Review

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Individual and social immunisation in insects

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Immune systems are able to protect the body against secondary infection with the same parasite. In insect colonies, this protection is not restricted to the level of the individual organism, but also occurs at the societal level. Here, we review recent evidence for and insights into the mechanisms underlying individual and social immunisation in insects. We disentangle general immune-protective effects from specific immune memory (priming), and examine immunisation in the context of the lifetime of an individual and that of a colony, and of transgenerational immunisation that benefits offspring. When appropriate, we discuss parallels with disease defence strategies in human societies. We propose that recurrent parasitic threats have shaped the evolution of both the individual immune systems and colony-level social immunity in insects.

Multi-tiered defensive strategies

Parasites, incorporating both macro- and micro-parasites (the latter including pathogens) are widespread in nature. They show high adaptability and impose a strong selective pressure on their host organisms. As a consequence, hosts and parasites may engage in a coevolutionary arms race [1–5] leading to the evolution of complex host resistance mechanisms, among others immunisation (Box 1) [6]. Immunisation leads to the protection of the host against a disease-causing agent (mostly parasites) upon secondary exposure to the same agent [7]. Immunisation against a parasite can occur either by a general immune upregulation, which provides unspecific protection against a broad range of parasites, including the focal one, or by a specific immune memory, effective against the same parasite. Decreased host susceptibility after immunisation may be mediated by either (i) increased resistance, that is, a higher capacity of the host to reduce parasite loads; or (ii) a higher tolerance, where the host can cope with higher levels of the parasite [8].

The mechanism of such specific immune memory is intensively studied in vertebrates, where it is based on antibodies and memory cells being produced during the immune reaction, at the first encounter with the parasite. These memory-providing humoral and cellular components of the immune system are stored in the body and can be immediately accessed during repeated exposures with the same parasite, leading to faster parasite elimination, and only a mild or asymptomatic case of the disease [7]. Recent work suggests that immune memory may not rely exclusively on these changes in the so-called adaptive or acquired arm of the immune system, but can additionally depend on innate components of the vertebrate immune system [9].

The past decade revealed that protective immunisation also occurs in several invertebrate species against a wide range of parasites [10–24], despite the fact that they lack T cells and antibody-producing B cells, which play an important role for immune memory in vertebrates. Immunisation in invertebrates involves examples of both general unspecific immune protection [12] and memory effects – termed immune priming – which shows specificity at the genus [21], species [15,18] and strain [11,14,24] level. In any case, the immunological mechanisms underlying the observed immunisation in invertebrates are still elusive [10,11,25,26].

Given its protective effects, immunisation has been incorporated into medicine as a highly successful tool to prevent infections. As early as the ninth century, people practiced variolation or inoculation (Box 1), where immunisation is induced by low-level infections [27,28]. As a result of the inherent risk of high-level infections occurring during the process, this practice has been replaced by modern vaccination (Box 1), starting in the 18th century, where immunisation is induced via killed or attenuated pathogens (e.g., surface components or toxoids) [29]. Not only do vaccinations prevent individuals from contracting infectious diseases, they also benefit nonimmunised group members via herd immunity (Box 1) [30]. Herd immunity refers to the fact that, once a pathogen-dependent proportion of group members is immunised through either natural infection or vaccination, the disease can no longer successfully transmit to new hosts and will eventually go locally extinct in a population, freeing the nonimmunised minority from the risk of infection.

In addition to herd immunity, which is a pure epidemiological 'numbers game', protecting the fraction of susceptible individuals in an otherwise immune group [31], societies have evolved further mechanisms of disease control, by collectively achieving social immunity (Box 1) [32–36]. In particular, the eusocial colonies of social insects (social bees, wasps, ants and termites) – but in a wider sense also other group-living insects [37–39] and

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Box 1. Terminology in individual and social immunisation

Immunisation versus immune priming (memory)
Immunisation refers to a reduced susceptibility to a parasite upon secondary contact with the same parasite [7]. The phenomenon of immunisation may arise by two underlying mechanisms: (i) a specific immune memory (termed immune priming in invertebrates) to the particular parasite [11,14,15,21,24]; or (ii) a general immune upregulation that promotes an unspecific protection against a broad range of parasites [12]. To disentangle these two underlying mechanisms, it is not sufficient to demonstrate reduced susceptibility upon secondary challenge with the same parasite, but is also required to test whether the protection includes other parasites, or not.

Individual versus social immunisation
Immunisation can protect an individual organism from infection upon secondary parasite encounter (individual immunisation) [7]. It can also act at the society level, where the susceptibility of group members is reduced after initial parasite contact of other individuals of the group. This phenomenon of social immunisation has been demonstrated in the social insects [56–59], where nestmates that had previous social contact to parasite-exposed individuals receive a protection that makes them less susceptible to disease when the group is challenged by secondary parasite contact. Social immunisation is thus more than the sum of individual immunisation of all group members as it spreads across social group members.

