Urban architecture – A cognitive neuroscience perspective

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Biography: Kate Jeffery is Professor of Behavioural Neuroscience at University College London. Originally trained in medicine, for the past 25 years she has been at University College London researching the neural basis of spatial representation. Her main interests are in how the sense of direction is configured, and in the three dimensional properties of the brain's map of space. She is an elected Fellow of the Royal Society of Biology and Royal Institute of Navigation (RIN), and a founder of CogNav, the RIN Special Interest Group that aims to link researchers and industry experts who share an interest in navigation.

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Abstract

The rapid urbanization of the past century has led to an accelerating demand for urban design that caters for city-dwellers in both physical and psychological domains. The field of architecture has begun to cultivate more analytic approaches to city design, in order to enable quantification and hypothesis-testing of design principles. In parallel, the cognitive science of human navigation has been developing rapidly, fuelled by neuroscientific findings from rodent research. The time seems ripe to bring these disciplines together. This article reviews some of the most salient neuroscientific discoveries of recent decades and shows how these discoveries, and the design principles that emerge from them, can add important constraints on architectural design. By taking these cognitive constraints into account it is argued that urban spaces – particularly large, complex ones such as transport termini and convention centres – can be made more navigable and able to provide a better experience for users.

Key words

spatial cognition; wayfinding and navigation; neuroscience; architecture; memory

Introduction

Architecture is ultimately about space, and architectural forms are assimilated and interpreted by the brain's spatial-processing system (Banaei et al. 2017), which supports both spatial cognition (thinking) and spatial emotion. Spatial cognition is the mental faculty that takes in information about the spatial surroundings, transmitted via the senses – especially vision – and assembles it into a subjective percept that lets a person experience, understand and use the space optimally (Burgess 2008). The spatial cognitive system is closely linked to the emotional processing system (Saarimäki et al. 2016), and so architecture needs to provide spaces that are not only usable but also provide positive subjective experience.

Architecture as a discipline has traditionally relied upon centuries of accumulated experience to develop its design principles, and in recent decades has also begun to deploy quantitative tools, such as space syntax, that allow for theory-aided design and the testing of hypotheses. However, one field of knowledge that is potentially informative but has not yet been generally incorporated into architectural practice is spatial cognitive neuroscience. This is a discipline of psychology focusing on spatial knowledge, which has been propelled in part by a recent set of neurobiological discoveries, originally made in rodents, that have profoundly shaped our understanding of how the brain processes space. These discoveries have revealed an entire brain system devoted to the processing of navigable space, and have also shown that this system underpins memory for life events: so-called episodic memory.

The fundamentals of spatial cognition are highly relevant to architecture, and so the aim of this article is to outline them and to suggest ways in which they may help inform architectural thinking. In particular, it will be argued that such principles can help the design of spaces that are less confusing and more 'legible'. And finally, some speculations will be offered about how design that works with, rather than against, natural navigation processes also may make spaces more intuitive, less stressful and more emotionally positive, and may enable people to engage at a deeper level with their cities.

The cognitive neuroscience of space

The hippocampus, the place cells and the cognitive map

In understanding the cognitive neuroscience of space, by far the most important advance in the past century has been the discovery that there is an entire brain system, the hippocampal system (Fig. 1), that is specialised for the processing of larger-scale space.

Attention was first drawn to this brain region by a groundbreaking case study published by neurosurgeon William Scoville and neuropsychologist Brenda Milner (Scoville and Milner 1957), reporting the calamitous effects of a brain operation intended to cure a disabling case of epilepsy but which unexpectedly left the patient, Henry Molaison, profoundly amnesic (Corkin 2013).

Insert Figure 1 near here

Motivated by this unexpected discovery of a memory system in the brain, in the 1970s neuroscientist John O'Keefe began recording the electrical signals from single neurons using hippocampally implanted microelectrodes in awake, behaving rats. He found to his surprise that many neurons in the hippocampus would become active whenever the animal ventured into particular places in the box (different places for different neurons; Fig. 2). Over the course of many recordings O'Keefe determined that what these neurons were responding to was not any simple sensory feature of the box, or even a complex combination of simple features, but rather something far more abstract – 'place'. He thus named these neurons 'place cells', and he and his colleague Lynn Nadel proposed that the hippocampus is the site of the brain's construction of a mental map of space, which they called a 'cognitive map' (O'Keefe and Nadel 1978).

Insert Figure 2 near here

Over the ensuing years/decades, the cognitive map theory of the hippocampus steadily gained experimental support and important principles began to emerge. The first was that a distinction can be made between space organised relative to the body,

called ‘egocentric’, and space organised relative to the outside world, called ‘allocentric’ (Proulx et al. 2016). Egocentric space is the preserve of a different brain area, the parietal lobe (Fig. 1; Byrne, Becker, and Burgess) which is engaged when the problem to be solved, such as picking up a cup, involves space that has a specific and fixed relationship to the body. People with strokes affecting the right parietal lobe lose the ability to represent the left side of space – they leave food on the left sides of their plates, neglect to shave the left side of the face, draw a clock with no numerals on the left, copy only the right side of drawings using only the right side of the page and so on (Fig. 3). In a famous study of Italian stroke patients, Bisiach and Luzzatti (1978) found that although people could not describe the buildings on the well-known Piazza Del Duomo that lay on the left relative to their imagined viewpoint, they could describe these same buildings if they imagined themselves on the opposite side of the square, such that these buildings were now on the (imagined) right. Thus, the parietal lobe is not a permanent store for information about the location of the items relative to each other, but is needed to represent where they are in egocentric (self-related) spatial coordinates.

Insert Figure 3 near here

By contrast, the kind of space that engages the hippocampus is allocentric space, which is organised relative to the outside world – nearer the door, by the river, at the west end of the building, etc. Place cells seem in some sense to be allocentric because a place cell is active (‘fires’) whenever the animal is in that place, regardless of which way it was facing or what it is looking at. This can only be done if the brain has

stored the relationships of the environmental features to each other, independently of the animal's own location.

Maps vs. routes

Psychologists quickly picked up the cognitive map theory and began exploring the role of the hippocampus in guiding navigation behaviour. It soon became apparent that rats with experimentally induced damage to the hippocampus, surgical or chemical, have difficulty navigating (Morris et al. 1982). Human studies found that mental mapping deficits become evident even if the damage is only one-sided, as with epileptic patients post-surgery (Maguire et al. 1996). These findings also fitted with the observation that people in the early stages of Alzheimer's disease, which starts in the peri-hippocampal region, frequently complain of getting lost as one of their earliest symptoms (Coughlan et al. 2018). Perhaps the most well-known finding from studies of humans has been Maguire's famous studies of London taxi drivers (Woollett, Spiers, and Maguire 2009), finding activation of the hippocampus during imagined or virtual-reality navigation, and structural changes in the hippocampus of experienced taxi-drivers.

