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Review

Lateralized perception: The role of attention in spatial relation processing

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ABSTRACT

Any spatial situation can be approached either categorically – the window is to my left – or coordinately – the glass is 20 cm away from the bottle. Since the first description of the distinction between categorical and coordinate spatial relation processing, it has often been shown that they are processed by at least partially different underlying mechanisms, mainly located in the left and right hemisphere, respectively. A number of recent studies have suggested that spatial attention plays a particularly important part in the perception of space: categorical processing benefits from a local focus of attention, and coordinate processing profits from a global focus of attention. This suggests that the lateralization pattern is modified by the concurrent size of the attentional focus, and is consequently more dynamic than previously thought. Therefore, a thorough revision of earlier theories on spatial relation processing is in order. In this review, we present a new model on lateralization of spatial relation processing that explicitly describes the role of spatial attention.

Contents

1. Introduction

When we interact with our environment, its spatial features are crucial to us. There are different ways to deal with these spatial features. If someone asks us where we left the car keys, we can respond with something like: 'I left them on the coffee table in the living room'. On the other hand, when we want to pick up those keys, it does not help much to know they are on the table; we need to know their exact location with respect to our hand in order to plan and execute our movement. These two examples illustrate the two main types of spatial relation processing. The first example shows that we can process spatial relations between objects in an abstract, propositional way, which is termed *categorical*. We can use this type of spatial relation to give directions or memorize where we left things. In contrast, in the second example we use the precise, metric properties of spatial relations, or *coordinate* spatial relations, when we navigate or grasp objects.

The characteristics of these spatial relations are in part dictated by the type of 'coordinate system' that is used to represent spatial characteristics. Such coordinate systems can be either egocentric (observer based) or allocentric (environment based) (see

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e.g. Klatzky, 1998; Majid et al., 2004). In an egocentric coordinate system, these spatial relations by definition concern the relation between an external object and the observer, such as 'the car is to my left' or 'I am closer to the library than you are'. Neurophysiological studies on primates indicate that visual space is constructed many times over, according to a variety of frames of reference, each attached to different parts of the body and possibly subserving different functions (Dent 2009, Graziano and Gross, 1995). Neuroimaging in humans confirms that one of the topographic maps of the parietal lobes is based on a head-centered coordinate frame (Sereno and Huang, 2006). A plurality of sensorimotor action spaces can be related to specific effectors that have the ability to move independently from the rest of the body (e.g. hand, head, and eye). In such motor-oriented frames of reference, spatial relationships between two locations can be coded in terms of the movements required to act or move from one to the other (Paillard, 1991).

In an allocentric coordinate system the relation concerns two objects or parts of objects that are defined according to a reference frame whose fulcrum is located outside of the observer‘s body. Examples of spatial relations from an allocentric perspective are: 'the church is to the North of the square' and 'you are 200 meters West from the library'. Crucially, both categorical and coordinate spatial relations can be applied within these different frame of reference and coordinate systems (see also Ruotolo et al., 2011a,b; Ruggiero et al., 2012). In this review we focus on the direct comparison of categorical and coordinate spatial relations, regardless of the coordinate system used. All that is discussed here can equally apply to spatial relation processing in an egocentric as well as an allocentric or object-based perspective.

The distinction between categorical and coordinate spatial relations is not only reflected by clear differences in functionality, but also refers to different underlying processing mechanisms. Although described earlier by McNamara (1986), Kosslyn (1987) provides the first elaborate theoretical framework to understand the differences between categorical and coordinate processing. He introduced the idea that the two types of spatial relations are processed by two different subsystems in the human brain, which have lateralized due to evolutionary processes. Categorical spatial relation processing is thought to be lateralized to the left, whereas coordinate spatial relation processing is argued to be right lateralized.

