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Architecture, Space and Information in Constructions Built by Humans and Social Insects: a Conceptual Review

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Abstract

The similarities between the structures built by social insects and by humans have led to a convergence of interests between biologists and architects. This new, de facto interdisciplinary community of scholars needs a common terminology and theoretical framework in which to ground its work. In this conceptually oriented review paper, we review the terms “information”, “space” and “architecture” to provide definitions that span biology and architecture. A framework is proposed on which interdisciplinary exchange may be better served, with the view that this will aid better cross fertilisation between disciplines, working in the areas of collective behaviour and analysis of the structures and edifices constructed by non-humans; and to facilitate how this area of study may better contribute to the field of architecture. We then use these definitions to discuss the informational content of constructions built by organisms and the influence these have on behaviour, and vice versa. We review how spatial constraints inform and influence interaction between an organism and its environment, and examine the reciprocity of space and information on construction and the behaviour of humans and social insects.

1. Introduction

Living systems are both constructions and constructors [1,2]. At the fundamental level, organic molecules self-assemble into organic compounds (e.g. proteins, DNA) that build organelles and cells [1]. Cells in turn can assemble themselves into tissues, organs, and ultimately fully functional organisms [3–8]. Organisms modify their environment to build functional structures that will protect them (e.g. bird nests) and help them acquire the resources that they need for their development, survival and reproduction (e.g. spider web) [9–11]. Finally, organisms in societies can combine their building efforts to achieve constructions that no single individual could produce on its own, as is exemplified by termite mounds and human skyscrapers, which can be several hundreds - or even thousands - times larger than the individuals that build them [11,12].

Social insects in particular have long fascinated biologists by their ability to mold their environment to their needs [13–16]. Some species of ants are known to clear debris and vegetation to form large trail networks the size of a football field, connecting their multiple nests to various resources [17–19]. Others have mastered the art of tunneling to build underground networks of galleries connecting chambers housing their workforce, brood, food stockpiles, and even subterranean fungus garden [20–25]. Many species of ants, termites, bees and wasps build structures by accumulating material (e.g. wax, saliva-imbibed soil or vegetable fibers) that will form walls, pillars, floors and ceilings [14,26–35]. Finally, some ants and bees use their own bodies as construction material, attaching to each other and creating dynamical structures such as bridges, ladders, holds and temporary nests [12,36–49].

The complexity and diversity of structures built by social insects is reminiscent of that of human beings [50]. Their construction rules are however radically different. Unlike human-made constructions that are most often composed of inert and standardized units assembled in a precise order, social insect constructions are built from more plastic and irregular components, and their assemblage results from distributed processes of self-organization with little to no supervision [13,51,52]. As a result, their structures are less standardized, but more capable of adjusting their conformation in response to changes in the conditions in which they are placed [12,37,38,53,54].

The parallels and divergences between the structures built by social insects and by humans have sparked a lot of interest in the architectural community [55–60]. The natural world has been an inspiration for architects since antiquity, with biology becoming a key influence on design thinking at the turn of the C19th; when the analogical influence turned to interest in how biological systems develop and evolve (see Mertins, 2007; Steadman, 1983) [61,62]. Coupled with the computational capacity to simulate natural systems architects are today exploring the self-organising and emergent morphologies of biological phenomena to rethink how buildings and cities are designed [63–71]. The emergent, adaptable and situated structures built by social insects offer intriguing insights in particular for architects to re-evaluate not only the sustainable aspects of the human built environment but to question the distinction between cognitive phases of human architecture (i.e., between design, construction, and occupancy stages) and to think about these as continuous. (see Soar, 2016) [72].

Recently, biologists and architects have starting coming together to form a new community, interested in understanding the construction mechanisms used by social insects and their potential applications in human-made structures [55,73]. As is to be expected between two disciplines that have existed in parallel with little interaction, terminology has quickly become the first obstacle to creating a theoretical framework in which to ground the emerging field. During discussions preceding the writing of this manuscript, the authors have identified three concepts in particular that rendered their mutual understanding difficult: architecture, space, and information. In what follows, we will first try to reconcile the somewhat liberal use by biologists of the concept of architecture with the more institutional definition that architects have of it. We will then discuss the concept of space in architecture and biology, and how social systems use space both as a source of information and a mean to encode social information. Finally, we will discuss the idea of information itself and the effects of architecture on information flow and processing in social systems.

2. Scope of the review

One of the problems with interdisciplinary work is language, and is what may be termed the baggage individual disciplines bring to the table. Essentially, terminology can be a barrier for interdisciplinary exchange. Key terms, such as architecture, space and information have long conceptual histories, such that even their everyday use is awkward. Closer inspection only muddies the water further because of the way different disciplines claim the high ground with regards their specific outlook. “Space” for example is from one side an enclosure (i.e. it has boundaries) and the other the void (i.e. the volume contained within these boundaries). Our capacity to mathematically articulate spatial scenarios gives the impression “space” is something we have generally mastered conceptually, but the fact that a concise definition evades us implies otherwise.

Another case in point is the title of this paper, which is loaded with conceptual connotations. “Architecture”, for example, is principally concerned with the human built environment. It is the practice of designing buildings and articulating how to build the design; not forgetting how to explain the rationale behind the design to demonstrate why that design should be built. Professional architectural societies, such as the Royal Institute of British Architects (founded to facilitate and promote the advancement of architecture) guard the term specifically as referring to buildings designed by architects, and the Architects Registration Board (ARB), the statutory body for the registration of architects in the United Kingdom, protect the term in law. Yet these terms (architecture; architect) are often borrowed to refer to complicated structures and artefacts, such as software applications and circuit boards, recognised as products of intentional design. This trend is particularly apparent within the frame of this special issue, which is concerned with constructions built, particularly, by social insects and comparisons that may be drawn between such structures and the human built environment.

The authors, a biologist and an architect, brought together through their interest in the natural world and specifically the structures creatures (other than humans) construct, have sought to establish a ground on which interdisciplinary exchange may be better served by discussing definitions of fundamental terms that span biology and architecture. Our primary goal is to aid better cross fertilisation between disciplines, working in the areas of collective behaviour and analysis of the structures and edifices constructed by non-humans; and to facilitate how this area of study may better contribute to the field of architecture.

3. Toward an interdisciplinary framework

3.1. Are social insects architects?

Architecture has many meanings. For instance Steven Holl said, during his acceptance speech for the 2012 American Institute of Architects Gold Medal, that “architecture is an art bridging the humanities and sciences” [74]. Thomas Mayne, at his Pritzker Prize acceptance speech, said that “architecture is a way of seeing, thinking and questioning our world and our place it” [75]. Claiming social responsibility as its most definitive attribute Samuel Mockbee asserts “architecture is a social art. And as a social art, it is our social responsibility to make sure we are delivering architecture that meets not only functional and creature comforts, but also spiritual comfort” [76]. Diebedo Francis Kere echoes Mockbee: “architecture is not just about building. It's a means of improving people's quality of life” [77].