Animal studies also revealed that not *all* navigation tasks are affected by hippocampal damage. Those that are spared include route-based tasks that do not require a mental map (Packard and McGaugh 1996). An example of route-based navigation would be travelling to work along highly familiar streets; a type of navigation that is done automatically and without thinking. Such habit-like navigation depends on a learned set of landmarks together with egocentric responses (e.g., 'go down to the corner and turn left'), and is the preserve of a third brain system, the striatum (Hartley and Burgess 2005). The striatum dominates in behaviour control whenever the behaviour is familiar, well-rehearsed and does not require much flexibility

of thought. As we will see later, this distinction between map-based and route-based navigation becomes important when considering how to design for a heterogeneous population, some of whom may be using a map and some a route-based strategy.

How does a place cell know where it is?

What information does a place cell use to determine whether it should fire or not? The literature on this is vast, and growing daily, but a few broad principles have emerged.

The first is that a place cell needs to know about 'context' – that is, which environment or situation is the animal currently in? Place cells are active differently in different contexts (e.g., different colored rooms) or if the animal has to do one type of task vs. another type of task (Markus et al. 1995; Wood et al. 2000) even if the spatial layout of the environment is the same. Findings like these suggest that a distinction is made between incoming information about the bare bones of the spatial layout and information that fleshes this out into a meaningful, rich representation of 'spatial context' (Jeffery et al. 2004).

The second important type of information is direction. When a place cell is recorded in a rotationally symmetric environment such as a square or circular arena, the cells can nevertheless break this symmetry and fire nearer one wall than another (Jeffery et al. 1997). Something must, therefore, be telling them which wall is which. This something is almost certainly the head direction cells, described in the next section, and it seems that the direction system is absolutely fundamental to the construction of a mental map.

The third important type of information comes from the environment boundaries. The importance of boundaries became evident in a study by O'Keefe and Burgess (1996) in which they moved the walls of a box independently and found that

different cells ‘followed’ different combinations of walls. The pattern that emerged suggested that the cells are sensitive to how far the rat is from the walls (Barry et al. 2006), meaning there much be some kind of distance-measuring process occurring – we now think this may be due to the grid cells (see below).

There is now good evidence that humans have place cells too (Ekstrom et al. 2003). The extent to which the above properties of rodent place cells are preserved in humans remains unknown. However, the finding that rodent brains treat different kinds of information differently, based on their spatial infomativeness (e.g., whether a feature seems like a boundary) suggests that we should be sensitive to this possibility in humans too. This becomes relevant in thinking, for example, about what format to use in presenting information to people.

Head direction cells and the cognitive compass

In the years that followed the discovery of place cells, researchers began to explore the brain regions connecting to the hippocampus in order to try and identify the routes for incoming information. In the mid-1980s, Jim Ranck reported the discovery of “head direction cells” (Ranck 1984). A given head direction cell becomes very active when the rat faces in a particular direction, irrespective of where in the environment the animal was. Ranck proposed that together, the cells act like a compass, creating the sense of direction and telling the hippocampal system which direction is which.

Head direction cells have since been found in many brain areas and form a widespread system. Studies of the system have produced many insights concerning spatial perception. The first of these is that the cells depend on a continuous interplay between information coming from stationary environmental features – landmarks – and information coming from the animal’s movement through space, such as when it turns

its head, or walks around a corner. Neuroscientists think of this as the distinction between ‘setting’ and ‘updating’ the sense of direction.

A second insight is the importance to orientation of rotational asymmetry in the visual landscape. Rotational symmetry refers to the visual similarity that occurs if the environment looks the same when viewed from different facing directions. In a rotationally symmetric compartment, what typically happens is that the spatial cells guess at which of the possible directions (based on vision) is correct, and then maintain that orientation with the help of the movement-detection system mentioned above (Jeffery et al. 1997). In a circular room with no doors then visual rotational symmetry is infinite, and the system is entirely reliant on motion-detection (sometimes called path integration) to maintain a stable signal. And in fact, in such situations the signal typically drifts after some time, because there is nothing to reset it.

Grid cells and the cognitive odometer

As described earlier, place cells have information about how far the animal is from the environmental boundaries. Where does this information come from?

The answer to this question, or at least part of it, emerged from a paradigm-changing finding of “grid cells” in the entorhinal cortex (Hafting et al. 2005), which is the brain region that funnels sensory information into the hippocampus. Grid cells seem a little like place cells: however, instead of just one or a few firing fields, the cells produce many fields. Remarkably, these fields are evenly spread across the surface of the environment, producing a hexagonal pattern that has a strange, crystalline beauty, and is quite unlike anything ever seen from a brain before (Fig. 4). Grid cells are thought to form the metric basis for the cognitive map – something like a map grid, but hexagonal.

Insert Figure 4 near here

The finding of grid cells electrified the field, and less than a decade later the Mosers were awarded a half-share of the 2014 Nobel Prize in Physiology or Medicine for the discovery. The other awardee was O'Keefe, for his discovery of place cells. The reason that place and grid cells have been considered so important is that they demonstrate beyond all doubt that the brain constructs a map-like representation of space, incorporating information not just about locations but also about the relationships between them such as directions and distances. This is by far the most abstract representation yet found in the brain, and it proved that space is intrinsic to our conception of the world. Recent evidence suggests that humans have grid cells too (Jacobs et al. 2013; Doeller, Barry, and Burgess 2010), and speculation is beginning that perhaps humans use this system for more than just space (R. A. Epstein et al. 2017).

Human navigation

The findings from rodents concerning the spatially coding neurons has shown us that the brain separates out the business of spatial processing in a modular way, with landmark-processing handled by one circuit, self-motion by another, direction by another, distance by yet another, and so on. We have also learned that these modules interact at so many levels that in some senses they aren't really modules at all, so much as criss-crossing rivers of information flow. But what about studies of human navigation brain circuits?

