On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence

Gerry Jager a, b, Albert Postma a, b

a Psychological Laboratory, Utrecht University, Heidelberglaan 2, NL-3584 CS Utrecht, The Netherlands
b Department of Psychiatry, Magnus Institute of Neuroscience, University Medical Center, Utrecht, The Netherlands

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Abstract

This article reviews current evidence on the hemispheric specialization hypothesis for two types of spatial relations representations; categorical versus coordinate [Psychol. Rev. 94 (1987) 148; J. Exp. Psychol.: Percept. Perform. 15 (1989) 723]. Categorical representations capture general properties of the spatial structure of a visual stimulus, without defining the exact metric properties. Coordinate representations specify precise spatial locations of objects or parts in terms of metric units. It is claimed that a hemispheric difference in contribution to the computation of both types of spatial relations representations exists, in which the left hemisphere is specialized for the computation of categorical spatial representations while the right hemisphere is specialized for the computation of coordinate ones. Several forms of research (experimental, computer simulations, patient studies and neuroimaging studies) are reviewed. In general, there is convergent evidence for a conceptual separation of coordinate and categorical processing, with strongest indications for a relative right hemisphere advantage in encoding coordinate spatial relations, and weaker support for left hemispheric categorical specialization. The pattern appears to be critically linked to receptive field properties of the two hemispheres and as such is modulated by certain elementary visual characteristics of the displayed stimuli.

Keywords: Categorical and coordinate spatial relations; Hemispheric mechanisms

1. Introduction

Visual information processing critically depends on establishing spatial relations between elements in the visual display. In general, two types of spatial relations or representations can be distinguished [17,21,28]. Coordinate relations specify precise spatial locations of objects or object parts in terms of metric units and give exact distances. In turn, categorical relations form general, abstract codes, capturing basic relational and invariant spatial information in the visual world. They assign a spatial configuration or a range of positions to an equivalence class (such as above/below, left/right, inside/outsdie of) without defining the exact metric properties. The need for this distinction derives from the fact that the two relations would serve different purposes in guiding behavior. Broadly speaking, there are two contexts in which people use spatial information. First, people use spatial information to guide actions (moving the eyes towards an object, reaching, navigating, etc.). In this context, the brain needs specified metric spatial information because simply knowing the cup to be ‘on’ the table is not enough if we want to reach for it. That is, we do not just grope about, but make a precise movement towards the cup. Second, people need spatial information for identifying objects or scenes. In case of identifying ‘a cup on the table’ the brain does not need a specified metric spatial representation. Representation of the abstract spatial relations between the cup and the table, such as ‘the cup is on the table’, is sufficient. Moreover, this type of general, abstract representations of spatial relations is important in the identification and recognition of objects under various viewpoints and in various positions [26].

Assuming that there is an essential distinction between categorical and coordinate representations, it seems straightforward to consider the engagement of different underlying neural substrates as well. Kosslyn et al. [28] proposed that the left cerebral hemisphere would be involved specifically in categorical processing, whereas the right hemisphere should be more specialized in computing coordinate information. In particular, the posterior parietal lobes seem involved [22]. According to the original theory, this hemispheric difference could have several reasons [8,28]. First,
one reason lies in the fact that the left hemisphere is
dominant for language processing in right-handed people.
Because of the importance of category-formation in many
aspects of language, it was conjectured that the left hemi-
sphere might be dominant for categorical processing in gen-
eral, including that used in visual spatial processing. Second,
there is evidence that the right hemisphere plays a dominant
role in navigational processes and attentional search, in
which coordinate representations are critical [28]. Finally,
the lateralization in processing spatial relations might be the
consequence of hemispheric differences in the use of input
from low-level visual neurons with relatively large receptive
fields versus input from low-level visual neurons with rela-
tively small receptive fields. Neurons differ in their recep-
tive field sizes, which overlap to differing degrees. That is,
low-level visual neurons with large receptive fields receive
input from relatively large regions of space and their recep-
tive fields have a certain overlap, while neurons with rela-
tively small receptive fields, which do not overlap as much,
define particular (small) areas of space. Based on the devel-
OPment of computational models, Kosslyn and coworkers
[8,25,26] argued that categorical processing is facilitated by
attending to the outputs of neurons with relatively small,
on-overlapping receptive fields. Focusing on one object,
the receptive fields for the surrounding space are grouped
into separate ‘bins’ that have specific categorical relations
relative to the objects being focused on, allowing the brain to
categorize the relation of a second object that falls into one
of these bins, relative to the first one. If on the other hand
outputs from neurons with relatively large, overlapping re-
ceptive fields are attended to, effective coarse coding is (that
is, coding of larger regions of space) facilitated. This situ-
ation allows the brain to localize an object precisely, based
on the specific profile of activation, by combining signals
from neurons with overlapping receptive fields (cf. [8]).