One thing that is, however, common to all these quotes is that architecture is something other than just a building. Architecture, claimed Jay A. Pritzker “is intended to transcend the simple need for shelter and security by becoming an expression of artistry” [78]. In this context, a building is considered as no more than the sum of its parts. Architecture, however, is other than that. The whole takes on an independent existence from the parts it is made of, as an observer will perceive it as a distinct object from the objects it is composed of. If this is what the architects claim then how does the term, and mindset, transfer to edifices formed by non-humans? If architects and biologists are indeed concerned with developing interdisciplinary collaborations (to study, for example, ant nests), we need to dispel the notion of architecture being exclusive to humans and consider it from a non-anthropocentric perspective.

Vitruvius (c.80-70 BC - c.15 BC), author of *De Architectura libri decem* (commonly referred to as “The Ten Books on Architecture”) [79], regarded as the first book on architectural theory, and often referred to as the first architect, asserted architecture to have three qualities: Firmitas, Utilitas and Venustas. Henry Wotton, a C17th translator, interpreted these terms as “firmness” (well constructed) and “commodity” (functional) for the first two, with Venustas being less well defined and often interpreted as “beauty” or “delight”. We take on the latter version on the premise that it implies something ephemeral and other than the sum of the parts, whilst beauty has connotations of the beholders eye and is tied to subjective concerns of taste and style. The first two concepts are unlikely to cause controversy between architects and biologists; both disciplines actually expresses them in similar terms as we will discuss below. Delight, however, will require more consideration on our part. Indeed aesthetics - which makes the whole “other” than the sum of its parts - is a concept difficult to operationalize in the scientific study of animal behavior, and we will attempt to find a middle-ground on which biologists and architects can build upon.

3.1.1. Firmness

Vitrivius’ “firmness” is understood as the physical properties of a construction that guarantee its structural soundness, at the very least for the time the building is needed. These properties depend on trade-offs between many factors including construction material and methods, technological advances, substrate composition, environmental conditions, and costs. Architects use tools from physics, engineering and economics to balance these different factors and plan accordingly the construction process. Biologists use a similar set of tools to measure biological structures, characterize their construction process, and ultimately determine the balance of constraints made by the animals.

Architects and biologists are, for instance, equally interested in measuring the physical properties of construction material. Weight, density, strength and deformability are all determining factors in choosing construction material for buildings. Animals themselves are sensitive to the physical properties of the construction material. Termites, for example, preferentially dig through non-load-bearing over load-bearing wood, and build thicker load-bearing clay walls when attacking loaded wood [32]. Architects rely on tools from materials science and engineering to select materials with desirable physical properties, and from applied physics for combining these materials in a structurally sound manner. Software tools like Oasys’ GSA Building enables detailed analysis of structural solutions providing accurate prediction of material performance, how a structure interacts with the ground and the impact of footfall on irregular structures [80]. Autodesk’s Insight 360 platform permits architects to simulate and analyse building energy and environmental performance so they can approach the design process with understanding of factors leading to better building performance outcomes throughout the building lifecycle [81]. Biologists rely on similar tools to quantify the physical properties of animal constructions. For instance, Cole et al. (2001) conducted a comparative study of the physical properties of nest paper in three species of wasps, showing that the fibre composition of the paper might explain differences in thickness and tensile strength between nests [26]. In termite mounds, King et al. (2015, 2017) used structural (e.g. mound geometry) and dynamic (e.g. air flow) measurements to demonstrate that a “simple combination of geometry, heterogeneous thermal mass, and porosity allows the mounds to use diurnal ambient temperature oscillations for ventilation” [82,83]. Finally, and somewhat bridging architecture and biology, the physical qualities of termite mound soil have inspired researchers to evaluate their use in human-made constructions, such as in compressed earth bricks [84] and pavement material [85].

This commonality of tools and approaches provides opportunities for direct interactions between biology and architecture. Indeed, the standardized language of physics and engineering is particularly useful to transfer "technology" between the two disciplines. Case in point, the passive ventilation system of termite mounds has inspired the design of several buildings [86], such as the Eastgate Centre in Harara, Zimbabwe for instance [87]. The study of the physical and mechanical properties of social insect constructions may therefore be the most obvious starting point for collaborations between architects and biologists, and the one that is most likely to generate direct applications of the building principles of natural systems.

3.1.2. Commodity

Vitrivius' "commodity" refers to the efficient organization of spaces and systems that support the functions of the construction. It determines how the different parts of the building are used by its occupants and the benefits that they receive from it, relative to other possible organizations of the building. This concept is critical to both human-constructions and biological structures, as it links form and function with each other. Unlike "firmness" which is studied with tools from physics and engineering mainly, "commodity" in architecture and biology is more often characterized with methods from behavior and psychology, with a particular interest in the interaction between the organization of the structure and the distribution of behaviors within.

A first concern of both architects and biologists is the spatial separation of functions that might have an adverse effect on each other. An obvious example is the spatial segregation of feeding locations from excretory areas in order to reduce the spread of infections. In human-made buildings, this segregation is achieved by the physical separation of food storage, cooking and consumption areas from the lavatories. Segregation of function can also be enforced by social conventions and regulations that makes certain behaviors acceptable in some locations only (e.g. smoking bans inside publicly accessible buildings). Similarly the spatial separation of functions is also present in structures built by social insects (see Section 3.2.2).

Another common interest of architects and biologists is in determining how efficiently a structure is used, and how its organization balances different, often contradictory uses. In architecture, this can have important implications in terms of, for instance, building safety (e.g. during an evacuation) [88], economic consequences (e.g. time spent by customers in store aisles) [89], and access (e.g. to favor space use by certain categories of users). In social insect constructions, researchers more often look at issues of resource accessibility [17], information flow [90], and nest defensibility [91]. In any case, biologists and architects use here again similar tools to measure and predict the efficiency of a structure relative to one or more of these objectives. For instance, researchers and practitioners in both disciplines regularly employ agent-based model to determine how the spatial organization of a structure affects the distribution of individuals, be they ants in a network of galleries [92] or humans in an art gallery [63]. Fitting such models to data from human and non-human systems allows for direct comparison between them, as has been done multiple times in studies of building evacuation for instance [93–97].

Finally, tools from graph theory can be used to measure the efficiency of a structure in terms of connectivity between its different parts. It has been used to characterize structures built by social insects such as ant and termite nests [23,91], and ant foraging trails [17,18], but also human-made constructions such as urban settlements [71,98], communication networks [99], water distribution systems [100,101], and transportation networks [102]. More specifically graph theory has been applied in architectural design as a method of describing building form and a way of automatically generating plan arrangements [62,103]. For instance Space Syntax theory describes how connectivity and integration of areas within buildings and cities epitomises human social relations, and through mapping the heterogeneity within architectural forms correlates topological relations between building and settlement configurations and people (see Hillier, 1996; Hillier & Hanson, 1986) [104,105]. Such approaches also allows for direct comparisons between human-made and insect-made networks that can be indicative of common building principles. For instance, Buhl et al. (2006) showed that street networks in non-planned settlements have similar cost-efficiency trade-offs as the emergent structure of ant tunnelling networks [98]. As in the previous section on "firmness" this commonality of tools and analysis language should allow for more frequent collaborations between architects and biologists.