The bulk of the neuroscientific study of human navigation circuits has involved brain scanning, also called neuroimaging or fMRI (functional magnetic resonance imaging), which reveals which brain areas a person is using when they think in certain ways. Neuroimaging studies of human navigation have also relied on another rapidly advancing technology, virtual reality (VR), which allows people to have an experience that resembles moving through the world, even though they are lying in a brain scanner. VR is an important tool, although it misses one crucial aspect of such movement which is the sense of acceleration. Despite this limitation, VR and fMRI together make a powerful combination and have not only validated the rodent findings in humans but have also contributed a number of important new insights. For example, several brain regions have been discovered in the human brain that are involved in the processing of visual scenes and the extraction of scenes that are place-like. The parahippocampal place area (PPA) is one of these – it responds when subjects are shown photos of places, but not when they are shown photos with similar image statistics that are of objects (Epstein and Kanwisher 1998). This area also activates when subjects explore, with their hands, models of places (Lego rooms etc; Wolbers and Buchel 2005), suggesting that the area is involved in the mental conceptualization of place. Another area that is commonly activated, retrosplenial cortex, seems to have a role in the processing of directionally useful landmarks, explaining the strange finding of Auger, Maguire and colleagues that people who have difficulty deciding how permanent (landmark-like) an object (for example, a wheelie bin) is also have the greatest difficulty in navigating (Auger, Mullally, and Maguire 2012; Auger and Maguire 2013). And finally, a brain area that has not been studied in rats but which seems to reliably show up in human brain scans, called precuneus, may have a role in forming mental imagery (Cavanna and Trimble 2006).

The emotional processing systems

As well as the spatial systems described above, an important set of neural circuitry contributes to emotional processing of space. Attributing emotional positivity or negativity – called 'valence' – to a space is fundamental to survival and involves ancient circuits in the brain, which learn very rapidly. One can acquire a deep and lasting fear of a place following one single brief unpleasant experience there. Such 'fear conditioning' methods are used in the laboratory to study the emotional circuits and have revealed the importance of a small, almond-shaped structure called the amygdala, buried deep in the temporal lobe (LeDoux 2003). The amygdala is probably involved in several types of emotional processing, but fear is its most prominent role, and people with damage to both amygdalae are often strangely unable to experience fear, or recognise it in others (Adolphs et al. 1994; Fox and Shackman 2017). Many experiments have shown that the amygdala and hippocampus work together to support the learning of fear responses to unpleasant places (Chaaya, Battle, and Johnson 2018), which occurs rapidly and is long-lasting. The part of the hippocampus that has most interconnections with the amygdala, called "ventral hippocampus" in rats and "anterior hippocampus" in humans, has been implicated in anxiety states in normal subjects, and also in anxiety disorders, including post-traumatic stress disorder (Lopresto, Schipper, and Homberg 2016).

One important role for the spatial emotional system concerns threat-induced escape, which is the rapid flight to safety that most species exhibit when frightened (De Franceschi et al. 2016). This is a type of navigation that involves very ancient, subcortical brain systems, and is automatic. Some evidence suggests the role of a structure called the superior colliculus in directing such escape (Evans et al. 2018). If so, this might have implications for the design of fire exits etc., because panicked

escape may not involve the mental mapping circuits in the same way as ordinary navigation.

The other side of the spatial-emotions coin concerns the learning of positive associations with places. One important system is the ventral (deep) striatum, and in particular a tiny nubbin of grey matter within it called the nucleus accumbens. This is a structure which is best known for its role in addictive behaviours – it is activated when a person experiences a pleasurable reward such as food, sex or drugs, and reinforces the actions that led to the reward (e.g., lighting a cigarette, putting it in the mouth, inhaling etc.; Berridge and Kringelbach 2015). An amazing experiment conducted in rats recently found that if place cells were activated experimentally while a rat was asleep, simultaneously with activation of the ventral striatum, then when the rat awoke it would go to the place signalled by the activated place cells (De Lavilléon et al. 2013). The implication is that the association of the place cells for the place and co-activation of the reward centre caused the rat to form pleasant associations about the place.

There are other emotions associated with spatial processing as well – curiosity is an important one. Curiosity arises when a situation is novel and the subject is driven to explore. When placed in a new environment, most animals, including humans, will explore, suggesting that the brain has a drive to reduce environmental uncertainty. It is easy to see why this has survival value – knowing if there are predators nearby, and checking out the escape routes or food sources etc, is obviously adaptive. While normal animals eventually habituate to their new environment and stop exploring it, rats with damage to the hippocampus keep exploring (Teitelbaum and Milner 1963), consistent with a failure to form spatial memory of the layout of the environment. Interestingly, people with Alzheimer's disease show similar patterns of restless exploring, called

wandering (Cipriani et al. 2014), which may also result from a failure to form a memory of the layout a place.

Another type of spatial emotion is territoriality, which refers to the sense of ownership and mastery of a space that is characteristic not just of humans but of many other territorial species. Territories are usually defended against conspecifics (members of the same species) and is thus a social emotion as well as a spatial one, requiring knowledge not just of the space in one's territory, and the boundaries, but also of which other individuals belong there and their relative places in the dominance hierarchy. Increasing evidence suggests that the hippocampus may be involved in social recognition and processing of social relationships (Kumaran et al. 2016) as well as space/memory, possibly because of the close link between places and their inhabitants.

Architectural design principles emerging from cognitive neuroscience

The foregoing discussion has highlighted a number of discoveries emerging from the cognitive neuroscience of space that suggest some principles that are relevant to architects designing spaces for people to navigate in. This section presents the most salient ones, some of which are already an established part of architectural practice and some of which may be novel.

Setting the sense of direction

Perhaps the first and most important insight is the primacy of the sense of direction in establishing a coherent sense of space. The initial anchoring of the direction sense is achieved using previously encountered, and thus familiar, landmarks – if the environment is new then the system maintains the direction it was signalling when the previous environment was exited. The direction sense is then supported by a combination of continued perception of landmarks, together with the continuously-

running process of movement-tracking, often called ‘path integration’.

This registration process is tremendously important for the establishment of an integrated cognitive map. If a person enters a room without some type of linking information to create a directional consistency with the previous room then the sense of direction will establish an arbitrary orientation, which may be hard to alter when the discrepancy is discovered. Most of us have had the experience of learning the wrong orientation of a region – perhaps a part of a city – relative to its neighbouring regions, and never managing to correct the error despite repeated return visits there. However, our built spaces often deposit people somewhat arbitrarily in new spaces – in an elevator lobby, at the top of a staircase, or a station concourse from an escalator etc. Designers should consider the benefits of providing compass information the moment people arrive in the new space – or perhaps even earlier (e.g., on the steps of an escalator) so that the sense of direction can immediately set itself correctly in register with the outside world.