The theory on the categorical-coordinate distinction
claims that the left hemisphere may use more input from
low-level visual neurons with small, non-overlapping recep-
tive fields than the right hemisphere. In contrast, the right
hemisphere may be biased in the opposite direction, using
more input from neurons with overlapping, large receptive
fields [8,25,26]. These hemispheric differences in the use of
input from lower-level visual neurons are consistent with
findings of differential hemispheric sensitivity towards dif-
ferent channels or bands of low-level sensory information,
for instance spatial frequency patterns [3,17,18,26]. As the
hemispheric specialization theory evolved over time, it was
suggested that hemispheric differences in attentional biases
might also contribute to differences in spatial processing.
For many tasks, it seems not possible to attend to both large
and small regions of space at the same time. So, there is a
need for two separate types of attentional biases, one for
small regions of space and one for large regions. The left
hemisphere is viewed as having an attentional bias toward
processing information from small regions of space, partly
because it tends to monitor information from neurons with
relatively small and non-overlapping receptive fields. The
right hemisphere is thought to have an opposite attentional
bias toward processing information from larger regions of
space, induced in part by the right hemisphere’s tendency
to monitor information from neurons with relatively large
and overlapping receptive fields [3,8,22,24].

Kosslyn’s original proposal inspired a large number of
several studies. Sometimes, disaccord findings have been
reported (see later). Almost 15 years later, the question is
how strong the supposed hemispheric differentiation for cat-
ergical and coordinate relations really is. As such, it was the
purpose of the present study to present a critical overview of
the currently existing literature. Four lines of evidence were
considered: experimental (visual half field) studies, com-
puter simulations, patient lesion studies, and brain imaging
work. In addition, an attempt was made to determine the
factors, which may contribute to the lateralization pattern
(see also [5,57]).

2. Functional dissociations

Studies aimed at obtaining functional dissociation be-
 tween categorical and coordinate processing in the left and
right hemisphere all have employed the visual half field
methodology. The visual half field methodology is charac-
terized by selectively presenting a stimulus for a very short
period to one visual half field at the time. As a consequence,
one hemisphere has access to the stimulus before the other.
A relative left hemisphere advantage (faster RTs, fewer er-
rors) is expected for a categorical task, whereas superior right
hemisphere performance should be observed for the coordi-
nate conditions. Most of these experiments have a handsome
design using the same set of stimuli in all conditions. For
example, a line with a dot either above or below it is flashed.
What differs is the sort of judgment subjects are instructed
to make, i.e. is the dot below or above the line (abstract cat-
ergical judgment) or is it, for instance within 1 cm of the
category or not (precise coordinate judgment).

The first studies on the categorical-coordinate relation
distinction simply looked at finding visual field effects, in-
dicating functional lateralization. For example, Hellige and
Michimata [15] compared categorical and coordinate judg-
ments using stimuli consisting of a small dot and a horizon-
tal bar. In the categorical task, subjects were asked whether
the dot was above or below the bar, while in the coordinate
task they had to decide whether the dot was further or less
than 2 cm apart from the bar. Both tasks were presented very
briefly (150 ms) to the left, center and right visual fields,
respectively. It was reasoned that if the two tasks did rely
on a single process, i.e. if categorical and coordinate spatial
relations were not distinct, then there should be no differential performance on both tasks between both hemispheres. However, their results showed that the coordinate task was performed better by the right hemisphere, whereas the categorical task was performed better by the left hemisphere. Later investigations focused more on the factors modulating lateralization patterns. Two modulators, which have been considered, are gender and handedness. Both women and left-handers are associated with distinct patterns of lateralization [36,47,58], and thus, gender and handedness may affect categorical and coordinate performance in a special way. Other factors include task difficulty, response mode, practice, and feedback. Finally, characteristics of the actual stimuli, such as display features and exposure duration, have proven to be important.