Over the years, many experimental studies have been performed concerning this distinction, which have enabled a fine-tuning of the original theory (see for review, e.g. Jager and Postma, 2003; Laeng et al., 2003; Laeng, 2014). Recent empirical studies have brought new evidence to the table and point toward a substantial role of spatial attention in explaining differences between categorical and coordinate processing. This offers a novel theoretical perspective. Therefore, an up-to-date review of current evidence and the impact of these findings on the theoretical framework underlying categorical and coordinate spatial relation processing is called for. In this review, we first provide an overview of the main experimental work on spatial relation processing, particularly recent work. Then we discuss what this tells us about the nature of spatial relation processing, and focus on the role of spatial attention in particular. We present a new framework to fit the experimental findings on how spatial attention affects spatial relation processing and its lateralization. Lastly, we will explore how spatial relation theory translates to human visual perception in general.

2. Empirical evidence

Soon after Kosslyn's first publication on the topic of spatial relation processing (Kosslyn, 1987) numerous behavioral studies attempted to empirically prove the distinction (e.g. Hellige and Michimata, 1989; Kosslyn et al., 1989; Koenig et al., 1990; Bruyer et al., 1997; Wilkinson and Donnelly, 1999; Banich and Federmeier, 1999). These studies were mainly aimed at verifying the double dissociation of type of spatial relation and hemisphere. Typically, very simple stimuli were used in these studies. The dot-bar stimuli have been used in most of these early studies. These stimuli consist of a horizontal bar with a dot presented either above or below the bar, at varying distances, as illustrated in Fig. 1. The categorical

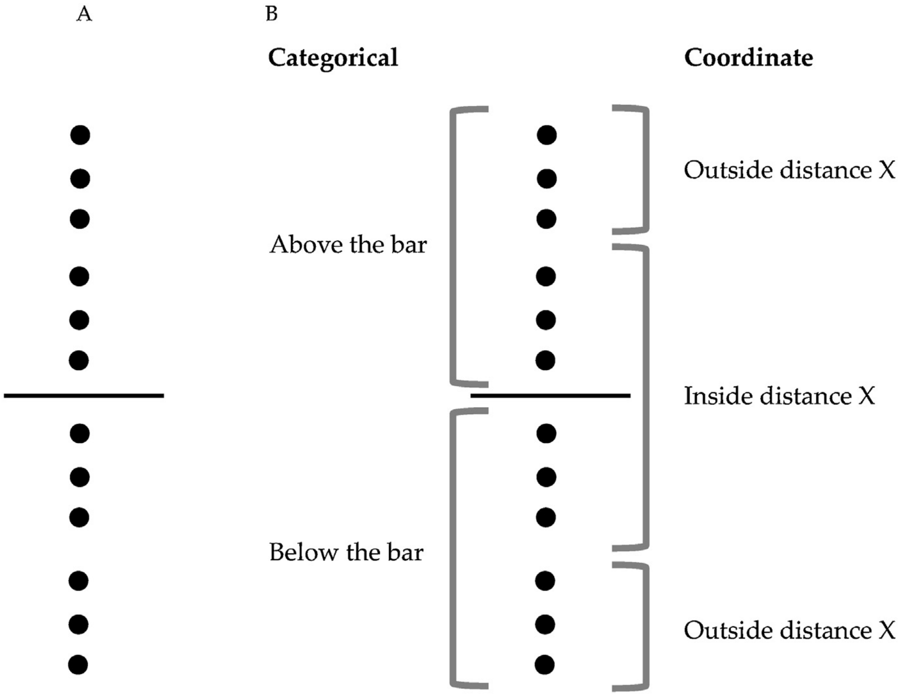

Fig. 1. The often used dot-bar stimulus, (A) with all possible dot positions, (B) dots above the bar belonged to one spatial category, the dots below the bar to the other spatial category, and dots within a particular distance of the bar belonged to one type of coordinate relation, dots not within this distance belonged to the other type of coordinate relation. Note the during the task, only one dot position would be visible.