Within-lifetime versus transgenerational immunisation
Individual immunisation can occur within the lifespan of an individual (within and across developmental stages [12,15,18,21,22,62,67,68]). Similarly, social immunisation makes insect societies (or some of their group members) less susceptible to the same disease at a later stage of the colony lifetime [56–59]. Transgenerational immunisation refers to a transfer of immunity from the parental to the offspring generation; at the individual level from mother/father to offspring [14,19,69,70,75,76] and at the society level from maternal colony to daughter colony [73]. Similar to within-lifetime immunisation, the phenomenon of transgenerational immunisation may also rely mechanistically on either an unspecific general protection, or on specific transgenerational immune priming.

Active versus passive immunisation
Individual as well as social immunisation may occur either actively or passively, via an active increase in the personal immune response of the focal individuals or through a passive means. At the individual level, active immunisation can be caused by natural infections and vaccinations with dead or attenuated pathogen strains. Passive immunisation is achieved by the transfer of immunologically active molecules, such as antibodies, either naturally during maternal transfer to the foetus or newly born young, or in health care during passive vaccination [7]. Within insect societies, group members may similarly be protected passively by transfer of protective immune molecules [59] or actively when raising an own immune response following a signal elicited by the exposed individual or transfer of the parasite during social contact [58].

Variolation (inoculation) versus vaccination
Since the 18th century, human medicine has made use of the beneficial effects of immunisation by vaccination with dead or attenuated pathogens, which trigger a specific immune response, yet cannot cause severe disease [126]. Vaccination succeeded the similarly efficient yet more risky intentional transfer of low exposure dosages of infectious pathogens, as practiced since the ninth century in Asia, termed variolation or inoculation [27,28].

Herd immunity versus community immunity (via contact immunity)
Susceptible individuals benefit from the presence of resistant (either naturally immunised or vaccinated) group members by herd immunity. This is because parasites can only persist in populations where they can be transmitted to new susceptibles at a specific, parasite-dependent rate. If the number of resistant individuals is high, the disease will go locally extinct, so that susceptible individuals are freed from the risk of infection, despite being susceptible to the disease [30,31]. In contrast to herd immunity, contact immunity refers to the process where group members become protected against infection by an upregulation of their own immune system, in response to social contact with others. Vaccination with live attenuated pathogens (for example, after oral polio vaccination [114–116]) often renders the vaccinated individuals shedders of the attenuated strains, which are then transmitted to the close social environment, and thus often vaccinate other family members, leading to acquisition of community immunity in these close social groups.

Individual versus social immunity
Individual immunity comprises the behavioural and physiological disease defences of individual organisms – that is, their individual parasite avoidance and hygiene behaviours, as well as their physiological immune systems. Social immunity arises through collectively performed anti-parasite defences of a group of individuals, either achieved jointly or conducted towards each other [32]. It consists of sanitary behaviours, physiological defences, as well as modulation of interaction frequencies [32,34,35,79]. In the narrow sense, it has been defined as the cooperative actions performed in societies, such as the colonies of eusocial insects, but it has been recently suggested to also include other forms of social care like parental care, in a broad-sense definition of social immunity [38].

vertebrates such as primates [40] – collectively perform anti-parasite behaviours [41–46], use antimicrobial substances [47–52], and are thought to modulate interaction frequencies [32,35,53] among colony members to effectively mitigate disease spread in their crowded, highly related societies, which would otherwise be at great risk of epidemics [32,35]. One particular component of social immunity arising in societies is social immunisation (Box 1); a process that parallels individual immunisation at the level of the colony [54]. Social immunisation refers to an improved protection of the colony as a whole (also referred to as 'superorganism' [54,55]), after the encounter of one or several of its members with a parasite, independent of the fate of the exposed individuals [56–59]. In other words, previously naïve group members become protected against a parasite brought into the group by other members, making them less susceptible to the same parasite upon secondary exposure, thereby leading to immunisation of the colony.

We here elaborate on recent advances in the study of immunisation in invertebrates, particularly insects, both at the individual and society level. We discuss evidence for the existence and specificity of individual immune priming and present current hypotheses on the potential underlying mechanisms. We further introduce the known cases of social immunisation and describe their mechanistic bases where identified. Moreover, we separate immunisation within the lifetime of an individual or society from transgenerational effects. While our focus lies on insects, as individuals and as eusocial societies, we develop analogies to humans and their societies.

Individual immunisation

Evidence of individual immunisation

Invertebrates, particularly crustaceans and insects, were recently found to show immunisation at the level of individual organisms, which can be specific [11,14,15,18,21,24]. This phenomenon is equivalent to the