2.1. Gender

Generally, it is thought that functional hemispheric asymmetries are more pronounced in males than in females [58]. Therefore, one can expect that this also applies to the categorical-coordinate dichotomy. More specifically, the lateralization (interaction between task and visual field) should be more pronounced for male than female subjects. In addition, gender differences can be task specific. Traditional spatial tests, such as the Mental Rotations and Space Relations tests endorse male superiority for spatial tasks. However, Silverman and Eals [52] argue that these traditional spatial tasks depend on specific spatial abilities, which tap more precise geometrical spatial processing, such as performing accurate mental transformations. In contrast, females would outperform males on tasks that require subjects to recall spatial configuration of objects, a more categorical process.

Note that as such gender of the subjects may influence performance on the categorical-coordinate dichotomy. One possible modulation is that males, showing slightly higher functional lateralization in general than females, would be most likely to demonstrate the proposed categorical-coordinate lateralization as well. Another possible gender related difference is that males are superior on the coordinate tasks whereas females are better on the categorical tasks. However, as can be seen in Table 1, most studies did not reveal a more pronounced lateralization of coordinate and categorical processing in men, as males and females could not be differentiated in their performance on both types of tasks. Neither could a general superior coordinate performance in men be contrasted with better female scores for the categorical task [15,28,31]. One exception is the study by Rybash and Hoyer [49], who reported men to outperform women initially for right hemisphere processing on coordinate tasks while women performed better on the categorical tasks. The latter clearly does not support the traditional view that males outperform females on all visuospatial tasks, but fits the more recent notion that there is considerable variation as to which spatial dimensions might show genders sensitivity and in what direction (cf. [46]). Apparently, perception of elementary spatial relations shows a different pattern than visuospatial transformations. Interestingly, Postma et al. [44,46] observed that men were better in an object location memory condition, which tapped fine-grained positional processing, whereas there was no gender difference for a condition, which involved relative, categorical positional information. However, this evidence only indirectly bears upon the categorical-coordinate distinction and is incomplete.

2.2. Handedness

In contrast to gender, differences in handedness seem to have a clearer effect on the categorical-coordinate dichotomy. According to Hellige et al. [16] it has often been reported that right and left-handers do not so much differ in pattern of asymmetry, but the mean asymmetries are often less pronounced in left-handers because in a group of left-handed individuals the direction of the asymmetry is more variable. Based on this, one can expect a less pronounced hemispheric asymmetry between coordinate and categorical spatial processing in studies that include left-handed subjects. Most studies a priori controlled for possible influences of atypical cerebral lateralization in left-handers by testing

Table 1

Evaluating the empirical support for the susceptibility of the categorical-coordinate dichotomy to methodological factors

<table>
<thead>
<tr>
<th>Study</th>
<th>3</th>
<th>5</th>
<th>15</th>
<th>16</th>
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<th>30</th>
<th>36</th>
<th>41</th>
<th>48</th>
<th>49</th>
<th>56</th>
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</thead>
<tbody>
<tr>
<td>Gender (males &gt; coordinate; females &gt; categorical task and show less lateralization)</td>
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<tr>
<td>Mode of response (manual &gt; vocal in showing expected lateralization)</td>
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<tr>
<td>Practice (more practice diminishes coordinate advantage of right-handers)</td>
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<td>Feedback (feedback strengthens the expected lateralization)</td>
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<tr>
<td>Display luminance (black-on-white background &gt; lateralization than white-on-black)</td>
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<tr>
<td>Stimulus exposure duration (short duration &gt; lateralization than long)</td>
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= support; ± = weak support; ± = no support/difference; – = rejection. A blank is given when a factor was no subject of interest in the study.
only right-handed subjects. In two studies, the effect of differences in handedness was assessed more explicitly [16,31]. Interestingly, in both cases the hypothesized hemispheric specialization was only confirmed for right-handed subjects but not for the left-handers. Moreover, Kosslyn et al. [28] observed that lateralization effects increased with the strength of handedness (comparing relatively strong and relatively weak right-handed subjects). Apparently, there is a positive correlation between the strength of handedness and the potential to obtain the predicted categorical-coordinate pattern: with more strongly right-handed subjects, cerebral lateralization of the dichotomy is more pronounced. However, for left-handers there is seemingly no such correlation. They show a right hemisphere advantage for both the coordinate and categorical tasks [16], and this is independent of strength of the hand preference.

