of likely driving inputs: from layer 3 of a lower area, relaying directly to layer 4, and from layer 5 of the same lower area relaying, via the thalamus, mainly to layer 3.

It is normally assumed that the hierarchical development of sensory representations is primarily constructed by the direct, ascending cortical pathways that represent a wider range of features at a higher level of precision. The second-order thalamic input should therefore adopt a different kind of role, and one reasonable inference is that it plays a part in spatial selective attention. Again, using the visual system for illustration, there is a well-documented anatomical and psychophysical overlap between the control of eye-movements and the deployment of covert attention, a consideration which helps to make sense of the fact that the layer 5 outputs to the pulvinar originate from neurons also communicating with the superior colliculus. Hence, assuming that the layer 5 outputs carry an object-selective signal, they could act via the pulvinar to exert a regulatory influence over the transcortical networks formed by the information-rich, superficial layers - specifically, perhaps, to propagate object-selective bias between the different kinds of object descriptions found in different visual areas.

The subsequent reciprocal interaction between layer 6 and the pulvinar could be more analogous to the corticogeniculate system, at least insofar as many layer 6 neurons have apical dendrites and axonal collaterals arborising within the pulvinar terminal zone (layer 3, as opposed to layer 4). The neural dynamics of the interaction are certainly unknown but, commensurate with an attentional process, it is at least worth noting that the topography of cortico-pulvinar relationships is considerably less precise than that of corticogeniculate relationships, permitting neural competition to develop over broader stretches of cortical maps, and hence between objects at separate, distinct spatial locations.

Epilogue

The complexities of cortical circuitry are nothing short of fiendish, and

the problem of integrating genetic, morphological and physiological details from diverse cortical areas and across diverse species is a worthy challenge to the burgeoning science of neuroinformatics. Though inconsistencies abound, the fact that some trans-areal, trans-specific generalisations are possible, and justified, is a quite remarkable observation. Following the strategy of 'know thine enemy', it appears that the cortical fiend has some interesting habits, which we can usefully begin to tag with some shorthand, functional labels.

Further reading

- Anderson, J.C., and Martin, K.A.C. (2006). Synaptic connection from cortical area V4 to V2 in macaque monkey. J. Comp. Neurol. 495, 709–721.
- Barone, P., Batardiere, A., Knoblauch, K., and Kennedy, H. (2000). Laminar distribution of neurons in extrastriate areas projecting to visual areas V1 and V4 correlates with the hierarchical rank and indicates the operation of a distance rule. J. Neurosci. 20, 3263–32681.
- Douglas, R.J., and Martin, K.A. (2004). Neuronal circuits of the neocortex. Annu. Rev. Neurosci. 27, 419–451.
- Guillery, R.W., and Sherman, S.M. (2002). Thalamic relay functions and their role in corticocortical communication: generalizations from the visual system. Neuron 33, 163–175.
- Lund, J.S., Hendrickson, A.E., Ogren, M.P., and Tobin, E.A. (1981). Anatomical organization of primate visual cortex area VII. J. Comp. Neurol. 202, 19–45.
- Miller, R. (2002). Wheels within wheels: circuits for integration of neural assemblies on small and large scales. In Cortical Areas: Unity and Diversity, R. Miller and A. Schüz eds. (London: Taylor and Francis), pp. 423–458.
- Rockland, K.S. (1997). Elements of cortical architecture: hierarchy revisited. In Cerebral Cortex, Vol. 12, Extrastriate Cortex in Primates, K.S. Rockland, J.H. Kaas, and A. Peters eds. (New York: Plenum Press), pp. 1243–1293.
- Shipp, S. (2003). The functional logic of cortico-pulvinar connections. Phil. Trans. R. Soc. Lond. B 358, 1605–1624.
- Shipp, S. (2005). The importance of being agranular: a comparative account of visual and motor cortex. Phil. Trans. R. Soc. Lond. B 360, 797–814.
- Sillito, A.M., Cudeiro, J., and Jones, H.E. (2006). Always returning: feedback and sensory processing in visual cortex and thalamus. Trends Neurosci. 29, 307–316.
- Thomson, A.M., and Bannister, A.P. (2003). Interlaminar connections in the neocortex. Cereb. Cortex *13*, 5–14.
- West, D.C., Mercer, A., Kirchhecker, S., Morris, O.T., and Thomson, A.M. (2006). Layer 6 cortico-thalamic pyramidal cells preferentially innervate interneurons and generate facilitating EPSPs. Cereb. Cortex 16, 200–211.
- Yoshimura, Y., Dantzker, J. L. M., and Callaway, E. M. (2005). Excitatory cortical neurons form fine-scale functional networks. Nature 433, 868–873.