As mentioned earlier, rotational symmetry is also problematic for the head direction system. Rotational symmetry occurs surprisingly often in architecture (Fig. 5) and has the potential to be confusing, and to require a high cognitive load to process, because people need to keep track of their movements and cannot reorient by using the visual appearance of their surroundings in isolation. Note that while rotational symmetry can be infinite, as in a circular building like the ones in the first column of Fig. 5, it can also be of a lower order – twofold, fourfold etc – and yet still be confusing. In twofold symmetry, the visual scene looks the same when viewed from opposing directions – in such cases, an uninterrupted path integration signal is needed to prevent confusion. Sometimes this process fails – a famous example is the wrong-way touchdown of Jim Marshall, sometimes called “the most embarrassing moment in NFL

history", in which he confused the two directions of the Kezar Stadium (Fig. 5, middle) and scored an own goal.

Mirror symmetry, on the other hand, does not create this same problem. A mirror-symmetric environment does not have any rotationally ambiguous viewpoints (Fig. 5, right) and thus the visual scene can always be used for reorientation, placing minimal load on the movement-tracking system. Symmetry can be broken in other ways too – for example by use of colour/shading, large features, or by introducing parallel curvatures to corridor walls.

Insert Figure 5 near here

A third important insight from neurobiology studies has been that the head direction system prioritizes landmarks that are far away over those that are nearby. This makes sense, because nearby landmarks change their relative direction as one moves around – a chair is not a good indicator of global direction whereas a mountain is. In our built environments we rarely provide distant landmarks for orientation – some cities have them naturally, in the form of mountains, but more often than not the only visible landmarks are tall buildings, which are directionally unstable (and often have rotational symmetries).

One type of information that does not help orient the head direction system – at least not readily – is signage. Signs and text, which we developed very late in human evolution, are processed by brain regions that do not directly connect to the head direction system, and need to be routed through a circuitous path that probably includes the frontal lobes. While signs can be helpful, they do not engage the navigation directly and naturally in the way that environmental geometry and landmarks do.

Maps vs. routes

As mentioned earlier, the hippocampal system is used for cognitive mapping, but a different system, the striatum, is used when movement through a familiar space is automatic and habit-like. Studies of the interplay between these systems find that they appear to compete with each other – the more the hippocampus is being used, the less the striatum, and vice versa (Poldrack et al. 2001).

The existence of two navigation systems is relevant to the design of spaces that people navigate through, particularly if these are high-throughput, as in a transport terminus. In an underground train system, for example, some people will be following a familiar route – they might be commuting, and follow this route every day – and will therefore be on autopilot, using familiar landmarks such as doorways and stairs to organise their action sequences. Such travellers are likely to be disrupted by changes to local landmarks such as construction hoardings, or forced detours. Other people might be in unfamiliar territory and will be unable to use a route-based habit. These people will, due to natural variations in the population, comprise a mixture of those who prefer to use a map-based strategy where they can, and those who prefer to use a route-based one no matter what. Both populations need to be catered to in order to create a positive experience of the space (see below) but they have different requirements: route-based travellers need signs and symbols, while map-based travellers need global compass information so that they can integrate their visual surroundings into a cognitive map.

Spatial emotions and spatial unease

Because of the close association between the spatial mapping and emotional processing systems, design of spaces needs to account for the types of emotions they might elicit. The new discipline of neuroaesthetics has started to look at how the beauty of perceived

objects and spaces is processed by the brain (Chatterjee and Vartanian 2014). Space also has a role to play in shaping emotions via the affordances it offers for certain kinds of action such as escape, concealment or surveillance.

We saw earlier that exploring and orienting within a new environment is a priority for many species, including humans, and we also know from study of other behavioural systems such as hunger, thirst, sex etc. that drives are associated with tension, and satisfaction of drives with pleasure. This leads to the idea, supported by subjective experience, that being un-oriented in an environment, or not knowing its layout, is a source of tension or stress in humans, whereas satisfying the exploratory drive, remaining oriented and cognitively mapping the space is associated with relief of tension, and pleasurable experience of the space. Here we introduce the term 'spatial unease' for this sense of not feeling oriented or mapped within a space, and propose further that good architecture minimises spatial unease (unless it is playing with it for aesthetic reasons) while poor architecture exacerbates it.

Public buildings abound with uneasy spaces, in which people are given insufficient orientation information to stably set or reset the head direction system, or to align it with other nearby spaces. Uneasy spaces are also those where not all parts are available for exploration (visual or actual). Spaces that lack linking information with other spaces and that require many body turns to traverse, such as underground (subway) tunnel systems, contribute to spatial unease because although the route is obvious, no map can be made during its traversal.

Spatial unease may also arise when the entrances and exits are not obvious, or when it is hard to get from one place to another due to obstructions to routes such as atria or staircases. This may be partly because unavailability of ready ingress/egress disables the threat escape system described earlier, but it may also have a cognitive

explanation. Increasing evidence suggests the importance of the environment's affordances for movement, to use a term introduced by Gibson (1986), in allowing apprehension and mapping of a space. For example, it seems that walls and doorways are of importance to place cells (O'Keefe and Burgess 1996; Spiers et al. 2015), and the grid cells form better grids when an environment is easily traversed than when it is not (Casali, Bush, and Jeffery 2019). This notion of affordances, which is a psychological construct, links with space syntax, which has long identified environmental features such as connectedness and line of sight (and hence traversal) with navigation. The role of movement affordances in shaping the spatial map is just beginning in neurobiology research, but it seems likely that in the near future it will connect with architectural framing of the same issues.

Conclusions

In summary, then, this article has set out to outline some of the recent advances in the cognitive neuroscience of space, deriving mainly from rodent studies, that have relevance to architecture. Foremost among these discoveries are the unearthing of a spatial mapping system, study of which has revealed that the brain uses different types of information in different ways. In designing spaces for human use it becomes important to understand how these different types of information are used. This article also highlights emerging research into environmental affordances and their role in shaping the cognitive map. In the future, it is to be hoped that architects will reach out to their cognitive neuroscientist colleagues so that the resulting knowledge exchange can productively enhance city design, and make spaces more easily navigable, and less stressful and more pleasing, for an urban population that grows ever-denser.

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References

Adolphs, R., D. Tranel, H. Damasio, and A. Damasio. 1994. "Impaired Recognition of Emotion in Facial Expressions Following Bilateral Damage to the Human Amygdala." *Nature*. doi:10.1038/372669a0.

Auger, Stephen D, and Eleanor A Maguire. 2013. "Assessing the Mechanism of Response in the Retrosplenial Cortex of Good and Poor Navigators." *Cortex* 49 (10): 2904–2913. doi:10.1016/j.cortex.2013.08.002.