2.3. Task difficulty

An undesired possible confounding factor could be that the two spatial tasks simply differ in difficulty. Bruyer et al. [5] argued that categorical judgments as implemented in most tasks are almost by definition easier than coordinate judgments. That is, categorical judgments are made within a discrete frame defined by a very limited number of responses, generally two, whereas coordinate judgments have to be made on an infinite scale as the exact metric coordinates have to be computed. The functional lateralization thus could simply arise because one hemisphere (viz. the right hemisphere) is better in performing more difficult computations. Taking also into account that left hemisphere advantages for the (simpler) categorical tasks are usually weaker or completely absent, this could be a plausible alternative explanation. Therefore, Kosslyn et al. [28] systematically manipulated task difficulty for both categorical and coordinate tasks, using error rates and response latencies as indices of task difficulty. They found no evidence for an effect of task difficulty per se. Others have looked at differences in task difficulty within the coordinate or categorical tasks [5,42,50]. For example, a coordinate decision whether a dot is within 1 cm of a horizontal line or not, is much easier when the stimulus configuration includes two elements which are ‘obviously’ more than 1 cm from one another [50]. This type of task difficulty manipulation tends to interact with the lateralization of categorical-coordinate distinction. Right hemisphere superiority is attenuated for easy coordinate decisions [5,42,50]. In turn, it might even become visible for harder categorical judgments. One solution to this apparent confusion is that easy stimuli in general are processed preferably in categorical fashion while difficult stimuli tend to engage a coordinate approach [42].

2.4. Mode of response

Responses can be manually or vocally. In the former situation, subjects produce key press responses either by the middle and index finger of a single hand, the index fingers of both hands, or by pressing simultaneously with the two middle fingers or the two index fingers. The various response modes may engage the two hemispheres to different extents. A vocal response would mainly be generated by the left hemisphere. Unimanual responding recruits the contralateral hemisphere (and should be counterbalanced over subjects or trials). Simultaneously, pressing a finger of each hand is most neutral with respect to hemispheric engagement. Overall, response mode seems not an important factor. Bruyer et al. [5] reported that a vocal mode of response slightly attenuated the hemispheric distinction between coordinate and categorical tasks, but did not make it disappear. Kosslyn et al. [28] reported no changes in performance on categorical and coordinate tasks, when mode of response was changed from manual to vocal.

2.5. Effect of practice

Several studies have indicated that an initial right hemisphere advantage for processing coordinate spatial relations disappears after the first blocks of trials [28,37,49]. It was suggested that with practice subjects develop new categories or verbal labels for the coordinate distances, which in turn would favor the left hemisphere or at least mask the right hemisphere advantage [28]. Intriguingly, Michinata [37] reported that not only the right hemisphere advantage for coordinate judgments but also the left hemisphere advantage for categorical judgments quickly disappeared with practice. In addition, the right hemisphere advantage even reversed to a left hemisphere advantage in the coordinate tasks. Banich and Federmeier [3] reasoned that subjects might apply more than one strategy that enables them with practice to process a coordinate task in a categorical manner. One such strategy might be triggered by the computer screen itself becoming a reference frame that can preclude the need to calculate metric spatial relations between the items on which the judgment should be based. Banich and Federmeier thus varied the vertical positions of the stimuli over the screen, thus, prohibiting the use of the computer screen as a frame of reference. Strangely enough, now the lateralization of the categorical-coordinate dichotomy was restricted to the final blocks of trials! So, although there is reason to believe that the categorical-coordinate dichotomy is influenced by practice, the exact mechanisms are still open to debate.

2.6. Feedback

Feedback is in some ways similar to practice. Subjects can benefit from feedback by improving their judgments on both categorical and coordinate tasks, as with practice trials. However, feedback should be most important for calibrating...
judgments in the coordinate tasks while the categorical tasks are normally too easy to benefit from feedback. As such, providing feedback can bias the results\(^3\) [5]. As can be seen from Table 1 feedback has not been investigated systematically. In some studies feedback was given, in others not. Most authors, however, did not comment on possible effects of feedback, with one exception [5]. Although Bruyer et al. reported that removal of feedback on performance seemed to eliminate the lateralization of the categorical-coordinate distinction found in a previous experiment, it remains unclear why removal of feedback had little effect on accuracy or response latencies, and both types of tasks were not differentially affected by it. In short, for the time being it is hard to verify whether and to what extent feedback is of influence.