3.1.3. Delight

Finally, Vitrivius' "Delight" is generally understood as an aesthetic quality, defined in terms of style, proportion or visual beauty, and is symptomatic of how architecture is a visually dominant discipline. That architecture is dominated by a concern for the visual is long held [106], and the visual sense has played a significant role in our evolution as a species. This emphasis has driven cultural and technological development; which has in turn reinforced the prominence of our visual sense (see Cairns 2017) [107]. But "delight" is not specifically attuned to the visual and there is a growing sense that architects should account for a wider sensorial domain in the artefacts they create [108,109]. Indeed "delight" infers something of pleasure or joy, which is open to all sensation and sources of stimulation, and thus encompasses all senses.

If we follow the definition professed by Frederick Kiesler, that architecture is emotional, what distinguishes architecture from building is that the former evokes emotion [110]. Such a definition sidesteps the moral high ground of architectural practice and schools, because it states simply that architecture affects and causes emotion. Understanding architecture as such allows one (1) to transcend boundaries, because it relates to the sensing emotive capacity of the observer, and (2) to consider architecture a product of perceptual systems that perceive stimuli (see Gibson, 1966) [111].

So, whether a construction, built by social insects or humans, can be considered architecture or not is open to interpretation. As such we are faced instead with philosophical traditions and how one sees the world, and thus one's place amongst those things they share it with. We must ask then, if we are to accept the term "social insect architecture" whether ants, for example, have aesthetically-triggered emotions? We cannot sidestep this question.

While it is obvious that the nests of social insects have specialised functional dimensions [112–114], the question of whether they are also built aesthetically is difficult to address scientifically. There are no doubt that in the eyes of a human observer, social insect nests are beautiful objects [16]. However, whether they are in the eyes of an ant or a honeybee is more complicated to answer. Social insects can react and associate meaning to a wide variety of stimuli [115–119], but whether they derive emotions from these stimuli is unknown - or at least undiscussed in the litterature. Some species of social insects seem to be decorating their nests with artifacts which function is not immediately evident (e.g. the pebbles and twigs on meat ant nests [120]). But are these true aesthetic artifacts built with the intention of triggering emotions, or more simply construction patterns resulting from the evolutionary history of the organism, for instance as a mechanism for nest recognition? [120] And if the latter, doesn't it apply as well to human artifacts? After all, our senses and cognitive processes are also the products of our evolutionary history, therefore our aesthetic experiences should be as well [121].

Taking a non-anthropocentric view we need to relinquish the idea that aesthetics is an intellectual pursuit, and that it may be a judgement (or act) based on the assignment of value to something. The concept of aesthetics was originally coined by the philosopher Alexander von Baumgarten (1741-1762), who argued aesthetics is the study of the plenitude and complexity of sensations [122] (also, *cf*. Gibson, 1966) [111]. When Kant took up the concept he drained it of its sensory plenitude, revising its significance to contemplation and judgement of beauty (see Howes and Classen 2013) [123]. If we take a step back (to Baumgarten) we may consider the edifices built by social insects, from the organism's perspective as having some aesthetic quality - whatever that might be. We may conclude then that architecture (in its widest sense) is a product of behaviours that support and enhance physiological and social needs. On the one side, to provide protection and shelter. On the other, to shape and manage activity. The former applies to all constructions by humans and animals. The latter to social organisms in particular (humans and most typically social insects), which use their constructions as a form of enabling device to organise actions and define social conditions [113,124].

Therefore we propose that what truly separates construction from architecture is that the reaction of an organism to the former cannot be distinguished from its reaction to a similar artifact resulting from extraneous processes (that is processes foreign to that organism). Architecture, on the contrary, carries a social information that has the potential of affecting the behavior of organisms beyond the simple physical constraints imposed by the organization of the structure on them. A builder assembles a construction, but makes it architecture by embedding messages in it - be they intentional to prompt or provoke behaviour or unintentional in which case they may be a by-product of the builders behaviour or happenstance.

3.2. Construction as a way to shape space

One of the main outcomes of construction is - arguably - the organization of spatial relationships between individuals, their activities and their environment. Through construction organisms - be they humans or social insects - partition their environment into distinct zones that can support different functions (e.g. feeding vs excreting) and separate different habitats (e.g. outdoors vs indoors) or different populations (e.g. employees vs customers). This partitioning necessarily creates spatial relationships between the separated elements. This may seem obvious to the reader, yet the idea of space only appeared in architectural discourse in the late 19th Century, when it became important in two ways: first as the embodiment of human activity inside the architectural form [125] and second when it became aligned to aesthetic ideas in an attempt to define beauty [126]. The issue of space thereafter became a central topic in architecture, initially in terms of sensorial engagement with the environment [127]. (See van de Ven, 1987 for a concise history of how the idea of space has developed in architectural theory) [128].

The issue of space is also central to biology at all levels of biological organization. From the partitioning of biochemical reactions within cells [129] to the influence of large-scale environmental patterns on species distribution [130], measuring spatial relationships is critical to understanding life in general. In the context of this review, we are more specifically interested in how organisms reshape their environment through their building behaviour, and how in return the resulting constructions impose spatial constraints that direct further behaviours. These two questions apply similarly to humans and social insects, and the main goal of this section is therefore to identify research themes common to biologists and architects and to draw comparisons between their respective approaches.

For this purpose, we propose here that the spatial character of built constructions can be approached from three complementary and non-mutually exclusive angles. By no means do we claim that these angles are the only possible, but we think that they should encompass most of the research issues related to space and construction:

1. First, we will consider that constructions almost always separate an outside from an inside world, most often for reasons linked to protecting the organisms from some aspects of their environment.
2. We will also discuss the role of the spatial organization of the construction and its interaction with behaviour in segregating functions within a population and in channeling the individuals' activities.
3. Finally, we will examine how the spatial configuration of the construction can itself generate functions that benefit the organisms without necessarily requiring their active participation.

3.2.1. Constructions provide protection

The primary function of construction is arguably to provide shelter to organisms from adverse conditions in their environment. An enclosed, insulated space will for instance be less subject to climatic variations such as changes in temperature and humidity levels, thereby facilitating an organism's homeostatic regulation. Walls and ceilings also offer barriers that can shield - for a time at least - an organism from any physical threat, such as falling objects or predators. Therefore one of construction's most important purpose is to create a separation between an outside, often unsafe and unpredictable world, and an inside, more stable and less dangerous one.

Social insects are masters at building fortresses to protect their colonies from intruders. Their nests range from simple holes in the ground or in vegetation [131,132], to vast underground complexes of chambers interconnected by tunnels and housing sometimes several millions of individuals [133,134]. Like human strongholds, the nests of social insects are organized to limit outside access, with only a small number of entrances (often a single one). In many species, specialized workers - often called soldiers and morphologically distincts from the other workers - are found guarding these entrances against intruders [135,136]. In some species of ants and termites, these 'guards' have even evolved morphological and/or behavioral adaptations allowing them to plug the entrances with their own bodies, quickly preventing access to the inside of the nest when under attack [12,131,132,137,138]. Outside the fortress, several species of social insects also build protected passages that connect the nest to resources sometimes hundreds of meters away. These passages can be underground tunnels as in leaf-cutting ants and some termite species [133,139–141], mud tunnels (shelter tubes) built by termites along tree trunks [142,143], or even 'living' walls that *Dorylus* ants form along their trails out of their own bodies [144].

