH Guide for Care and Use of Laboratory Animals and were approved by the local animal care committee. Cells were determined to be from MT by their physiological characteristics (directionality and receptive field position and size) as well as by the position of the electrode in the cortex. We also recorded from MST cells, finding similar but larger attentional modulations to those reported here.

Stimuli. Random dot patterns were created by plotting bright dots at a density of 5 dots per deg square within a circular stationary virtual aperture on a dark computer monitor. Dots moved coherently at the preferred speed of the neurons and were re-plotted to the opposite side when they crossed the border of the aperture. The size of the aperture was chosen so that the stimulus did not exceed the boundaries of the classical receptive field.

Trials. Every trial started with the appearance of the fixation cross. After it was foveated, a stationary RDP (the cue) signalled the location of the 'target'. The monkey then depressed a lever. 200–300 ms later the cue disappeared (Experiments 1 and 2) or moved for 400 ms (Experiment 3). After a blank interval of 65 ms (Experiments 1 and 2) or 270 ms (Experiment 3) two moving RDPs appeared, one (the 'target') at the location of the cue and one (the 'distractor') at another location. The monkey's task was to release the level when the target changed speed or direction (which occurred at a random point

between 270 and 4,000 ms after target onset) and to ignore changes in the distractor. Failure to respond within a reaction-time window, responding to a change in the distractor or deviating the gaze (monitored with a scleral search coil) by more than 1° from the fixation point caused the trial to be aborted without reward. The change in the target and distractors was selected so as to be challenging for the animal. In experiments 1 and 2 the animal correctly completed, on average, 79% of the trials, broke fixation in 11%, might have responded to the distractor stimulus in 6% and responded too early or not at all in 5% of the trials. In Experiment 3 the corresponding values are 78, 13%, 8% and 2%. In none of the three experiments was there a difference between the performances for the two possible targets. Differences between average eye positions during trials where one or the other stimulus was the target were very small, with only an average shift of 0.02° in the direction of the shift of position between the stimuli. Only correctly completed trials were considered. Firing rates were determined by computing the average neuronal response across trials for 1,000 ms starting 200 ms after the beginning of the target stimulus movement.

Tuning curves. Tuning curves were derived by fitting the responses to the 12 directions presented with gaussian functions: $r_{null} + dirGain \times \exp^{(-0.5*(dir - prefdir)^2/width^2)}$. The four parameters of a gaussian curve capture the four features of a direction-selective cell: preferred direction ($prefdir$), response to the anti-preferred direction (r_{null}), the directional gain ($dirGain$; the maximal response modulation) and the selectivity or tuning width ($width$; the range of directions the neuron responds to).

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Poleward shifts in geographical ranges of butterfly species associated with regional warming

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Mean global temperatures have risen this century, and further warming is predicted to continue for the next 50–100 years[1–3]. Some migratory species can respond rapidly to yearly climate variation by altering the timing or destination of migration[4], but most wildlife is sedentary and so is incapable of such a rapid response. For these species, responses to the warming trend should be slower, reflected in poleward shifts of the range. Such changes in distribution would occur at the level of the population, stemming not from changes in the pattern of individuals' movements, but from changes in the ratios of extinctions to colonizations at the northern and southern boundaries of the range. A northward range shift therefore occurs when there is net extinction at the southern boundary or net colonization at the northern boundary. However, previous evidence has been limited to a single species[5] or to only a portion of the species' range[6,7]. Here we provide the first large-scale evidence of poleward shifts in entire species' ranges. In a sample of 35 non-migratory European butterflies, 63% have ranges that have shifted to the north by 35–240 km during this century, and only 3% have shifted to the south.

We analysed distributional changes broadly spread over the past century for non-migratory species of butterfly whose northern boundaries were in northern Europe and whose southern boundaries were in southern Europe or northern Africa. We excluded some data where circumstances suggested that range boundaries were controlled or altered by non-climatic factors. This yielded a subset of sufficient quality for us to detect distributional changes predicted by models of global warming, yet is unbiased with respect to such changes. However, because data for some species were excluded at either their northern or southern boundaries, we

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