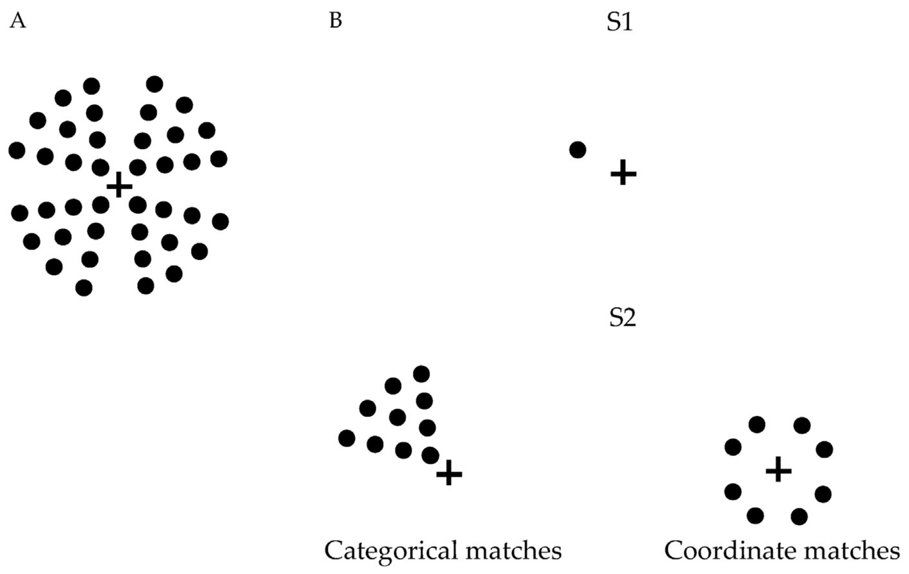

Fig. 2. Version of the cross dot stimulus, used in working memory designs, (A) with all possible dot positions, (B) with a given dot position for the first stimulus (S1), the dots shown as S2 that would match categorically are shown on the left, and the dots that would match coordinately are shown to the right. Note that during the task, only one dot position would be visible for both S1 and S2.

instruction in this case, was to indicate whether the dot is 'above' or 'below' the bar, regardless of distance. The coordinate instruction in turn, was to focus on the distance and indicate whether the dot is 'within' or 'not within' a predetermined distance, regardless of side. An important feature of this design was that the stimulus layout was identical and only the instruction varied between the two versions of the task.

In these behavioral studies, a visual half field design was used to assess lateralization patterns by means of response times and accuracy for stimuli presented to the left or right visual field. This approach was soon followed by studies in which lateralization was determined with more direct and precise measures of brain activity: positron emission tomography (PET), functional magnetic resonance, imaging (fMRI and MEG), electroencephalography (EEG), and transcranial magnetic stimulation (TMS). In the vast majority of these studies, the lateralization pattern was further substantiated (e.g. Baciu et al., 1999; Kosslyn et al., 1998; Trojano et al., 2002, 2006; van der Ham et al., 2009; Franciotti et al., 2013). Several studies on patients with unilateral brain damage also supported these findings (e.g. Laeng, 1994; Palermo et al., 2008; van der Ham et al., 2011, 2012a,b,c). Overall, the parietal cortex seemed of particular importance; left parietal cortex was mainly linked to categorical processing, whereas the right parietal cortex was involved mostly with coordinate processing. Yet, the original theory as proposed by Kosslyn needed some attenuation. Most of the foregoing findings indicate that the lateralization pattern is not mutually exclusive: both hemispheres are involved in processing each type of spatial relations, but they show a clear bias toward one of the two types.

Aside from the many techniques that have been used to study this dichotomy, various task designs have been applied as well, facilitating different research questions. The first number of studies was designed to study spatial relation processing in perception: a response was required to a briefly presented, simple stimulus. Results from these studies illustrate how we process the spatial features of visual stimuli. Later experiments also focused on spatial relation processing in working memory task designs, in which two sequentially presented stimuli were compared (e.g. Laeng, 1994; van der Ham et al., 2007), and in a mental imagery paradigm (Michimata, 1997; Palermo et al., 2008) where clock faces had to be imagined. These studies have shown that the typical lateralization pattern reflecting separate processing mechanisms can also be generalized to visual working memory and mental imagery.

