

events originating in the retina. Note, this is in contrast to results from somatosensory cortex where the influence of peripheral inputs on cortical patterns decreased with age [6].

Siegel *et al.* [3] end their paper with an interesting discussion of how these two distinct patterns might subserve different activity-dependent functions during development. L-events, driven by propagating retinal waves, may provide an instructive 'training' signal for retinotopic map formation that is amplified by cortical circuits. Support for this hypothesis was recently provided by a study of somatosensory cortex, where spontaneous firing patterns are implicated in the formation of somatotopic connections between the thalamus and the barrels of the somatosensory cortex [16]. In contrast, H-events, with their high synchronicity and larger depolarizations, may drive homeostatic regulation of overall synaptic weights. Here, support comes from growing evidence that patterned activity can influence circuit development in a variety of ways beyond simple Hebbian competition. For example, the temporal patterns of activity in individual neurons can greatly influence early developmental events such as neurotransmitter phenotype or growth cone response to activity molecular cues like those provided by ephrins or N-CAMs [17]. In addition, different activity patterns can influence different aspects of map refinement. For example, in retina, some features of waves drive retinotopic refinement while other features drive eye-specific segregation [18]. As these activity-dependent mechanisms become elucidated, the distinct patterns of activity and their process of generation will take on growing importance.

An unresolved issue of cortical development is whether spontaneous activity plays a role in preparing the cortex for sensory input. This idea has been proposed by a recent study in rodents and preterm infants [19] because, at eye-opening, there is a sudden sparsification of spontaneous firing patterns [7,15], a pattern reflective of adult sensory cortex. By identifying distinct sources of the spontaneous network activity in developing cortex, Siegel *et al.* [3] have enabled the development of experiments that can test these hypotheses directly.

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Face Recognition: Lessons from a Wasp

The golden paper wasp is a social insect whose colony members have the remarkable ability to recognise each others' faces. New research shows that this species is singularly skilled at learning about faces, opening interesting perspectives on convergent evolution of specialist cognitive abilities in insects and vertebrates.

Aurore Avarguès-Weber

Humans have a remarkable capacity to learn and recognise familiar faces. We can view a friend from several years ago in an unfamiliar environment and still instantly identify them. Detailed studies on human face recognition have shown that faces are a special

type of visual pattern for which we have unique expertise [1], underpinned by a specialised region of the brain, the fusiform face area, which shows increased selective activity for face processing [2]. Other mammals, including sheep [3] or macaques [4], have impressive face processing capabilities associated with



Figure 1. Golden paper wasps on their nest. Each wasp *Polistes fuscatus* possesses a distinct face mask, thus allowing individual recognition. New research shows that these wasps have specialised skills at learning to discriminate faces of conspecifics. Such patterns to them have higher salience than the appearance of natural prey types or abstract visual patterns. (Image courtesy of Michael Sheehan.)

specialised brain areas for facilitating reliable recognition.

Needless to say, this conspecific recognition ability is likely to be crucial in all aspects of social organisation, including family and group cohesion, partner choice or pair stability, social hierarchies, networks, and ingroup/outgroup classification. Nevertheless, social organisation in the insect societies, such as wasps and ants, was, until recently, thought to be mediated entirely without individual recognition; their societies, while running like smoothly oiled, highly efficient machines, or superorganisms, were thought to be held together entirely by cues, such as the nest-specific scent, that identified groups rather than individuals. Recent work by Elizabeth Tibbetts and colleagues [5], however, has shown that in a certain species of paper wasp (*Polistes fuscatus*), individuals recognise one another individually (Figure 1). In this species, multiple queens cooperate to found a nest in spring, but the ‘alpha queen’ monopolises the right to lay eggs, and beneath there is a linear hierarchy of individuals that is determined by aggressive interactions. However, individual recognition allows everyone to know their place in the hierarchy, so positions do not need to be reinforced by further duels whenever two individuals meet.

A new study by Sheehan and Tibbetts [6] demonstrates that in this

species, too, the ability to learn and recognise conspecific faces is a highly specialised one, commensurate with its unusual lifestyle. The wasps were placed in a T-maze in which one picture in a pair was associated with a ‘safety zone’ in one arm of the maze, while in the other arm an image was paired with mild electric shock. Tested subjects show superior learning performance for the discrimination of conspecific faces compared to simple geometric patterns or pictures of caterpillars (their typical prey). Further support for the notion that face recognition in this species is indeed a specialised ability comes from the observation that subjects are also better at recognising realistic conspecific faces than scrambled images of such faces or antenna-less faces. This demonstrates that wasps indeed recognise the images as faces, rather than as arbitrary visual stimuli paired with unpleasant experiences.

Interestingly, wasps of a related species (*P. metricus*) did not show a comparable facility to process wasp faces, although they did show similar abilities for the other categories of images. This species difference is in accordance with their respective natural behaviour: unlike *P. fuscatus* queens, *P. metricus* queens nest alone and therefore do not require face recognition abilities. This fascinating new research thus suggests convergent evolution towards specialized face recognition between vertebrates and an invertebrate whose social lifestyle generates a selective pressure for individual face recognition.