The nests of social insects are not built to resist physical threats only. Indeed many social insects species regulate the micro-climate within their nests in order to maintain stable living conditions, independent from variations of the outside environment [145]. Termite mounds are arguably the most striking examples of constructions by social insects capable of shielding the colony from changes in the external weather conditions [82,83,145–148]. The structure itself of the mound creates temperature gradients that in turn generates air currents, balancing the temperature within the nest and ensuring stable gas exchanges [82,83]. A similar phenomenon can be found in some leaf-cutting ant nests, which regulate the oxygen / carbon dioxide balance through passive air movements [35,149–152]. Social insects also regulate the internal conditions of the nest in a more active fashion. Bees, for instance, aggregate at the entrance of their hive on hot days and use their wings to move hot air outside the hive and cooler air inside [153–155]. Army ants, which form temporary nests called bivouacs out of their own bodies, increase or decrease the spacing between each other to regulate the internal temperature of the colony [156,157]. Finally, in many ant species digging nests into the ground, the workers relocate regularly their brood away or toward the surface as it heats up or cools down, in order to maintain the brood near their optimal development temperature [158,159].

Protection from the outside world comes at a cost for the colony. Evidently, the constant upkeep and remodeling of the nest structure takes away workers from other essential tasks such as foraging or taking care of the brood. A balance must therefore be found between maintaining the nests integrity and carrying on the other activities of the colony. It is evident that some species invest a lot of time and energy in building and maintaining their nests (e.g. African and Australian termite mounds; the vast underground nests of *Atta* ants) while others barely improve the pre-existing cavities in which they nest (e.g. rock ants and turtle ants). Do complex - and therefore costly to build and maintain - nests evolve only in species with a strong need for protection - against predators or the environment -, or is nest complexity secondary to evolving efficient behaviors to accomplish the other tasks necessary for the survival of the colony? To our knowledge, there has been no systematic study of this trade-off.

Like the ants, humans have long built structures for defence and protection from the climate. Both functions are fundamental form-generating forces in human architecture, but as architects have embraced advancements in technology the influence climate has on human construction has lessened. Similar to the strategies of ants described above, humans have occupied hollows in the ground, carved out underground buildings and networks, and capitalised on features of the landscape to regulate the micro-climate within dwellings and maintain stable living conditions. Dwellings built in the ground, such as the Matmata houses in the Sahara and the Opal miner’s houses in Australia use a layer of earth as coolant, and Réso, a network of underground tunnels in Montreal provide protection during the long winter. In Naours, France, an underground settlement includes a bakery and chapel. In southern China the circular Tulou buildings are designed to offer protection from the monsoon rain, and in Normandy aerodynamic roofs provide protection from harsh Atlantic winds (See Piesik, 2017 for a review) [160].

Whilst societies have long constructed buildings using local materials and inherited construction techniques (vernacular architecture) to provide protection, innovation in the use of materials means the result is not simply a consequence of assembling gathered materials in a rudimentary way, but creatively transforming them. Ashanti huts, for example, have a wooden frame with a roof of branches on top, on which a layer of beaten mud is supported. Contrary to what you might expect the thick heavy walls don’t support the roof, so structurally they act as curtain walls. This may be due to cultural influence, but it is also likely a result of climatic reasoning. An advantage of this construction is the phasing, providing shelter quickly while the walls are erected (see Rapoport, 1969) [161].

Glass, is perhaps one the most important innovations in modern building, and has changed the way we perceive the difference between inside and outside space. It blurs the lines between the two by providing physical protection but visual connection. In turn this changes the way we behave and how we think about space. It is interesting to look back at how the issue of space arose in architectural discourse and came to inform the modernist ideal of how space is deemed to flow from one area to another. The conflation of inside and outside was central to the architectural ideology of Leberecht Migge (1881-1935), who promoted the interpenetration of architecture and landscape through rational geometric lines with extensive use of glass to connect the two. Glazed doors and windows formed the *Zwischenglieder* (interstices) between inside and outside to provide connection with nature, and greenhouses encircling houses providing thermal protection in winter (see Haney, 2011) [162]. Migge's interstitial notion of space does not compartmentalise and it does not follow the general tendency to categorise the world into discrete units: between internal and external, and for example rooms by function. This controlled and ordered categorisation transfers to how we perceive and consequently organise space. We will come back to this in the next section.

3.2.2. Organization

Division of labor is a landmark of social life. Most social insects species are characterized by a strong behavioral, and also often physical differentiation between groups of individuals specialized in performing different tasks (e.g. foraging, brood tending, etc) inside the colony [163–166]. In many species, this division of labor is also characterized by the spatial segregation of tasks within the nest, with specialized areas dedicated to specific activities [163,167,168]. A typical example of this spatial organization of activities is the nest of leaf cutter *Atta* ants [20,133,134,169]. They are composed of a network of tunnels connecting chambers that are all dedicated to a specific task. Some chambers house fungus gardens that serve as primary food source for the colony. Others contain the brood at different stages of development. Finally, rubbish dumps are created inside and outside the nest, isolating the colony from the waste material it produces [170,171].

The spatial segregation of tasks has important consequences on the organization of the colony. Indeed, it has been shown that interactions are much more frequent between ants performing similar tasks [168], and that interaction rates are important regulatory signals for activating and inhibiting workers to perform particular tasks [172–175]. Because activities are segregated within the nest, workers specializing on a particular set of tasks are therefore more likely to interact with other workers with a similar behavioral profile, increasing their ability to share relevant information about their preferred tasks. Moreover, as workers transition toward other behavioral profiles as they age, they might relocate progressively within the nest toward areas better suited to their new preferences, possibly helped by the rate of interactions with workers of the same or of different behavioral profiles.

It is interesting to note here that the spatial segregation of tasks is not necessarily accompanied by the building of barriers to physically separate them. In ants and honeybees for instance, the brood is often grouped by type (e.g. workers vs drones) or developmental stage within a single space, without walls separating them [30,176,177]. Similarly, the content of honeybee comb cells is often organized spatially, with brood-containing cells grouped together in the center of the comb, surrounded by a band of pollen-containing cells, and then a larger peripheral region of honey-containing cells, but again with no physical barrier between these different areas [30,178].