Although the double dissociation of relation type and hemisphere is found in the convincing majority of these studies, the effects have shown to be sensitive to the methodology used. For instance, Baciu et al. (1999) showed that over time, participants started to categorize the coordinate task, as reflected by a shift from a right hemisphere to a left hemisphere dominance during the experiment. This has been explained with a critical and disadvantageous feature of the dot-bar stimulus layout. The dot could only appear at a fixed number of positions and the instruction entailed a categorization of distances into 'within' a particular distance and 'not within' a particular distance. Therefore, participants could well start to realize this limitation and categorize the distances instead of encoding them as exact distances. The cross-dot working memory paradigm (see Fig. 2) in which two distances were compared later solved this problem as participants continued to encode the exact distance, not a distance category in this type of task. Also the higher amount of possible dot positions avoided categorization. Another study (van der Ham et al., 2007) showed that categorical information decays slower than coordinate information. In a working memory task design, the interval between two stimuli therefore determines whether a double dissociation is found or not, typically it is found with an interval of 500–2000 ms.

In short, a large number of studies making use of various techniques and task designs demonstrate that there is a relative advantage of the left hemisphere in processing categorical information, and of the right hemisphere in processing coordinate information. Yet, specific task demands can affect this lateralization pattern.

3. Critical evaluation

A main point of criticism that can be made is whether it is really meaningful to study this distinction. What could we learn from such a distinction? Newell (1973) criticizes the tendency of psychologists to test binary distinctions, as supposedly these are typically not present in nature. Kosslyn (2006) argues against this statement, as for spatial relation processing such a clear distinction is present. In fact, the general idea behind lateralization of spatial relation processing should be viewed in a more general way. The brain is thought to 'divide-and-conquer' when it comes to processing information. If incoming information needs to be processed, it would be inefficient if both hemispheres would do this in the same way and then needed to communicate about this. Therefore, from an evolutionary point of view, lateralization, or the division of labor between the two hemispheres, will lead to more efficient and faster processing (see e.g. Hugdahl, 2000; Cook, 1986). Although categorical and coordinate spatial relations are generally thought to be based on partially separate processing mechanisms, sufficient evidence exists for it to be considered a clear binary, and lateralized distinction. Furthermore, we would like to argue that studying how we process spatial relations is meaningful, as it can be generalized to many areas of perception, as discussed later.

Despite the large amount of supporting evidence for the dichotomy, alternative explanations have been proposed as well. One prevalent alternative is that of space versus language. The traditional line of reasoning is that the right hemisphere typically processes spatial information, whereas verbal information processing is located in the left hemisphere. Therefore, it has been argued that in particular the left hemisphere advantage of categorical processing is due to the linguistic properties of this type of processing. In the dot bar task for instance, the use of propositions 'above' and 'below' suffices to solve the task. Kemmerer and Tranel (2000) argued there might be a triad instead of a dichotomy, with categorical relations split up into strictly spatial categories and verbal categories. They proposed that only the processing of verbal categories shows a left hemisphere bias. Yet, a number of studies argue against the fact that left lateralization is based primarily on the verbal content of processing. For categorical perception in general, it has been shown that pre-verbal infants show mainly left hemisphere activity when they categorize spatial orientations (Franklin et al., 2010). Also, no difference in lateralization pattern is found when people use labeled or unlabeled categories, indicating that language is not the main factor in the direction of lateralization (Holmes and Wolff, 2012). Within spatial relation processing in particular, the verbal nature of categorical stimuli could only explain for a minor part of the left lateralization (van der Ham and Postma, 2010). This is further substantiated by Suegami and Laeng (2013), who found that although categorical relations can be coded semantically as well as visuospatially, a left lateralization is found for both. As language processing is convincingly based in the left hemisphere, it is likely that it has some effect on the extent of lateralization when participants use verbal strategies to solve categorical tasks. Yet, given the current evidence it seems highly unlikely that language by itself is the determining factor in the direction of lateralization.