Auger, Stephen D, Sinéad L Mullally, and Eleanor A Maguire. 2012. "Retrosplenial Cortex Codes for Permanent Landmarks." *PloS One* 7 (8): e43620. doi:10.1371/journal.pone.0043620.

Banaei, Maryam, Javad Hatami, Abbas Yazdanfar, and Klaus Gramann. 2017. "Walking through Architectural Spaces: The Impact of Interior Forms on Human Brain Dynamics." *Frontiers in Human Neuroscience* 11 (September): 1–14. doi:10.3389/fnhum.2017.00477.

Barry, Caswell, Colin Lever, Robin Hayman, Tom Hartley, Stephen Burton, John O'Keefe, Kate Jeffery, and Neil Burgess. 2006. "The Boundary Vector Cell Model of Place Cell Firing and Spatial Memory." *Reviews in the Neurosciences* 17 (1–2): 71–97. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2677716&tool=pmcentrez&rendertype=abstract.

Berridge, Kent C., and Morten L. Kringelbach. 2015. "Pleasure Systems in the Brain." *Neuron* 86 (3): 646–664. doi:10.1016/j.neuron.2015.02.018.

Bisiach, Edoardo, and Claudio Luzzatti. 1978. "Unilateral Neglect of Representational Space." *Cortex*. doi:10.1016/S0010-9452(78)80016-1.

Burgess, Neil. 2008. "Spatial Cognition and the Brain." *Annals of the New York Academy of Sciences* 1124: 77–97. doi:10.1196/annals.1440.002.

Byrne, P, S Becker, and N Burgess. 2007. "Remembering the Past and Imagining the Future: A Neural Model of Spatial Memory and Imagery." *Psychol Rev*.

Casali, Giulio, Daniel Bush, and Kate J. Jeffery. 2019. “Altered Neural Odometry in the Vertical Dimension.” *PNAS*, pii: 201811867. doi:10.1073/pnas.1811867116.

Cavanna, Andrea E., and Michael R. Trimble. 2006. “The Precuneus: A Review of Its Functional Anatomy and Behavioural Correlates.” *Brain*. doi:10.1093/brain/awl004.

Chaaya, Nicholas, Andrew R. Battle, and Luke R. Johnson. 2018. “An Update on Contextual Fear Memory Mechanisms: Transition between Amygdala and Hippocampus.” *Neuroscience and Biobehavioral Reviews* 92. Elsevier: 43–54. doi:10.1016/j.neubiorev.2018.05.013.

Chatterjee, Anjan, and Oshin Vartanian. 2014. “Neuroaesthetics.” *Trends in Cognitive Sciences* 18 (7): 370–375. doi:10.1016/j.tics.2014.03.003.

Cipriani, Gabriele, Claudio Lucetti, Angelo Nuti, and Sabrina Danti. 2014. “Wandering and Dementia.” *Psychogeriatrics* 14 (2): 135–142. doi:10.1111/psyg.12044.

Corkin, Suzanne. 2013. *Permanent Present Tense: The Unforgettable Life of the Amnesic Patient*. Vol. 1000. Hachette UK.

Coughlan, Gillian, Jan Laczó, Jakub Hort, Anne Marie Minihane, and Michael Hornberger. 2018. “Spatial Navigation Deficits — Overlooked Cognitive Marker for Preclinical Alzheimer Disease?” *Nature Reviews Neurology*. doi:10.1038/s41582-018-0031-x.

De Franceschi, Gioia, Tipok Vivattanasarn, Aman B. Saleem, and Samuel G. Solomon. 2016. “Vision Guides Selection of Freeze or Flight Defense Strategies in Mice.” *Current Biology* 26: 2150–2154. doi:10.1016/j.cub.2016.06.006.

De Lavilléon, Gaetan, Marie Lacroix, Laure Rondi-Reig, and Karim Benchenane. 2013. “Explicit Memory Creation during Sleep: A Causal Role of Place Cell on Navigation.” *Nature Neuroscience* 18 (4). Nature Publishing Group: 1–39. doi:10.1038/nn.3970.

Doeller, Christian F., Caswell Barry, and Neil Burgess. 2010. “Evidence for Grid Cells in a Human Memory Network.” *Nature*. doi:10.1038/nature08704.

Ekstrom, A D, M J Kahana, J B Caplan, T A Fields, E A Isham, E L Newman, and I Fried. 2003. “Cellular Networks Underlying Human Spatial Navigation.” *Nature* 425 (6954): 184–188. doi:10.1038/nature01955.1.

Epstein, R, and N Kanwisher. 1998. “A Cortical Representation of the Local Visual Environment.” *Nature* 392 (6676): 598–601.

Epstein, Russell A., Eva Zita Patai, Joshua B. Julian, and Hugo J. Spiers. 2017. “The Cognitive Map in Humans: Spatial Navigation and Beyond.” *Nature Neuroscience*. doi:10.1038/nn.4656.

Evans, Dominic A., A. Vanessa Stempel, Ruben Vale, Sabine Ruehle, Yaara Lefler, and Tiago Branco. 2018. “A Synaptic Threshold Mechanism for Computing Escape Decisions.” *Nature* 558: 590–594. doi:10.1038/s41586-018-0244-6.

Fox, Andrew S., and Alexander J. Shackman. 2017. “The Central Extended Amygdala in Fear and Anxiety: Closing the Gap between Mechanistic and Neuroimaging Research.” *Neuroscience Letters*. doi:10.1016/S0041-3879(38)80104-5.

Hafting, T, M Fyhn, S Molden, M B Moser, and E I Moser. 2005. “Microstructure of a Spatial Map in the Entorhinal Cortex.” *Nature*.

Hartley, Tom, and Neil Burgess. 2005. “Complementary Memory Systems: Competition, Cooperation and Compensation.” *Trends in Neurosciences*. doi:10.1016/j.tins.2005.02.004.

Jacobs, Joshua, Christoph T. Weidemann, Jonathan F. Miller, Alec Solway, John F. Burke, Xue-Xin Wei, Nanthia Suthana, et al. 2013. “Direct Recordings of Grid-like Neuronal Activity in Human Spatial Navigation.” *Nature Neuroscience* 16 (9): 1188–1190. doi:10.1038/nn.3466.

James J. Gibson. 1986. “The Theory of Affordances.” In *The Ecological Approach to Visual Perception*, 127–137. New Jersey: Lawrence Erlbaum.