The existence of a spatial segregation of tasks without physical barriers is understood a the result of simple self-organizing processes of differential aggregation [177,179–181]. This suggests that different areas within a nest - with or without physical separation - might specialize in a particular type of task not because of their intrinsic characteristics, but because of social feedback loops between the workers: the more a task is performed at a location, the more likely it will be performed again at that location. For instance in a recent study, Czaczkes et al. (2015) showed that *Lasius* ants will preferentially drop their feces at specific locations within their nest (usually a specific corner of a specific chamber) [112], separate from other waste materials that are gathered in piles outside the nest (the 'trash') [112]. This behavior is most likely driven by social signals contained in the feces (e.g. pheromones) that stimulate ants to leave their feces where other ants have done it, leading to the creation of - effectively - toilets. This self-organized spatial segregation of tasks [182–186] is at odd with the way it is achieved in human constructions. Indeed, buildings built by humans are planned ahead and each room is pre-assigned a type of task, and then fitted with all the required features for users to accomplish these tasks.

The basic purpose of any building is to satisfy the physiological and social needs of the organism. On the one side, to provide protection and shelter; as discussed above. On the other, to shape and manage activity. The former transmits to all constructions: human and animal. The latter to social organisms (humans and most typically social insects), which build structures that act as a form of enabling device to organise activity and define social conditions. Scrutinizing built structures enables us to consider space retrospectively, as a system of social relations from which rules, or patterns, of inhabitation may be extrapolated. For instance, Bill Hillier and Julienne analysed the organization of built forms and illustrated how the configuration of space changes when specified from the perspective of each distinct area constituting planned arrangements [104]. Identifying the heterogeneity of built forms they revealed buildings to be systems of activity defined by the dynamics of social and cultural goings-on. Similarly, analysis of social insect nest structures illustrates intricate spatial arrangements and the social structure of the colony [91,187].

Working out the organization of a building is one of the most important and taxing aspects of architectural design. The task of organising the numerous criteria of a building programme was identified by Horst Rittel and Melvin M. Weber as “wicked”, because planning problems tend to be combinatorially hard [188]. The typical approach to organising a building is to flatten the problem, so that the activities to be housed can be planned. This has led some, like Paul Coates (2010), to claim the way architects traditionally organise a building is most unnatural [66,189]. Inspired by the way natural systems are understood as pattern making and problem solving, architects are today looking to the replication of phenomena in biology and computer science (such as flocking [190], stigmergy [190–193], branching systems [193], food foraging and nest construction [194], replication [195,196], and so forth) as an alternative approach to modelling form and structure that evades the traditional top-down centralised decision making process of configuration. This has opened up a whole new way of thinking about configuration in architecture, which is bottom-up and generative, and reminds us of Migge’s interstitial notion of space whereby internal and external domains are conflated and flow into one another (see previous section).

The architect Frederick Kiesler (1890-1965), who was strongly influenced by biology [61,197], promoted a notion of space extending Migge. He considered space to be continuous, or endless. Not in sense of the void but in terms of a line for which both ends meet. This notion of space, which is evident in both the organisation and materiality of his work (see Bognar 2003) [198], was informed but what he saw as a fundamental distinction between how humans construct and what he observed in nature. “Nature [,he says,] builds by cell division towards continuity whilst man can only build by joining together into a unique structure without continuity” [199]. His point being, humans construct through brute force (connecting parts together to form a whole: we bolt, glue and force elements together). In non-human constructions parts merge, overlap and conjoin one another as a consequence of self-organising and emergent processes. The concept of stigmergy describing social insect nest construction is a case in point, which we will come back to in Section 3.3.2. Kiesler sought to emphasise how we organise space and devise the arrangement of matter is tied to how we comprehend space and distinguish spatial relations.

3.2.3. Function building

An organism's fitness is not determined by its personal morphological, physiological and behavioral phenotypes only. It is also influenced by phenomena that result from its activity, but are not a physical part of its being [200]. This 'extended phenotype' includes structures built by the organism and that provide it with services increasing its survival and reproductive success. The nests of social insects colonies are exemplars of extended phenotypes that have played a critical role in their evolutionary history [201,202]. Besides providing protection (as discussed in Section 3.2.1) and a mean to organize the colony's activity (as discussed in Section 3.2.2), the architecture of the nest itself can generate other complex emergent functions for the benefit of the colony.

Perhaps the most well known example of a function that it 'outsourced' to the nest architecture by social insects is that of ventilation, permitting the regulation of temperature, humidity and respiratory gas composition within the nest [35,82,83,146,151,203–206]. This is a common occurrence in large ant and termite nests, which depth - and therefore insulation - could render air exchanges with the surface difficult in the absence of dedicated ventilation mechanisms. While ventilation can be actively performed by some social insects (e.g. in bees [145,153,155]), it is often achieved passively by nest structures that can harvest naturally-occurring physical phenomena. For instance, it was shown that the interaction between wind and nest structure - and in particular the orientation of nest openings relative to wind direction - was responsible for ventilation in the large nests of the leaf-cutting ant *Atta vollenweideri* [35,151,206]. A similar mechanism was found to be responsible for nest ventilation in the termite *Macrotermes michaelseni* [204]. In termites, the mound that covers the nest can also be built so that daily temperature fluctuations caused by the sun heating part of the mound generate convective flow driving the ventilation of the nest [82,83].

In all the examples above, the structure of the nest itself performs the function, independently from the behavior of the organisms that built it. In many cases however, the function of the structure only becomes apparent when in interaction with the behavior of the organism. For instance, topological and geometrical features of ants and termites networks of foraging trails and nest tunnels have been shown to guide the movement behavior of the workers [19,23,91,92,207–212], for instance facilitating the collective selection of the most efficient route within the network. In this case, the structure does not have a function by itself, but one is created when interacting with the behavior of the organisms.

Similarly, the structure of human constructions perform functions independently to provide and maintain suitable living conditions and support physiological and social needs. A classic example of the former is passive ventilation; termed "natural ventilation" to emphasise the lack of mechanical equipment to provide air exchange. The Eastgate Centre, mentioned earlier, is one example. Another is the Palace of Westminster's historic ventilation system designed in the 1840's by physician David Boswell Reid to serve the House of Commons and the House of Lords. These two debating chambers are internal spaces that have no external walls of their own. Reid's elaborate scheme includes more than 2,000 vertical shafts, smoke flues and ventilation channels, some up to 200m long, providing fresh air collected from towers and led through an intricate network to the basement of the building, where it was heated during winter, and released though outlets in the chambers. This included outlets placed in the seating, so fresh air was delivered directly to occupants [213].

More recently, Mesiniagra tower, designed by Ken Yeang, is a bio-climatic skyscraper in Malaysia, where the sun is a prime factor in design. Louvres provide protection from the sun, but Yeangs design was informed by the path of the sun, so the buildings form also acts as a shading device reducing solar gain [214]. The form and shape of buildings can also act as a device to distribute people and control the flow of movement. Crowd disasters are a prevailing issue [65,215,216] which has led to extensive data collection to investigate the dynamics of crowd behaviour [217,218]. Serial incidents at the Hajj, Mecca, has resulted in the reorganisation of the Hajj, and specifically a new design for the Jamarat bridge. Different levels serve pilgrims coming from different areas and directions to reduce crowding on the Jamarat plaza.