Once again, the social insects force us to reconsider a particular cognitive faculty as the prerogative of large-brained vertebrates [2–4]. In insects like the honeybee various other cognitive faculties have been discovered in recent decades [7], such as concept learning (such as ‘same’, ‘different’, ‘above’, ‘below’ and so on) [8,9] or top-down processing (prior knowledge positively influencing visual perception) [10]. Studying cognitive processing in social insects can thus be an important starting point for reassessing the complexity necessary to reach certain levels of cognitive processing [11], as well as opening new avenues toward the understanding of the comparative underlying mechanisms allowing social insects

and primates to solve complex visual problems.

Sheehan and Tibbetts’ work [6] opens possibilities for future research to understand the cognitive processes and its neural underpinnings involved in reliable face recognition. Can wasps, for example, recognise conspecifics in complex environments where faces are viewed at different rotational angles [12]? Are they particularly fast to analyse faces by comparison with other complex stimuli, as humans are [13]? *P. fuscatus* wasps are more accurate at discriminating faces than other visual stimuli, but might this be because of the behavioural significance of facial patterns, thus raising their level of attention or motivation for the discriminative task? So far, no obvious brain specialisation was found when the volume of brain areas were compared between *P. fuscatus* and a few other species of the same genus that do not possess the faculty to recognize one another individually [14], but more fine-grained explorations of the functional specialisation of neurons involved in face recognition remain to be performed [14].

Importantly, such studies in invertebrates open the door to highly controlled experiments, because there are fewer ethical concerns than in vertebrate experimentation, on the influence of early visual experience on the developmental stages of face processing [15]. These wasps might have, like humans, an innate attraction to conspecific faces [16,17], allowing their visual system to develop an expert skill at face recognition, based in part on individual experience. In humans, the capacity to process spatial configuration that is used as a broad object category definition — for example, two horizontally aligned eyes above a nose to define a human face — turns with experience into holistic processing, in which features bind together into a gestalt, so that the stimulus is processed as a whole [18], allowing fast discrimination between similar compound stimuli [19]. No evidence for holistic processing has been found so far in social insects, even if basic configural processes are used in honeybees [20], so this wasp species would be an ideal model to investigate such efficient recognition mechanism.

Answers to these exciting questions will reveal the similarities and/or

differences between how brains of very different sizes can process complex visual stimuli like faces, which has tremendous opportunities for understanding convergent evolution and possible implications for machine vision.

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Endosperm Imprinting: A Child Custody Battle?

Endosperm gene imprinting has long been speculated to control nutrient allocation to seeds. For the first time, an imprinted gene directly involved in this process has been identified.

Philip W. Becraft

Angiosperms and mammals are reproductively similar in that both produce extraembryonic filial tissues dedicated to nutrient acquisition from the maternal parent on behalf of the developing embryo. Interestingly, gene expression in both the endosperm and the placenta is subject to imprinting. That is, some genes show expression biases when inherited from the maternal versus the paternal parent. In mammals, there is substantial evidence that imprinting is important for placental development and fetal nutrition [1]. The analogous function of endosperm in plants suggests that imprinting might be important for similar reasons, but supporting evidence for this hypothesis has been lacking. In a recent issue of *Current Biology*, Costa *et al.* [2] provide the first functional evidence that imprinting of an endosperm gene impacts offspring nourishment.

Endosperm is a filial seed tissue that supports embryo growth and development and controls nutrient uptake by the seed. In the endosperm of cereals, transfer tissue forms at the interface with maternal pedicel tissues where vascular solutes are unloaded for uptake by the seed (Figure 1). Transfer cells are specialized for transport functions, and therefore function directly in nutrient acquisition by the seed. Endosperm is genetically identical to the embryo except endosperm cells are triploid, inheriting two copies of the maternally-contributed haploid genome and one paternal copy. The maternally- and paternally-inherited genomes are not functionally equivalent — there is a strict requirement for a 2:1 ratio of maternal to paternal genomes (2m:1p) for normal endosperm and seed development, even in *Arabidopsis* with a mostly transient endosperm [3–5]. Although endosperm requires a strict genomic ratio for normal development, embryos

are able to tolerate varying genomic imbalances, including either maternal or paternal haploidy.

The adaptive implications of endosperm triploidy, genomic imprinting and the requisite genomic ratios have been subject to much theoretical debate and the 'parental conflict' hypothesis most often comes to the fore. In outcrossing species, all the individuals of a brood share the same female parent but typically have mixed paternal parentage. The parental conflict model posits that offspring compete for limited maternal resources and that male parents enjoy a selective advantage when their progeny successfully outcompete siblings with different pollen parents. Conversely, female parents maximize their selective advantage when fitness is evenly allocated amongst their progeny by limiting resource acquisition to equitable levels. Hence, each parent has conflicting interests in the allocation of resources among the progeny. Accordingly, the female is proposed to suppress the expression of growth-promoting genes while the male inhibits genes that limit growth. Alternatively, the 'coadaptation' hypothesis proposes that maternally-expressed genes improve, rather than limit, progeny fitness and should therefore promote seed growth