A second alternative explanation that has come up is that of difficulty. Typically, processing categorical relations is easier to do than processing coordinate relations. Sergent (1991a,b) was the first to therefore suggest that instead of a dichotomy of categorical and coordinate, it might be a continuum between easy and difficult. The more difficult a task would get, the more the right hemisphere would get involved. Although Sergent's point of view was experimentally disproven by Kosslyn et al. (1992) and Slotnick et al. (2001), this point has also been used to explain experimental results by Van der Lubbe et al. (2006) and Martin et al. (2008) in later studies. Yet, a more recent fMRI study van der Ham et al. (2012a,b,c) again demonstrated that task difficulty itself cannot explain for the lateralization patterns found (see also Franciotti et al., 2013). It cannot be denied that there are adherent difficulty differences between categorical and coordinate processing, but when reviewing the evidence, difficulty does not seem to determine the lateralization pattern.

4. Attentional scope

Given that categorical and coordinate spatial relation processing are markedly distinct at a neurocognitive level and cannot be merely explained by characteristics like involvement of language or task difficulty, the question remains what exactly is the nature of spatial relation processing? A number of recent studies suggest a novel, appealing answer to this question, by looking into spatial attention and more specifically the size of attentional scope. Spatial attention is not an entirely new element in the ideas on spatial relation processing. Actually, in his first report Kosslyn (1987) already commented on the issue. He described the purpose of spatial relation interpretation as looking up the location of the relevant part and directing attention to this location, leading to the output of instructing the attention-shift subsystem to shift attention accordingly. He proposed that for both categorical and coordinate interpretation this process is the same, except for the nature of the representation used to do this, which is either categorical or coordinate. Several behavioral studies indicate that the difference in representation – categorical or coordinate – is closely related to the size of the attended location. Categorical processing is found to benefit most from a local, small focus, whereas coordinate processing seems more efficient with a global, large focus of attention. In several experiments this same pattern was found when manipulating the area participants attended to (Okubo et al., 2010; Michimata et al., 2011; Borst and Kosslyn, 2010; Laeng et al., 2011; Franconeri et al., 2012; Franciotti et al., 2013). Moreover, the same attentional pattern was also found in the absence of experimental manipulations. In a case study, patient NC showed great difficulty in processing coordinate information in particular, which coincided with a clear local bias, as opposed to the global bias generally found in human visual perception (van der Ham et al., 2012a,b,c). In line with this, it has also been shown that children with right hemisphere damage show a combination of impairment in global focus and coordinate judgments (Schatz et al., 2004). Furthermore, with retinotopic mapping of fMRI data, it has been shown that participants directed their attention more locally when they were asked to give categorical responses, as compared to coordinate responses (van der Ham et al., 2012a,b,c).

The interpretation of this dissociation between categorical and coordinate processing in terms of size of attentional focus revives an older idea about spatial relation processing: the link to receptive field sizes. In a computational model (Kosslyn et al., 1992) the flow of information in processing categorical and coordinate information was simulated. This simulation showed that the categorical decisions benefited from the use of small receptive fields, whereas the opposite was found for coordinate information. This difference makes sense when considering the functionality of the two types of relations. The smaller, non-overlapping fields facilitate splitting up space into distinct areas, or categories, and large, overlapping fields facilitate 'coarse coding' (Hinton, 1981), which helps to derive precise metric information. This is substantiated by the studies showing that attentional focus is different between categorical and coordinate processing. An important addition provided by the spatial attention studies is that they show that it concerns a dynamic process: the size of the attentional focus seems to be attenuated according to the task at hand, rather than to be fixed (Fig. 3).