Control is a fundamental factor of institutional buildings, which is clearly evident in Jeremy Bentham's Panopticon. His design is a system of control allowing observation of prison inmates by a single watchman, without the inmates being able to tell whether or not they are being watched. The building acts as a device to prevent, or reduce, the likelihood of undesirable behaviour [214,219]. On a grander scale, Haussmann's plan for Paris remodeled the city to modernise it and also provide physical control of the population. He replaced many narrow streets, which allowed the revolutionaries' to establish barricades, with broad boulevards and avenues. Less obviously, the wider streets function as a form of psychological crowd control – a mob may be less likely to revolt due to the expanse making them feel less powerful [220].

3.3. Constructions as a way to shape information

All living systems communicate in some shape or form, be it through chemical emission (e.g. scent, pheromone), visual display (e.g. form, colour, movement), sound production (e.g. vocalisation, vibration) or electric currents, to inform others of their own state (e.g. mating status) or of the state of their environment (e.g. incoming danger) [221,222]. As hinted at in the previous section, communication can also be achieved through building. Indeed, each construction act, by modifying the content or configuration of the environment, has the potential of constraining or guiding future behaviours. In Batesonian epistemology, it is "a difference which makes a difference", that is an "elementary unit of information" [223]. If we accept that each feature of a construction potentially holds information - or even *is* information -, then we need to discuss the meaning of this concept in biology and architecture. In particular in this section, we will attempt to identify possible points of agreement and disagreement between the two fields in order to facilitate communication - no pun intended - and collaboration between researchers across the aisle.

The concept of information is rather proteiform in both the scientific and philosophical literature [224]. Scholars in all disciplines have already proposed an uncountable number of definitions of information. With this manuscript, it is neither our intent to introduce a new one, nor to discuss the relative merits of each existing definition. However in the following sections, we will often refer explicitly and implicitly to two of the most prominent definitions of information - that of Claude Shannon and that of Gregory Bateson - and we think it necessary to briefly describe and contrast them here.

Claude Shannon's idea of information [225] is motivated by the need to measure and mathematically describe information in order to quantify differences between messages (e.g. to detect transmission errors) and degrees of dependence between different signals (e.g. to detect phase synchronization between separate sources of information). Rooted in statistics and probability theory, Shannon's information has been hugely influential in many disciplines in science and engineering because of the analytical tools it provides for measuring and comparing the information content of random variables independently of their meaning. As Gibson points out, Shannon's information excludes the meaning of a stimulus to focus on the quality of message transmission from source to receiver [111].

Gregory Bateson's ecological view of information is rooted in the cybernetic idea of communication and organisation. The elementary unit of information, he claims, is a difference that makes a difference. He states, a difference that makes a difference is an idea. It is a 'bit', a "unit" of information [223]. This somewhat paradoxical statement deserves unpacking. Whilst Shannon's concept of information is about reduction of uncertainty Bateson implies a process of distinction. Both imply an observer, making choices, but Bateson infers a system classifying inputs or sensations subsequent to the ability to discriminate, initially between self and other, between things [226]. He describes a referencing system that perceives and thereby distinguishes [227,228], and accounts for how entities, be they cells, organisms or agents in a computer model, engage with *their* world. Bateson's unit of information is thereby also a unit of survival, whereby a difference is a matter of trial and error through which habits emerge. His concept of information is the basis for a theory of learning.

With these two approaches of information in mind, we will examine three general areas concerned with construction and information:

1. First, we will examine biological communication and information, and in particular the concepts of cues and signals and how they provide some evolutionary context to the present discussion.
2. We will then consider the concept of stigmergy and how construction can shape social systems by embedding information in the environment.
3. Finally, we will discuss the importance of explicitness in the perception of information and how this might help explain fundamental differences between constructions in humans and social insects.

3.3.1. Cues, signals, and biological information

In the behavioural sciences, information generated by an organism is traditionally separated in two categories: cues and signals [221,222,229]. Signals are any information transferring features that have evolved specifically to convey information about the signaller or its environment to receivers. It is generally understood as resulting from the coevolution of emitting and receiving apparatuses, as well as associated behavioral responses. Signals are also often - though not always - associated with the notion of intentionality, that is the organism controls when and where to broadcast the signal.

On the other hand cues are features that can be used by an organism to guide its behaviour, but that were not evolved specifically to convey information between a signaller and receivers. Think for instance of a predator following the scent of a prey animal. The prey animal has not evolved its scent nor does it intentionally release it to inform the predator, yet the predator can evolve an apparatus to perceive the scent, as well as associated behavioral responses. If a cue provides an evolutionary advantage to the emitting organism (e.g. if it attracts potential mates), it can then be selected for and become a signal. However, while signals are intrinsically biological in nature (i.e. a product of evolution), cues can also be obtained from nonliving entities, like the position of the stars in the sky or the direction of the wind.

Cues and signals play an integral role in the construction behavior of social insects. For instance, the construction behavior of some ant and termite species have been shown to depend on environmental cues such as the strength and direction of air currents or the presence of physical heterogeneities in the landscape (see for instance Jost et al, 2007) [230]. These cues can influence both the initiation of the construction process (e.g. environmental heterogeneities serving as anchor points of constructions in ants, termites and wasps) [14,29,231] and the final result of the building activity (e.g. walls aligned along the direction of air currents in ants and termites) [230]. Signals, on the other hand, are more often associated with coordinating the actions of the individuals in the colony. For instance, the addition of pheromones to the construction material in ants and termites has arguably evolved to encourage individuals to add to structures built by nestmates rather than to random environmental heterogeneities [14]. It could also represent the freshness of the material, therefore indicating structures under construction requiring additional actions by workers.

Similarly, environmental and contextual cues are fundamental factors influencing the building and formation of human constructions. Vernacular architecture perhaps best illustrates how determinants such as climate, availability of local construction materials, and the influence of local traditions has informed the design of human constructions. One of the most significant determinants is the climate (See section 3.2.1). Buildings in cold climates typically have few openings, windows are small or non-existent to prevent heat loss, and have high thermal mass or significant amounts of insulation. Conversely buildings in warm climates tend to be constructed of light materials to allow cross-ventilation through openings in the fabric of the building. The different aspects of human behaviour and environment has led to different building forms, evident in the variable contexts and cultures around the world [160,161,232]. Despite these variations all buildings are subject to the same laws of physics and hence demonstrate significant similarities, which are evident also in social insect constructions: see section 3.1.1.

However human constructions differ from that of insects in that they are also the product of socio-cultural factors that escape largely natural selection. As technology has advanced and human socio-culture has progressed with it, methods of construction have become more sophisticated and the form of buildings have evolved. Innovation and technological advancement allows architects to overcome constraints, such as those determining vernacular architecture. For example, the Gothic flying buttress was an innovation transferring gravitational forces to ground in a way that allowed walls to become lighter, which permitted greater expanses of glass and thereby daylight to flood a buildings interior. Applied to churches and cathedrals this technique of building provided a means to denote divinity and promote the authority of the church. So, human construction is not only informed by environmental/contextual information - like in social insects - but also enables cultural signs to be embedded in the construction itself. These signs develop through a process typically referred to as ‘cultural evolution’ [233–237], whereby knowledge, beliefs, languages, etc., are passed on from generation to generation (inheritance), modified over time, and may enter in competition with each other, leading to selection pressures not unlike that underlying natural selection.