2.7. Display features (luminance, polarity) and exposure duration

Elementary features of the stimuli to which subjects have to respond frequently have been found to affect the critical spatial decisions. Stimulus polarity appears critically important. Wilkinson and Donnelly [57] reported the expected results only with black stimuli against a white background. Similar indications follow from Hellige and Michimata [15] and Hellige et al. [16]. In her critique of the hemispheric specialization associated with the coordinate/categorical distinction, Sergent [50] noted that with high contrasts between target stimuli and background none of the supposed lateralization was found, whereas it appeared with lower contrasts. Contrast and luminance might specifically affect the contribution of cells with different receptive field sizes. Accordingly, Kosslyn et al. [26] emphasized that the two hemispheres have different receptive field properties, which in turn would cause different functional specialization in spatial tasks. The left hemisphere, being predisposed to input from visual neurons with smaller receptive fields, would be tuned to high frequency spatial information as well as be superior in categorial tasks. In contrast, the right hemisphere, being predisposed to input from visual neurons with relative large receptive fields, would be sensitive to low frequency spatial information and coordinate spatial information. Cowin and Hellige [10] removed high spatial frequency information from the stimulus by dioptric blurring. This resulted in a disruption of the performance of the categorical task but no lateralization was found for categorical processing. Recently, Okubo and Michimata [41] showed that removing low frequencies attenuated right hemisphere coordinate performance. It thus has been suggested that with low stimulus energy and low contrast in particular the right hemisphere advantage for metric decisions turns up. It should be noted however that Wilkinson and Donnelly [57] obtained a reversed contrast modulation. They showed that high contrast led to a right hemisphere advantage for the coordinate task. In this study, exposure duration and display polarity (black-on-white versus white-on-black) were also manipulated, and it was argued that these display parameters might be more important than contrast in generating the hemispheric asymmetry for the spatial relations processing.

While the foregoing underscores the fact that the visual half field technique depends critically upon presentation parameters, again the exact way in which this parameters work are somewhat variable. One interesting possibility is that both display luminance and—polarity exercise their influence on the dichotomy by the mechanism of changing ‘effective exposure duration’ of the stimuli. Effective exposure duration is dependent on exposure duration sec, but also on phenomena like visible persistence and pre- and post-stimulus masking [57]. Some display features may enhance the effective exposure duration of the stimuli, and consequently can disturb the visual half field methodology. When exposure duration exceeds a certain threshold, the stimulus is no longer selectively presented to only one hemisphere, and there is more opportunity for interhemispheric cross talk. For example, Wilkinson and Donnelly systematically manipulated stimulus exposure time and found a task × visual half field interaction only for the 100 ms exposure time condition, while it disappeared during the 200 ms condition. Thus, according to the results reported by Sergent [50] and Wilkinson and Donnelly [57], one could say that ‘viewing conditions’ should not enhance visible persistence of the retinal image of the stimulus, in order to reveal the categorical-coordinate distinction. This seems best served by black stimuli on a brighter background, presented for 100 ms [57].

3. Neural network simulations

In 1992, Kosslyn et al. conducted a series of neural network simulations in order to find additional insights into the hemispheric specialization hypothesis [26]. The authors realized that the results of studying neural network simulations do not necessarily generalize to the human brain, but network simulation studies seemed useful to investigate several assertions about the categorical-coordinate distinction. First, categorical and coordinate spatial relations representations are assumed to be clearly conceptually different. Second, computation of both sorts of representations is affected by increasing task difficulty, and third, the effects of stimulus quality and/or presentation parameters on the categorical-coordinate distinction can be accounted for by different computational mechanisms.

Three-layered feedforward networks were built and trained to compute categorical and coordinate spatial relations. After training, simulations of the bar-and-dot tasks

\(^3\) Still, how exactly feedback would work is unclear. On the one hand, it could support coordinate judgments and eventually allow for the discovery of right hemispheric superiority (by relaxing flow effects). On the other hand, it might help the establishment of categorical labels in the coordinate task, thus, working together with practice in the reverse direction.
were run, using the amount of error as an index of how well the network performed the tasks. The first part of the study assessed the conceptual difference between categorical and coordinate relations. Two types of networks were compared, each type performing both categorical and coordinate tasks simultaneously. In one type of network, all of the hidden units were connected to all of the output units (unsplit network), whereas in the other type of network, the hidden units were split in two groups, each group connected exclusively to the output units for one type of task (split network). It was reasoned that when two tasks rely on distinct computations, a split network would perform better than an unsplit network because of a reduction of interference from one form of computation on the other. As was expected, the results showed that the split networks generally produced significantly less error than did the unsplit ones. This supported the idea of the two types of spatial relations being conceptually different, that is, their representations are not logically intertwined.