Jeffery, K J, M I Anderson, R Hayman, and S Chakraborty. 2004. “A Proposed Architecture for the Neural Representation of Spatial Context.” *Neurosci Biobehav Rev* 28: 201–218.

Jeffery, K J, J G Donnett, N Burgess, and J M O’Keefe. 1997. “Directional Control of Hippocampal Place Fields.” *Exp.Brain Res.* 117 (1): 131–142.

Kumaran, Dharshan, Andrea Banino, Charles Blundell, Demis Hassabis, and Peter Dayan. 2016. “Computations Underlying Social Hierarchy Learning: Distinct Neural Mechanisms for Updating and Representing Self-Relevant Information.” *Neuron* 92 (5): 1135–1147. doi:10.1016/j.neuron.2016.10.052.

LeDoux, Joseph. 2003. “The Emotional Brain, Fear, and the Amygdala.” *Cellular and Molecular Neurobiology*. doi:10.1023/A:1025048802629.

Lopresto, Dora, Pieter Schipper, and Judith R. Homberg. 2016. “Neural Circuits and Mechanisms Involved in Fear Generalization: Implications for the Pathophysiology and Treatment of Posttraumatic Stress Disorder.” *Neuroscience and Biobehavioral Reviews* 60. Elsevier Ltd: 31–42. doi:10.1016/j.neubiorev.2015.10.009.

Maguire, E A, T Burke, J Phillips, and H Staunton. 1996. “Topographical Disorientation Following Unilateral Temporal Lobe Lesions in Humans.” *Neuropsychologia*.

Markus, E J, Y L Qin, B Leonard, W E Skaggs, B L McNaughton, and C A Barnes. 1995. “Interactions between Location and Task Affect the Spatial and Directional Firing of Hippocampal Neurons.” *J.Neurosci.*

Morris, R G, P Garrud, J N Rawlins, and J O’Keefe. 1982. “Place Navigation Impaired in Rats with Hippocampal Lesions.” *Nature*.

O’Keefe, J, and N Burgess. 1996. “Geometric Determinants of the Place Fields of Hippocampal Neurons.” *Nature*.

O’Keefe, J, and L Nadel. 1978. *The Hippocampus as a Cognitive Map*. Oxford: Clarendon Press.

Packard, M G, and James L McGaugh. 1996. “Inactivation of Hippocampus or Caudate Nucleus with Lidocaine Differentially Affects Expression of Place and Response Learning.” *Neurobiology of Learning and Memory* 72 (0007): 65–72.

Poldrack, R A, J Clark, E J Pare-Blagoev, D Shohamy, Moyano J Creso, C Myers, and M A Gluck. 2001. “Interactive Memory Systems in the Human Brain.” *Nature*.

Proulx, Michael J., Orlin S. Todorov, Amanda Taylor Aiken, and Alexandra A. de Sousa. 2016. “Where Am I? Who Am I? The Relation between Spatial Cognition, Social Cognition and Individual Differences in the Built Environment.” *Frontiers in Psychology* 7 (February): 1–23. doi:10.3389/fpsyg.2016.00064.

Ranck, James B. 1984. “Head-Direction Cells in the Deep Layers of the Dorsal Presubiculum in Freely Moving Rats.” *Society for Neuroscience Abstracts*.

Saarimäki, Heini, Athanasios Gotsopoulos, Iiro P. Jääskeläinen, Jouko Lampinen, Patrik Vuilleumier, Riitta Hari, Mikko Sams, and Lauri Nummenmaa. 2016. "Discrete Neural Signatures of Basic Emotions." *Cerebral Cortex* 26 (6): 2563–2573. doi:10.1093/cercor/bhv086.

Scoville, W B, and B Milner. 1957. "Loss of Recent Memory after Bilateral Hippocampal Lesions." *J. Neurol. Neurosurg. Psychiat.* 20: 11–21. doi:10.1136/jnnp.20.1.11.

Spiers, Hugo J., Robin M A Hayman, Aleksandar Jovalekic, Elizabeth Marozzi, and Kathryn J. Jeffery. 2015. "Place Field Repetition and Purely Local Remapping in a Multicompartment Environment." *Cerebral Cortex* 25 (1): 10–25. doi:10.1093/cercor/bht198.

Teitelbaum, H, and P Milner. 1963. "Activity Changes Following Partial Hippocampal Lesions in Rats." *J Comp Physiol Psychol.* 56: 284–289.

Wolbers, T, and C Buchel. 2005. "Dissociable Retrosplenial and Hippocampal Contributions to Successful Formation of Survey Representations." *J Neurosci*.

Wood, E R, P A Dudchenko, R J Robitsek, and H Eichenbaum. 2000. "Hippocampal Neurons Encode Information about Different Types of Memory Episodes Occurring in the Same Location." *Neuron*.

Woollett, Katherine, Hugo J. Spiers, and Eleanor A. Maguire. 2009. "Talent in the Taxi: A Model System for Exploring Expertise." *Philosophical Transactions of the Royal Society B: Biological Sciences*. doi:10.1098/rstb.2008.0288.

Figure captions

Figure 1. The three major spatial systems in the brain. The hippocampus (first image, dark blue) is closely related to the emotional processing amygdala (turquoise).

Figure 2. Recording of a place field. An electrode implanted into the hippocampus (blue structure) of the rat brain detects nerve impulses (called spikes). Each spike is identified and plotted as a red square on the place in the rat's exploratory path that the rat was at the moment the spike occurred – all the spikes from a particular neuron cluster in one place in the environment, called the place field.

Figure 3. Hemispatial neglect syndrome. Top: Clock faces drawn from memory by a patient with a right-sided parietal cortex stroke, showing neglect of the left side of the clock. Figure reproduced courtesy of Aikaterina Fotopoulou, University College London. Bottom: Copies of simple pictures made by a hemineglect patient: note the variable neglect of the left sides of the individual items, but also the left side of the whole page. Figure reproduced courtesy of Tania Nijboer and Antonia Ten Brink, Utrecht University.

Figure 4. Firing patterns of two grid cells, recorded by Giulio Casali in a 1.2m square environment using the same method as in Fig. 2. Note that each cell fires in multiple regions of the environment instead of just one, and also that there is a remarkably even spacing and consistent direction between these firing fields (shown by the yellow lines, which have the same length and are oriented at 120 degrees relative to each other). The regular spacing and orientation point to some process of direction- and distance-measuring, suggesting that the grid cells are integrating these two spatial parameters to enable processing of two-dimensional travel.