Based on the recent empirical evidence concerning the role of attentional focus, we present a new model to explain for the lateralization effects found for spatial relation processing. This model highlights that both task instruction and stimulus size have a pivotal role in predicting the lateralization effect. Task instruction reflects the original theory: a categorical task instruction will lead to a left hemisphere advantage, and a coordinate instruction to a right hemisphere advantage. Stimulus size has a major role in this

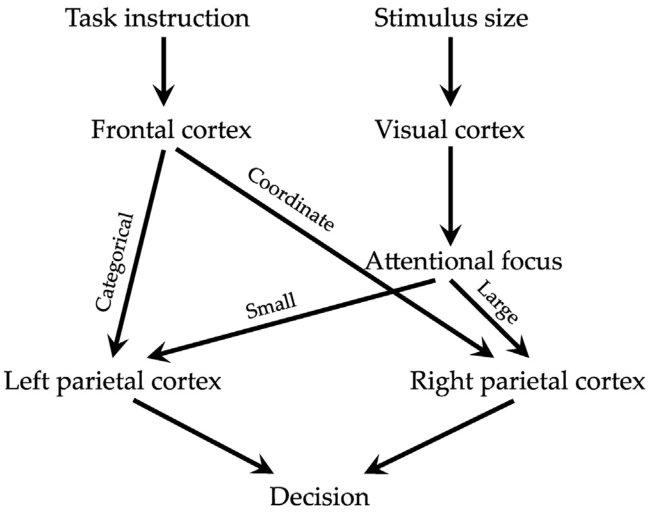

Fig. 3. The model of information processing resulting in a spatial relation decision. Both task instruction and stimulus size contribute to the lateralization pattern.

model. It refers to the size of the crucial elements of the visual stimulus and directly determines the attentional focus that is required for a specific spatial relations decision. When stimulus size is relatively small, the attentional focus will also be relatively small and lead to a left hemisphere advantage in processing. Conversely, a relatively large stimulus size will create a large area of attentional focus and consequently result in a right hemisphere advantage.

This new model highlights that lateralization in visual perception is not solely determined by task instruction. Attentional focus has been demonstrated to yield a considerable impact as well. The addition of stimulus size not only explains for the recent findings concerning small and large attentional scope and categorical and coordinate spatial processing, respectively, it could also account for variations in extent of lateralization found in different studies over the years. Precise stimulus features like size have been largely ignored over the years. The main criterion has been that the stimulus layout would be identical for categorical and coordinate decisions, in the sense that only the instruction would determine whether it was a categorical or coordinate task. Yet, the elements of those stimuli that are crucial for making a correct decision differ nonetheless. For instance, with the cross dot stimuli in Fig. 2, the categorical decision only requires to check one fourth of the total stimulus area (the second dot is either in that area or not), whereas for the coordinate decision, the entire stimulus area should be attended (the second dot can appear in any direction relative to the center). Therefore, it is important to realize there are two forces at work here.

5. Bringing together dichotomies in low-level perception

By discussing size of attentional focus, the local versus global dichotomy naturally comes to mind. This is another classical dichotomy proposed to describe human perception (e.g. Navon, 1977) that has been shown to be lateralized (e.g. Martin, 1979). Although it is an inherent continuous property, it is typically regarded as a dichotomy of ‘relatively small’ versus ‘relatively large’. A meta-analysis confirmed the general finding that there is left hemispheric specialization for local information and the right hemisphere shows an advantage in processing global information (Van Kleeck, 1989). Furthermore, the notion of receptive field sizes is directly related to the processing of high and low spatial frequencies, also a dichotomy with a distinct lateralization pattern. The commonly found direction of lateralization in spatial frequency processing tasks has been framed in the spatial frequency hypothesis; the left hemisphere is more proficient in processing high frequency and the right hemisphere in processing low frequency information (Sergent, 1983). This has been supported by a number of studies (e.g. Mecacci, 1993; Proverbio et al., 1997). Surprisingly little research has been done in which these different dichotomies have been directly integrated. Frequency manipulations have been applied in categorical-coordinate tasks to investigate a possible interaction. Okubo and Michimata illustrated that the coordinate right hemisphere advantage disappeared when low spatial frequencies were eliminated from the stimuli (Okubo and Michimata, 2002, 2004). The categorical left hemisphere advantage disappeared when high spatial frequencies were filtered out in the stimuli. Yet, such a relation between spatial frequency and spatial relation processing is contradicted by Niebauer and Christman (1999).