3.3.2. Stigmergy and spatial embedding of information

The notion discussed above that construction - whether by humans or insects - embeds information, that is can influence future actions of the builders or the users is reminiscent of the concept of stigmergy in biology. This idea was first introduced by Pierre-Paul Grassé in 1959 to describe the construction behavior of termites [191,238]. Grassé explains that the organization of the building activity does not depend on direct coordination between the workers, but rather on indirect coordination achieved through the modification of the structure under construction. Each time a termite worker adds or remove material from the structure, it changes the configuration of the local environment around it. This change will influence subsequent building activities at or around its location, either by the same worker or other workers in the colony. Coordination at the colony level emerges from the repetition of such stigmergic processes, giving the impression that the colony is following some sort of well-defined plan.

Since Grassé's original insight, stigmergic coordination has been found to play a role in most constructions built by social insects. For instance, the primitively eusocial wasp *Polistes* builds its nest out of paper it produces by mixing its saliva with plant fibers [26]. This paper is then turned into walls that will ultimately form a comb of hexagonal cells. During the building of the comb, cells are not added randomly to the structure under construction: wasps a more likely to add new cells where existing cells already form three or more adjacent walls [13,239]. As a consequence of this preference, multiple wasps can coordinate their building activity and will first complete existing rows of cells in the comb before starting a new one. The result of this indirect coordination is a round shaped comb with approximately one hundred and fifty cells and, more importantly, without holes. Other examples of social insect construction relying on stigmergic coordination include internal and external structures of nests in ants and honey bees [14,178], trail networks in ants and termites [240–242], and cemeteries and refuse piles in ants [114,230].

While it can be argued that stigmergy is a dominant organizational force in social insects construction, they also rely on other modes of coordination during building. In particular, environmental and social templates play an important role - often in combination with stigmergy - in determining the final shape of the construction [13,51]. For instance, *Macrotermes* termites adjust the size of their queen's chamber to match her size as she grows [243,244]. Similarly, rock ants (*Temnothorax albipennis*) adjust the size of their nest to the quantity of their brood [245–247]. In both cases, it is believed that volatile pheromones produced by the queen and the brood establish a chemical gradient around them that can be used as a template by the workers to determine the size of the construction. Environmental heterogeneities and gradients can also be used as templates by social insects, determining for instance the location at which a construction is initiated or its final orientation. Finally, social insects can use direct coordination to organize their building activity. This is the case for instance of the self-assemblages built by some species of ants (e.g. temporary nests, bridges, ladders) and bees (e.g. swarms, festoons) by attaching to each other [12,37,38,47,49]. While limited to a few species, these - quite literally - living architectures built through direct coordination have the advantage over stigmergic structures of being extremely plastic and reactive, sometimes assembling and disassembling in a matter of minutes or even seconds.

As a concept to describe the coordinated building activity of social insects the concept of stigmergy does not, on first inspection, easily transfer to human society and its architecture. However, Grassé's idea of stigmergy can been extended to encompass all forms of cues and signals that organisms - including humans - leave in their environment that have the potential of mediating indirect interactions between individuals [51,191,192]. Stigmergic traces represent the information that organisms embed in the spatial context and, together with environmental influences, they define a large part of the information landscape accessible to each organism.

In the social sciences, Grasse's original insight has been studied in the context of numerous forms of human activity, including the stock market, economies, traffic patterns, urban development and more besides [248–251]. One may claim even that the way architects design traditionally, through drawing sketches, is stigmergic; whereby a line drawn on the page breaks the homogeneity of the blank surface, and influences scribing the next line. Successive lines are added influenced by and influencing the developing pattern to mediate the development of an idea. Working in a team the same sketch is referred to and developed by others who are influenced by what they see and add to, adapt or emphasise aspects of the sketch. Building Information Modelling (BIM) uses a stored digital model, which is accessible to all members of a design team, who work on and develop the model in parallel, detecting clashes and developing the model collectively. Recently architects have begun experimenting with stigmergy literally as a method of generative design [252–257].

As mentioned above (see section 3.2.2), the capacity to use the computer to simulate the autonomy, emergence, and distributed functioning of natural systems provides architects a new way of producing form and structure, and to think about the organisation of areas constituting a building or city. Adjacency and circulation are fundamental concerns in organising architectural layouts, because of factors like the movement of people, material and information between areas, and/or the need to control or supervise one area from another. The nature of such problems has been characterised as “wicked” [188] because of the interrelatedness of the factors involved. The food foraging behaviour of ants, for example, has been explored as an alternative method of organising distribution networks in buildings and cities. Instead of placing activity areas in relation to one another based on convention the stigmergic behaviour of assorted artificial ant colonies has been utilised as a method of self-aggregation, and applied to generating the desired arrangements between activities in a building [258], and to generate primitive room arrangements [255]. Pussepp proposed a model whereby circulation is developed as an emergent by-product of global morphogenesis of the built form [259], and proposed a tool for generating outline urban arrangements often associated with unplanned settlements [260]. The stigmergic behaviour evident in insect societies and animals has also been adopted as a method of form finding [253,257,261]. Carranza and Coates, for example, used the trails left behind by a population of swarming agents as a scaffold to wrap a continuous surface around [253].

Whilst stigmergy has been applied as an alternative approach to organising buildings and form finding, the casual form of urban aggregation evident in medieval villages, Brazillian favelas and Chinese Hutongs exemplifies stigmergic configuration driven by environmental constraints, as with vernacular architecture, but urban aggregation of this type is also driven by associations with one’s neighbour. Whilst cities are prone to top-down planning by the authorities they have been shown to operate as a dynamic, adaptive system based on interactions with neighbours, feedback and decentralised distribution of people, goods, information and energy [70,262,263]. Consequently urban growth has been evaluated computationally and illustrated to replicate natural systems [66,264]. Coates demonstrated how the formation of early human settlements is underpinned by geometrical constraints that inform the arrangement of unplanned as well and planned urban arrangements through a combination of environmental feedback and simple local rules [265]. The algorithmic approach driving contemporary architectural design today is motivated by this comprehension of geometrical rules and stigmergic behaviour of agent-systems evident in shaping urban settlements and the configuration of buildings. Coupled with the capacity of social insect societies to unscramble the wickedness of certain problems (like searching for food), architects are today looking to the decentralised and distributed control evident in the behaviour of social insects and how they form the structures they build [13,51,194].

3.3.3. Explicit and implicit information

In the previous two sections, we discussed information from the point of view of the signaller: signals and cues are categorized based on whether the signaller has evolved them specifically to convey information about itself or its environment - or not (Section 3.3.1); and stigmergic traces are characterized by whether they persist in the environment even in the absence of the signaller (Section 3.3.2). In this section, we would like to shift the focus toward the receiver of the information. In particular, we would like to argue that information can influence the behavior of the receiver in either an explicit manner, or in an implicit one. We consider information as being explicit if the receiver has evolved - through natural or cultural evolution - perceptual and/or cognitive abilities to specifically give a meaning to this information. In other words, the organism has acquired dedicated processes to operate on the content of a piece of information (e.g. neural pathways) and react to it accordingly. This corresponds to all forms of information for which the organisms possesses a receptor and mechanisms to interpret the output of the receptor.