Department of Anatomy and Institute of Ophthalmology, University College London, Bath Street, London EC1V 9EL, UK. E-mail: s.shipp@ucl.ac.uk

Correspondences

Rapid advancement of spring in the High Arctic

Toke T. Høye^{1,2}, Eric Post³, Hans Meltofte¹, Niels M. Schmidt^{1,4} and Mads C. Forchhammer^{1,4}

Despite uncertainties in the magnitude of expected global warming over the next century, one consistent feature of extant and projected changes is that Arctic environments are and will be exposed to the greatest warming [1]. Concomitant with such large abiotic changes, biological responses to warming at high northern latitudes are also expected to outpace those at lower latitudes. One of the clearest and most rapid signals of biological response to rising temperatures across an array of biomes has been shifts in species phenology [2-4], yet to date evidence for phenological responses to climate change has been presented from most biomes except the High Arctic [3]. Given the well-established consequences for population dynamics of shifts in the timing of life history events [5,6], it is essential that the High Arctic be represented in assessments of phenological response to climate change. Using the most comprehensive data set available from this region, we document extremely rapid climate-induced advancement of flowering, emergence and egg-laying in a wide array of species in a high-arctic ecosystem. The strong responses and the large variability within species and taxa illustrate how easily biological interactions may be disrupted by abiotic forcing, and how dramatic responses to climatic changes can be for arctic ecosystems.

Most long-term records of phenological events are from north-temperate environments. Recent comprehensive studies from this region have reported





Figure 1. Advancement of phenological events in higharctic Greenland.

(A) The location of the study area, Zackenberg, Northeast Greenland. Image courtesy of The Living Earth, http://www.livingearth.com. (B) Temporal change in onset of flowering (plants), median date of emergence (arthropods) and clutch initiation dates (birds) estimated from weekly sampling in permanents plots (plants and arthropods) and neardaily surveys through the breeding period in a 19 km² census area (birds) during 1996-2005. Trends based on five to seven years of observations (small dots) and eight to ten years of observations (large dots) are red when statistically significant and otherwise blue. Trends in arthropod taxa marked by asterisks are likely to be biased.

advancements of 2.5 days per decade for European plants [7] and 5.1 days per decade across animals and plants globally [8]. In the Arctic, however, temperatures are currently increasing at nearly double the global average [1], and parts of the Arctic will experience even more dramatic climatic changes due to reductions in the extent of sea ice [9]. A long-standing prediction has thus been that the most rapid and dramatic biological responses to climatic changes would be found in the Arctic, where biological feedbacks are expected to further exacerbate abiotic changes [10]. Estimates of just how rapid and strong biological responses to climatic change might be in the Arctic have been hampered, however, by lack of temporally coherent, long-term data. Here we present long-term (1996-2005) phenological data, the results of concerted efforts to monitor biological changes across trophic

levels in a pristine ecosystem in high-arctic Greenland (Figure 1A; and see the Supplemental data available on-line).

Flowering dates in six plant species, median emergence dates of twelve taxa of arthropods, and clutch initiation dates in three species of birds have advanced, in some cases by over 30 days during the last decade (Figure 1B). Despite the relatively short time-series, more than 40% of the observed phenological advancements were significant at the 5% level. Corroborating jackknife procedures revealed that omitting the year to which the temporal trends (days of advancement per decade) were most sensitive (1996) resulted in even stronger trends in more than 90% of the time series analysed. The average advancement across all time series was 14.5 days per decade (see Supplemental data). Differences in species studied, the time periods covered and the spatial scale of observations

make accurate comparisons to trends reported from lower latitudes difficult. Nevertheless. the surprisingly large and rapid phenological advancements across taxa reported here from the High Arctic do suggest that responses are particularly dramatic in this region.

Whereas phenological responses at lower latitudes are primarily related to temperature, organisms in snow-dominated environments such as the Arctic are more influenced by snow cover. At Zackenberg, the inter-annual variation in phenology was positively related to timing of snowmelt in all time series where data on date of snowmelt were available (39 of 66 significant). Our spatially replicated sampling of plants and arthropods revealed considerable variation among sampling areas within a single ecosystem; moreover, the magnitude of the temporal trend in advancement was negatively related to the average date of snowmelt (plants: slope = -0.46, r = 0.62, P = 0.0023; arthropods: slope = -0.39, r = 0.23, P = 0.15; arthropods where trends based on less than eight years of observations were omitted: slope = -0.97, r = 0.53, P = 0.0034). During the last ten years, the date of snowmelt has advanced by on average 14.6 days (S.E. = 1.013) in the permanent sampling plots.

The extreme advancement of spring events across taxa documented here is unlikely to be sustained over multiple decades because of the limitations in phenotypic and genotypic plasticity. Nevertheless, the observed significant trends in time series were consistently negative and closely coupled to timing of snowmelt across a wide range of species. This clearly indicates that organisms in the High Arctic respond strongly and rapidly to climatic changes. Indeed, such dramatic phenological changes may weaken or even disrupt trophic interactions among species that are crucial to successful reproduction in this highly seasonal environment.