The second part of the study was concerned with a possible underlying mechanism of the hemispheric differences in processing categorical versus coordinate spatial information. As discussed previously, hemispheric specialization for types of spatial encoding might be a consequence of different predisposition to input from visual neurons with different receptive field sizes, and in sensitivity to spatial frequencies. To test this possibility, it was examined what kind of receptive fields the hidden units of different networks developed after they were trained to compute either categorical or coordinate relations. The results were as expected: networks trained to perform the categorical tasks developed smaller receptive fields than networks that performed the coordinate task. Further confirmation was found by ‘hard-wiring’ networks in advance with fixed-size receptive fields. Networks with larger receptive fields performed the coordinate task significantly better than the networks with small receptive fields, but the expected opposite pattern for the categorical task was not significant, although a trend was found in the expected direction.

Another interesting aspect from this study was that networks with different numbers of hidden units were used. It was found that when a network contained a relatively large number of input units, the sizes of the receptive fields did no longer affect performance on the two types of tasks differentially. It was suggested that this might account for Serger’s [50] findings regarding contrast. Serger only found support for the categorical–coordinate distinction when the stimuli were presented with low contrast, and accounted for the right hemisphere advantage in the coordinate tasks in assuming that it is generally more efficient in processing lower quality information. A large number of input units correspond with fine-grained encoding, i.e. high contrast. In case of high contrast information, both hemispheres operate equally efficient. Kosslyn et al. [26], however, suggested a slightly different explanation: when stimuli are presented with high contrast, more low-level neurons contribute input to the higher-level systems in both hemispheres. In this case, even the minimal overlap of the small receptive fields may be enough to encode metric spatial location in the left hemisphere. As a consequence the relative difference in hemispheric processing of categorical and coordinate relations disappears.

Cook et al. [9] criticized these network simulations on theoretical grounds and statistical artifacts (see for criticisms and replies: [9,25,27]). Central in their critique were some flaws in the design of the networks and the stimuli used by Kosslyn et al. [26]. Cook et al. [9] pointed out that at least in some trials, first-order correlations between input and output unit activities biased the results. Typically, the simulations employed bar-and-dot stimuli. In some trials, the position of the dot alone in the input array was sufficient for the network to compute that the stimulus had an ‘above-configuration’ (dot above the bar), while the position of the bar was in fact irrelevant to the computation. Thus, in those trials, the networks did not need to compute spatial relations. Much of the networks’ performance could be attributed to the high input-output correlations rather than to the processing of spatial relations. Recently, however, Baker et al. [2] reported new neural network simulations on categorical and coordinate processing, using simulation models that eliminate input-output correlations in the stimulus set. In line with their previous findings, a relative better performance on the coordinate tasks was obtained as the size of the network’s receptive fields increased.

4. Categorical and coordinate processing in patients with brain lesions

Another source of information about the categorical-coordinate distinction is based upon investigations of brain-damaged patients. One group of patients that has been examined was commissurotomized patients, or so-called split-brain patients [50,51]. This rather unique neurological condition has in general served neuropsychological research on the functional specialization of the cerebral hemispheres because there is no interhemispheric interference within these subjects. Besides commissurotomized patients, work with patients suffering unilateral focal brain lesions is relevant (cf. [30]).

4.1. Commissurotomized patients

One of the initial points of discussion regarding Kosslyn’s theory [21,28] concerned what exactly ‘specialized’ meant. Was the processing of categorical spatial relations exclusively the domain of the left hemisphere, and in turn, was coordinate spatial processing exclusively a right hemisphere matter, or was the dichotomy based on a relative difference in contribution between both hemispheres in the computation of the two types of spatial relations representation? This controversy has long been settled, as nowadays, it is generally accepted that the hemispheric difference is
a relative one. Nevertheless, Sergent [50,51] conducted her studies against the background of the initial debate concerning absolute or relative hemispheric specialization, interpreting Kosslyn’s theory as the two types of spatial representations being mediated by different hemispheres (cf. following the former option). Sergent examined the competence of the two hemispheres at processing spatial relations in split-brain patients. One study reported a visual half field experiment in which three commissurotomized patients participate [50]. Purpose was to determine whether each hemisphere would perform above chance in both categorical and coordinate tasks. In addition, reaction times (RTs) were analyzed as a function of visual half field to get more information about (differences in) processing efficiency. The main findings revealed that subjects performed significantly better than chance in each visual field condition for both categorical and coordinate tasks. In addition, there were no overall differences in RTs in relation to visual half field. Consequently, it was concluded that the two disconnected hemispheres both had the capacity to represent categorical and coordinate spatial relations and processed this information equally efficient. Only one patient showed differences in RTs, which were in favor of the right hemisphere in both tasks.