The ‘double filtering by frequency model’ created by Ivry and Robertson (1998) provides a theoretical framework for this particular topic. In their model they provide a unitary explanation of lateralization effects in visual perception. They base their claim on the premise that some of our perceptual systems make use of a Fourier analysis to describe incoming information, and that the left and right hemisphere have a bias toward processing high and low spatial frequencies, respectively. Their model is therefore based on the frequency characteristics of incoming stimuli. It proposes three separate and sequential stages of stimulus processing: sensory representation, selective filtering of task-relevant information, and asymmetric filtering by cerebral hemisphere of selected information. In the first filtering stage an attentional mechanism serves as a filtering system with regard to the frequency spectrum; the region selected in the spectrum can be as narrow or broad as required by the task performed. The actual lateralization does not occur until the second filtering stage, during which higher order analyses are taking place, for which each hemisphere has its preference. The processing in the left and right hemisphere is considered high-pass and low-pass filtering operations, respectively. As Ivry and Robertson (1998) state: “*The central hypothesis of the DFF theory is that the output of those filtering operations underlies many of the laterality effects reported in visual and auditory perception*”. These laterality effects are very likely to include local-global and categorical-coordinate processing. The authors indicate the model is a post hoc interpretation of experimental studies and new empirical input is necessary to examine its validity. The recent findings concerning attentional focus, described above appear to fulfill this need. As the local and global focus of spatial attention is directly related to categorical and coordinate spatial relation processing, respectively, these findings underline this model. Importantly, ‘task instruction’ as defined in the model does not seem to be restricted to spatial relation task instruction, but can easily be replaced by other types of spatial instructions, like local versus global.

6. Generalizing the dichotomy to higher level perception

With a new model reflecting the main findings concerning spatial relation processing, it is imperative to attempt to explore generalization of this theory. As mentioned earlier, the vast majority of fundamental studies providing information about how we process categorical and coordinate information use very simple stimulus layouts, consisting of lines, crosses, and dots. How do these findings relate to how we process visual information in real life? Several researchers have asked this question and looked into spatial relation processing within objects (e.g. Laeng et al., 1999; Saneyoshi et al., 2006; Saneyoshi and Michimata, 2009), faces (Cooper and Wojan, 2000), natural scenes (van der Ham et al., 2012a,b,c), and even in the dynamic process of navigation (Baumann et al., 2012). These studies have largely underlined the evidence from the studies with simple stimuli: a clear dissociation between the two types in terms of underlying processes. So, the distinction appears to hold regardless of visual complexity, meaning, and context. Yet, in a study on spatial relations in objects Amorapanth et al. (2010) apply some nuance to this: only part of the brain areas involved in spatial relation processing were separate, other areas appeared to be shared for both types. Taken together, it seems that the way in which we perceive the spatial relation information in the world finds its basis in the theories discussed here.

7. Conclusion

Over 25 years of research supports the view that categorical and coordinate spatial relations are processed by at least partially different underlying mechanisms, mainly located in the left and right hemisphere, respectively. Moreover, this distinction is found within perception (of either space or objects), working memory, and mental imagery. Several criticisms have been uttered in response to these findings. Yet, the alternative explanations for the findings recapitulated here do not match up to the existing theory: language only seems to play a minor part and a difficulty continuum seems highly unlikely.

Spatial attention plays a particularly important part in recent empirical studies on the perception of space. Categorical processing benefits from a local focus of attention, whereas coordinate processing is more efficient when a global focus of attention is applied. Therefore, the original theory on the role of receptive field sizes has been revived, and seems to be more flexible than previously thought. Furthermore, it also highlights the interplay between various dichotomies widely described within perception and in part supports Ivry and Robertson's Double Filtering by Frequency Model. We propose that the clear distinction between categorical and coordinate is closely linked to the continuous measure of attentional scope. The rigid distinction between the two can therefore be attenuated by this factor, as a result of experimental characteristics and innate preferences.

Finally, we see that the findings discussed here do not only reflect how we process simple laboratory stimuli, but also how we see the world. The dichotomy has shown to be a major factor as well in how we process objects, faces, scenes, and interact with our environment.

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