Supplemental data

Supplemental data, including experimental procedures are available at http://www.current-biology.com/cgi/ content/full/17/12/R449/DC1

Acknowledgements

We thank the Danish Environmental Protection Agency for supporting the monitoring programmes at Zackenberg Research Station, the Danish Agency for Science, Technology and Innovation for funding to MCF and NMS and numerous people for field assistance.

References

- Kattsov, V.M., Källén, E., Cattle, H., Christensen, J., Drange, H., Hanssen-Bauer, I., Jóhannesen, T., Karol, I., Räisänen, J., Svensson, G. *et al.* (2005). Future climate change: modeling and scenarios for the Arctic. In Arctic Climate Impact Assessment, (Cambridge: Cambridge University Press), pp. 99–150.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., and Bairlein, F. (2002). Ecological responses to recent climate change. Nature 416, 389–395.
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. S. 37, 637–669.
- Forchhammer, M.C., Post, E., and Stenseth, N.C. (1998). Breeding phenology and climate. Nature 391, 30–31.
- Both, C., Bouwhuis, S., Lessells, C.M., and Visser, M.E. (2006). Climate change and population declines in a long-distance migratory bird. Nature 441, 81–83.
- Beckerman, A., Benton, T.G., Ranta, E., Kaitala, V., and Lundberg, P. (2002). Population dynamic consequences of delayed life-history effects. Trends Ecol. Evol. 17, 263–269.
- Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A. et al. (2006). European phenological response to climate change matches the warming pattern. Glob. Change Biol. 12, 1969–1976.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. Nature 421, 57–60.
- Holland, M.M., Bitz, C.M., and Tremblay, B. (2006). Future abrupt reductions in the summer Arctic sea ice. Geophys. Res. Lett. 33, L23503.
- Chapin, F.S., III, Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P. et al. (2005). Role of land-surface changes in arctic summer warming. Science 310, 657–660.

¹Department of Arctic Environment, National Environmental Research Institute, University of Aarhus, Frederiksborgvej 399, DK-4000 Roskilde, Denmark. ²Department of Population Biology, Institute of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. ³Department of Biology, Pennsylvania State University, 208 Mueller Lab, University Park, Pennsylvania 16802, USA. ⁴Centre for Integrated Population Ecology, www.cipe.dk. E-mail: toh@dmu.dk

Can autistic children predict behavior by social stereotypes?

Lawrence Hirschfeld¹, Elizabeth Bartmess², Sarah White³ and Uta Frith³

Explaining and predicting behavior involves understanding others in terms of their mental states - the so-called Theory of Mind (ToM). It also involves the capacity to understand others in terms of culturally transmitted information about group membership, for example, which social groups exist in one's culture and which stereotypes adhere to these groups. This capacity typically emerges between 3 and 5 years of age, just like ToM understanding [1,2]. Are the cognitive capacities underlying ToM and stereotypes the same or do they provide independent means of understanding and predicting the actions of others? Children with autism have a profound inability to engage in everyday social interaction, as well as impairments in verbal and nonverbal communication, which have been attributed to a severe delay in ToM development [3,4]. If the use of stereotypes and mental

states were part and parcel of the same underlying cognitive process [5], then autistic children should have similar difficulties with both. We report here that 8-year-old autistic children with a mental age of 7, who fail ToM tasks, nevertheless know and use gender and race stereotypes just like normal children. This provides a powerful argument for the assumption of distinct processes in social reasoning [6] (see Supplemental data).

We assessed race and gender stereotype knowledge with the Preschool Racial Attitudes Measure (PRAM II) [7], which presents scenarios with outline drawings using a forced-choice format as shown in Figure 1. We also assessed the propensity to avoid the use of stereotypes in predicting a protagonist's behaviour by devising a novel Conflict task. Here, the child was presented with vignettes where one prediction could be made from an individual's current mental state or habitual preference, while a different prediction could be made from his or her social category membership. The mental state used was desire expressed as 'likes to', as it is virtually the first mental state that children understand [2]. We confirmed in a simple screening test that even our youngest and least able participants were able to grasp



PRAM – race trial 'Here are two girls. One of them is a friendly girl. She has lots of friends. Which one is the friendly girl?'

Conflict task – race trial 'Here are two women. This is Georgina (left) and this is Chloe. Georgina likes to help people. One of these women walked an old lady across the road. Which woman was it?'

PRAM – gender trial 'Here are two children. One of them has four dolls. Which one has four dolls?'

Conflict task – gender trial 'Here are two people. This is James and this is Grace. Grace doesn't like to cook for people. One of these people has baked biscuits. Which person baked biscuits?'

Current Biology

Figure 1. Examples of race and gender trials for each task.

The child sees a picture — life-like coloured line drawings of people with brown or pink skin — and hears a short vignette. In total, each child completed 24 race and 12 gender trials on the PRAM and 5 race and 5 gender trials on the Conflict task; in the latter task, different predictions can be made on the basis of stereotypes or desires.