There is some evidence that in split-brain patients at least some information is transferred between the disconnected hemispheres, what makes them not entirely free from reciprocal interference or interhemispheric communication [51]. Hence, in a sequel study, the capacity of the two disconnected hemispheres to share the outcome of their respective operations (conjoint processing) for the production of a single response (in this case, a categorical versus a coordinate judgment) was assessed [51]. How this conjoint processing influences the overall performance tells us something about possible differences between the two hemispheres at making the two kinds of spatial relation judgments. If one hemisphere takes control over processing (depending on the type of judgment), then bilateral performance (stimuli presented to both visual half fields simultaneously) is expected to be similar to the better of the unilateral conditions. For example, if the right hemisphere is specialized in coordinate processing then simultaneously presenting a coordinate judgment task to the left and the right hemisphere should not alter performance in comparison to right hemisphere presentation only, because left hemisphere processing will not add essential information. Alternatively, if the two hemispheres can operate simultaneously and in parallel on the same information, then bilateral performance should be better than either unilateral condition, or at least not weaker. In this case, a response can be made whichever hemisphere completes processing first because the hemispheres can share the outcome of their operations. Bilateral visual field presentation (or central visual field presentation) in general results in faster reaction times relative to unilateral visual field presentation, thus, indicating more efficient conjoint processing of spatial relations [15,50].

Sergent’s results [51] revealed again no indication that representations of categorical and coordinate spatial relations are produced by different hemispheres as all three patients performed above chance after left visual field and right visual field presentations of both categorical and coordinate tasks. In addition, enhanced performance in the bilateral presentation condition also implied functional hemisphere equivalence; presumably both hemispheres can implement the required operations. Finally, it seemed that visuospatial information in which both categorical and metric features were preserved, was transferred between the disconnected hemispheres. The data suggested a sort of implicit comparison of information from one hemisphere to another, and such a comparison could be made on both metric and categorical information. Sergent concluded that if the two disconnected hemispheres can compare their respective information on both categorical and coordinate features, it implies that both hemispheres are capable of producing the two types of spatial relations representations [51].

Overall, the split-brain patient studies did not find consistent support for the hemispheric specialization hypothesis for two types of spatial relations. However, inferences from commissurotomized patients about the normal brain require caution. Nevertheless, these studies contributed to the initial debate about absolute versus relative hemispheric specialization and made clear that if a hemispheric specialization for the processing of two types of spatial relations exists, it must be a relative one. Indeed, this point has repeatedly been made by Kosslyn. In the computer simulation of cerebral lateralization, there was a copy of each subsystem for each hemisphere [26,27].

4.2. Unilateral focal brain lesions

Laeng [30] reports two interesting and clever experiments with focal-lesion patients. He reasoned that, according to the hemispheric specialization hypothesis, patients with lesions in one hemisphere should become particularly ‘insensitive’ to changes in the spatial relations for which the hemisphere is specialized. Based on this view, he predicted a relative breakdown of categorical processing after left-sided lesions, while right-sided lesions would cause a relative breakdown of coordinate function. Laeng [30] tested this prediction by asking 62 patients, half with left hemisphere damage and half with right hemisphere damage, and a group of similar but neurologically intact control subjects, to perform two tasks. In one task (identity test) subjects were shown colour drawings of one or more objects, most of them representing animals (e.g. a large cat to the left of a small cat). After a short delay subjects had to decide whether another drawing was the same or different as the original drawing. In half of the items, the variant drawing would show a change in some categorical relation without a change in the coordinate relations between the objects (e.g. if the original drawing showed a large cat to the left of a small cat, the variant drawing may show a large cat to the right of a small cat, while
the distance between the cats remains the same). The other half of the items would show a variation in the coordinate relations while keeping the original categorical relations unchanged (e.g. the distance on the horizontal plane may be stretched or compressed). Interestingly, the two patient groups made the same numbers of errors, but of different types. Left hemisphere patients made on average more categorical errors than right hemisphere patients, while the last group made on average more coordinate errors. These effects were largest for patients with damage to the parietal lobes only, in comparison to patients with lesions affecting both parietal and temporal lobes or frontal lobes. In a way, it is surprising that parietal damage alone causes more explicit deficits in the performance of a spatial task than more extended damage including the parietal lobe. According to Laeng et al. [32], this finding might suggest that in patients with damage to the parietal lobes and other structures (especially temporal and frontal cortices), the focus of the lesion might be located more anteriorly. Therefore, the lesion might have less compromised a hypothetically functional area for spatial relations that would be located more central and posterior within the parietal lobe. For the time being, clearly this possibility needs further examination. In addition, it is plausible that more widespread lesions, or more diffuse damage, may cause distortions in other cognitive processes besides the spatial ones resulting in a more general decrement in cognitive performance. Therefore, certain spatial deficits might become less conspicuous and at least less selective.