Figure 5. Types of symmetry. Left column: these examples have infinite rotational symmetry, such that from within, they provide few visual clues as to facing direction. Middle column: some environments, such as this one, have lower order rotational symmetry which still lends itself to visual confusion. The Kezar Stadium shown here was the site of Jim Marshall's famous wrong-way touchdown, in which he lost his sense of direction and was fooled by the visual ambiguity into reorienting in the wrong direction. The right-hand column shows examples of mirror symmetry – equally

aesthetically pleasing, they do not confuse the head direction system since no two visual scenes are identical.

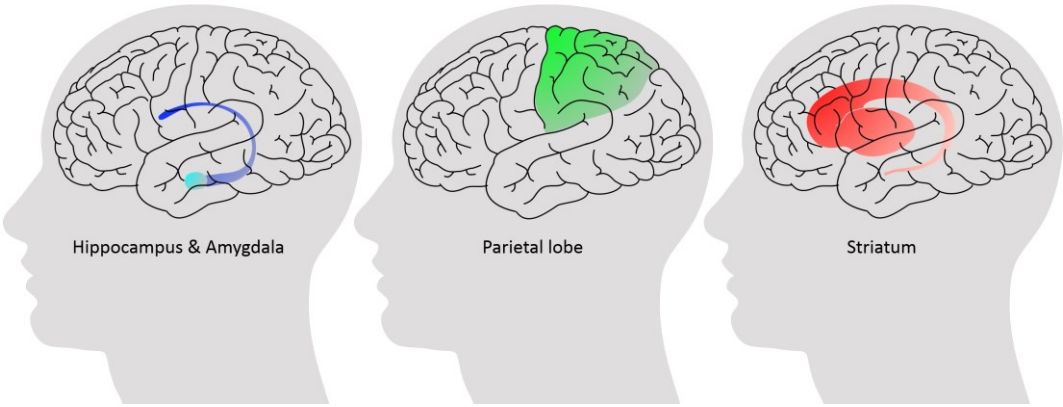


Figure 1

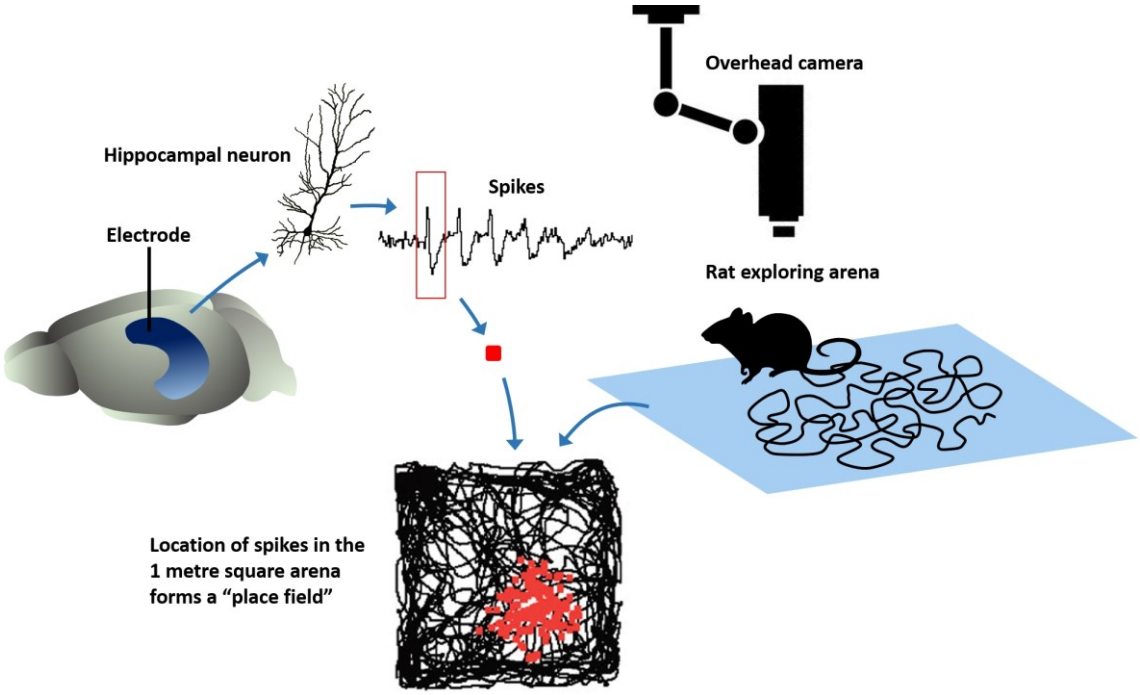
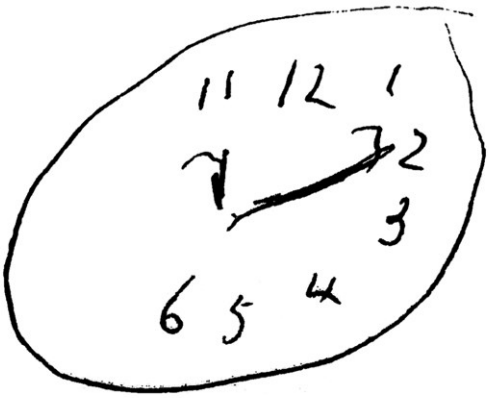

Overhead camera
Hippocampal neuron
Spikes
Electrode
Rat exploring arena
Location of spikes in the
1 metre square arena
forms a "place field"