Implicit information, on the other hand, corresponds to features that can modify the behavior of an organism without requiring this organism to process or even perceive the associated stimuli. In other words, they are features of the physical and social environment that do not have a meaning for the organism - the organism might not even be able to perceive them -, yet they may influence its actions in a manner that the organism cannot control. These are often external physical forces applied on the organism without its knowledge (e.g. the tide pushing planktonic organisms toward the shore) [266] or barriers that constrain the movement of the organism. In some species of ants for instance, it was found that the geometry of their networks of foraging trails is asymmetrical: when a forager comes back toward its nest and reaches a branching point, the trail heading toward the nest after the branching point deviates less (~30º) from the ant's original direction than the other trail (~120º) which leads away from the nest [17,209,210,212,267]. While one species of ants may be able to use this information explicitly to navigate its trail network [210], others do not seem to perceive the difference and simply follow the path of 'least resistance' [92,209]. As a result, they are more likely to find their way back to the nest and their foraging output will be increased up to 3 times, all this without requiring any navigational capabilities, spatial awareness or even the ability to detect the configuration of the branching point (as demonstrated using robots) [211].

Most studies on the building behavior and construction use of social insects involve characterizing explicit forms of information: pheromone deposits, tactile contacts, air movements, etc [14,230,268]. Few however have considered the importance of implicit information in shaping the collective behavior of the colony. Indeed one difficulty with studying implicit information, is that it is not always obvious to an external observer given the disconnection between this form of information and the sensory and cognitive apparatus of the organism. Yet, as in the example mentioned above, there is strong evidence that the topology and geometrical organization of the environment has an influence on the spatial distribution of organisms, even when they are imperceptible to said organisms. Therefore it should be explored more systematically in the context of social insect constructions.

Similarly, we can see examples of information that is embedded within the human built environment, and in architectural form, and how it too can have an influence on the behaviour of the perceiver. Again, this impact may be described as implicit or explicit. Winston Churchill's adage "we shape our buildings; thereafter they shape us" exemplifies the built environment a chief factor in determining behaviour. The correlation between perception of the environment and its implicit effects on well-being and behaviour has long interested psychologists [269]. The complexity of the built environment is a crucial factor contributing to human behaviour. Experiments measuring how the brain and body responds to different kinds of settings show people are bored and unhappy when faced with extensive bland facades, and by contrast, happy and stimulated by varied and permeable building frontages, which will in turn have an influence on where a person will choose to spend their time [270,271].

Quantitative theories and methods of analysing urban configurations, such as Space Syntax [272], illustrate the correlation between the geometrical composition of the built environment and social behaviour [104,105]. Graph based representations and statistical analysis of the structural properties of built form illustrates there is a direct correlation between the topology and geometrical organization of the environment and the spatial distribution of people and movement [273–275]. For example the least angular deviation along a route suggests the structure of the street network is itself the key determinant of pedestrian flow. A pedestrian will tend to choose routes that require the least amount of turns, and this will correlate to their perception of how well integrated the street is within a network, and consequently to pedestrian density. The implication is that configuration can have effects on movement which are independent of attractors [276,277].

The role of explicit information in the built environment is both more literal and more formalised. Road signs, and the demarcation of pathways is an obvious example. In extreme cases the function of the building is literally interpreted by the observer, such as “Big Duck”: a shop selling ducks and duck eggs that is built in the shape of a duck. However, a particular aspect that distinguishes the human use of information is our capacity to build arbitrary associations between things and to think metaphorically. Symbolism enables humans to communicate with other humans they don’t meet: i.e., symbols are an indirect form of communication, which are embedded and perceived throughout the built environment and have developed their associations (or meanings) through cultural evolution. A structure is symbolic when it acts as a vehicle of arbitrary content and the observer reads the embedded meaning, making architecture “other than” just a building: as discussed in section 3.1.3.

4. Conclusion

Humans have long since looked on the natural world as a source of inspiration, and observation of what other animals can do has driven us to achieve feats beyond our natural capabilities; such as being able to fly. The idea of late that simple creatures build complex and dynamic constructions has spurred researchers to investigate the mechanisms behind such phenomena, from the building of social insects nests to the formation of cells, tissues, organs and ultimately organisms. The complex and coordinated behaviours resulting from interactions between individuals in a collective has led scientists and engineers to question how this understanding may be applied to human-related problems. Architects, on the other hand, who are becoming more aware of the parallels between biological processes and design, as well as the artefact making capacities of animals are turning more to biology to explore innovative methods of problem solving and designing.

Whilst there is a long history of biology influencing architectural endeavour only recently have biologists and architects begun to meet and collaborate. As indicated at the start of this paper this union brings inherent difficulties, as each discipline claims its own high ground and concepts fundamental to both are viewed distinctly from either side. Perhaps none more so than the concepts of “architecture”, “space” and “information”, which are not only fundamental to the sciences and humanities but everyday understanding. Consequently we set out in this review to cross-examine these concepts in biology and architecture and to establish a framework within which fundamentals that span both disciplines are apparent and beneficial to both, with the view to better enabling cooperation in the study of constructions built by social organisms and how these structures influence, direct and manage behaviour of social systems.

The primitive framework established here provides a basis on which to build. Having examined the notion of architecture we have proposed an open definition spanning human and non-human constructs, and reviewed the concepts of “space” and “information” in relation to human and social insect constructions. Additional concepts, such as “emotion”, may be scrutinised and included to facilitate and bolster interdisciplinary discourse. The notion of delight is perhaps beyond scientific reason but aesthetics (if we refer to Baumgarten [122,123]) may be considered a fundamental aspect of all living systems. The key, we suggest, is to analyse the occurrence of internal-external relations established by perceptual systems in the process of distinguishing information about their world. The real issue is to avoid anthropomorphising the social insect and consider how the insect's perceptual system conveys information about its world. In so doing we should avoid seeking the meaning and establish the internal-external relations that inform, direct and lead to, for example, the termites pillar building activity.

Living systems are embedded in their environment, which, we have proposed, from the organism's perspective is a matter of relations and forms that influence behaviour. These features, which may be evolved (signals) or not (cues), perceptible (explicit) or otherwise (implicit), constitute environmental pressures which constrain and coerce the activity of organisms. Spatial constraints are a fundamental feature of living systems, both in their development and in their unfolding engagement with the world [278,279]. Evident, for example, in the building of self-ventilating mounds in termites, the rules that govern construction can be seen as productive constraints, because they are sensed by the organism that responds to it, giving it a meaning, and ultimately creating a functional pattern (the mound and its passive ventilation) that improves the colony's fitness. It is a fundamental character of natural systems that spans scales from abiotic to social systems. This semiotic perspective unifies architecture and biology and, we hope, could be the basis for a more formal collaborative language between the two disciplines.

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