Figure 2

From memory



Direct copy

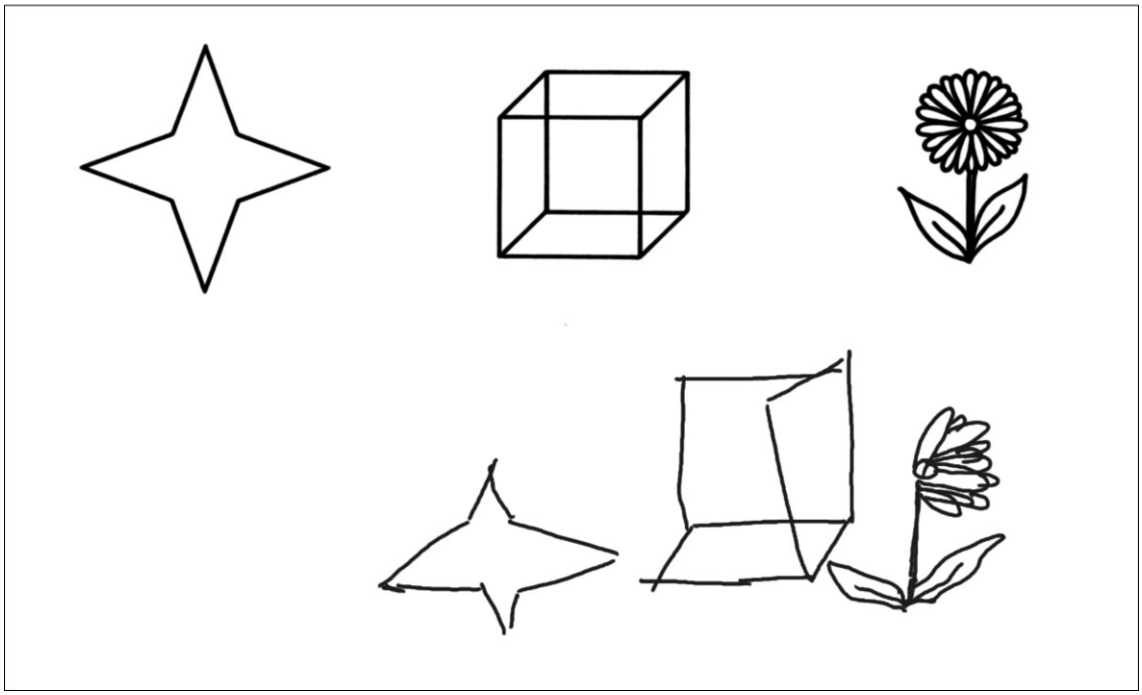


Figure 3

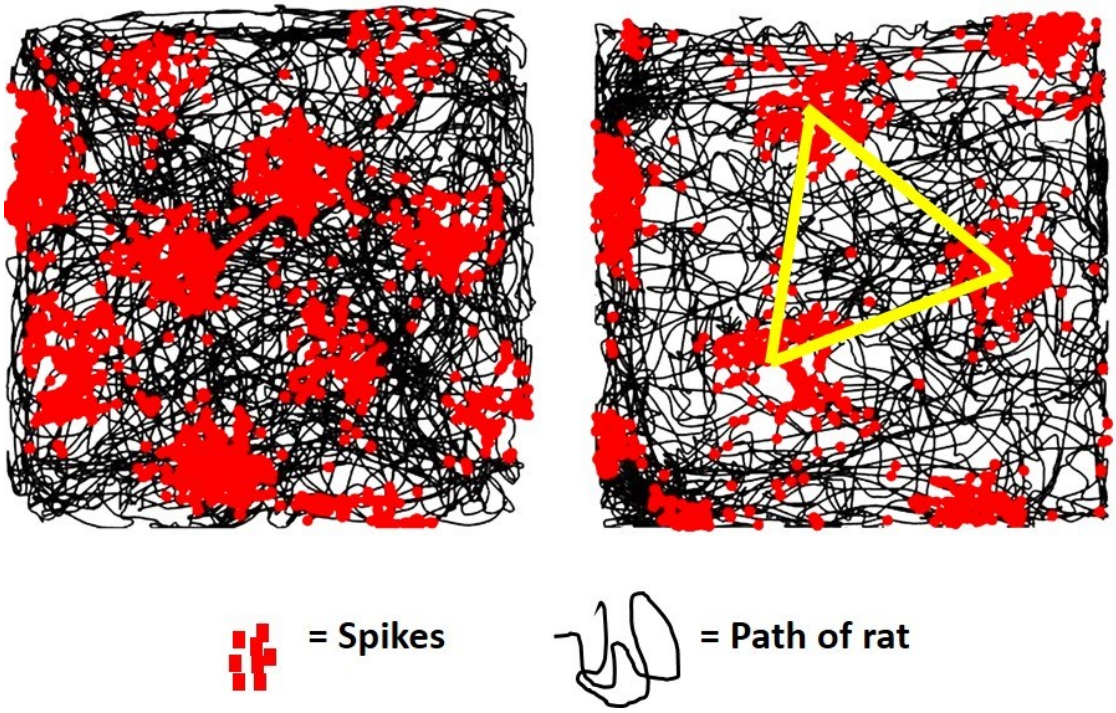


Figure 4

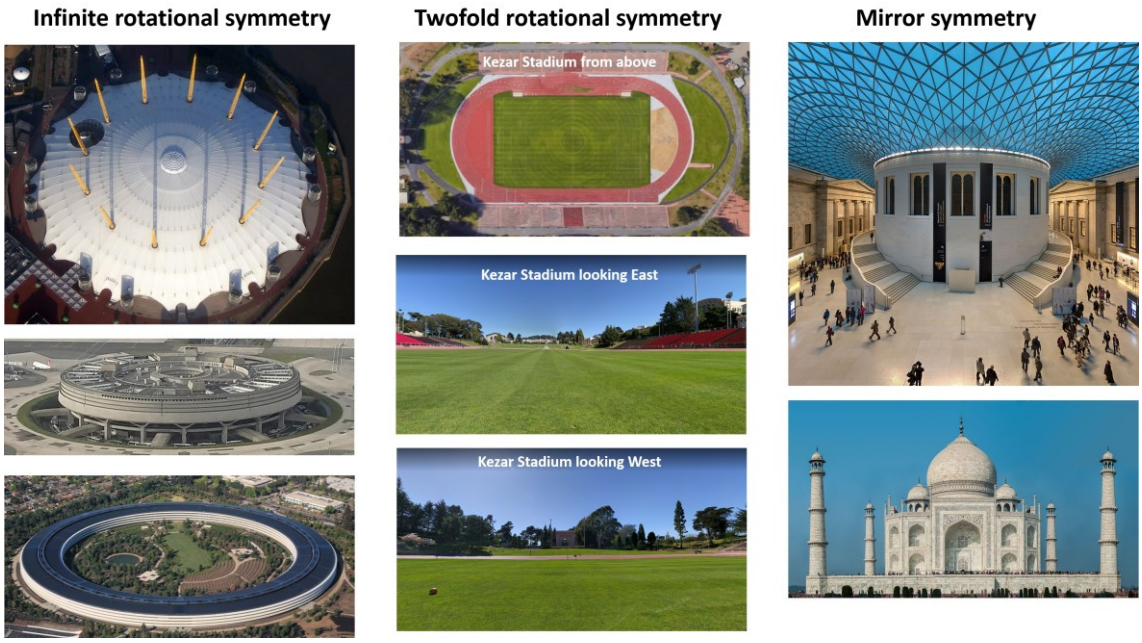

Infinite rotational symmetry
Twofold rotational symmetry
Mirror symmetry
Kezar Stadium from above
Kezar Stadium looking East
Kezar Stadium looking West

Figure 5