In Laeng’s other task (similarity test) [30], subjects were shown a drawing representing one or more objects and then were shown two variations; one had altered categorical relations and one had altered metric relations. Subjects had to indicate which of the two ‘looked more similar’ to the original drawing. It was predicted that left hemisphere patients would find the categorical transformed representations to be similar more often than right hemisphere patients and control subjects would, whereas right hemisphere patients would judge the categorical transformed representations as more similar less frequently than the control subjects would. The results confirmed the prediction. Although both lesion groups tended to choose the categorical transformations as most similar to the originals, the left hemisphere patients found the categorical variants more frequently similar than the right hemisphere patients or the control subjects, and the right hemisphere patients judged the categorical variants less frequently similar than control subjects did. Again, the effects were more pronounced when only the patients with parietal damage were examined.

Recently, a more indirect line of research has further corroborated the foregoing results. Kessels et al. [20] compared two aspects of object location memory. One concerns remembering the precise positions of a number of objects shown in a display, independently from which object is occupying the position. The other requires remembering object-to-positions links, i.e. which object is at which position, while the precise position is irrelevant (i.e. the to be linked positions were all marked). It has been conjectured that the former aspect rests upon coordinate processing whereas the latter entails categorical processing [43]. Accordingly, Kessels et al. [20] found that patients with a right hemisphere lesion performed significantly worse on the precise positional memory aspect, whereas left hemisphere stroke patients were impaired on object-location binding.

5. Brain imaging data

Kosslyn et al. [29] conducted a PET-study to investigate the brain circuits that are involved in the processing of the two types of spatial relations. It was proposed that the hemispheric differences in encoding a particular type of spatial relations are not so much due to hard-wired differences in outputs from neurons with different sized receptive fields, but due to the way attention was allocated. That is, the hemispheres may in fact have neurons with the same distribution of receptive field sizes, but the outputs from neurons with large receptive fields are processed preferentially in the right hemisphere, whereas those from neurons with small receptive fields are processed preferentially in the left hemisphere. This effect is due to attention allocation (see Section 1). Therefore, not only brain areas involved in spatial information processing sec will be activated when subjects perform categorical and coordinate tasks, but also areas involved in attentional processes. Consequently, a relative large network of brain areas should show up in computing the two types of spatial relations. Following Laeng’s patient work [30], the parietal areas were expected to be central in this network.

The results confirm the notion that apparently simple tasks activate large networks of brain areas and that processes that allocate attention selectively were involved in computing spatial relations (activation was found in many areas involved in visual attention, for instance the pulvinar nucleus and the superior colliculus) [29]. In addition, it was found that the two types of spatial relations activated distinct networks of areas: when directly compared, left hemisphere activation was present during the categorical task and predominantly right hemisphere activation during the coordinate task. Specific involvement of parietal lobes was only partly demonstrated. Two right parietal areas (a region in the right superior parietal lobe and a portion of the right precuneus, within the medial superior parietal lobe) were activated more when processing coordinate spatial relations than in case of categorical spatial relations. No indication, however, was found for left parietal areas that were consistently used to compute categorical spatial relations more than coordinate ones. Instead, in comparison between the test conditions, it seemed that left frontal regions were involved in categorical processing (relative to coordinate processing). It was argued that this failure to find the lateralized parietal differences might indicate that the relevant categorical processing is fast and ‘automatic’, therefore, causing no significant changes in regional cerebral blood flow in the left
and right parietal areas. Alternatively, the possibility exists that the parietal lobes do not contribute as much to the encoding of categorical spatial relations as was assumed [29].

In a fMRI-study Baciu et al. [1] assessed the involvement of the angular gyri (part of the parietal lobes) in the processing of categorical and coordinate spatial relations. There is some evidence that the right angular gyrus (Brodmann area 39) plays a critical role in tasks using precise metric information. In addition, lesions of the left hemisphere involving the left angular gyrus often result in Gerstmann’s syndrome, one aspect of which is a disruption of the ability to distinguish left from right, a typical categorical task [1,30]. The results showed that the right angular gyrus was activated more strongly than the left angular gyrus during initial performance of the coordinate task. Comparable to the practice effects found in visual half field studies, the involvement of the right angular gyrus was reduced after the first part of the examination, with a shift to an enhanced involvement of the left angular gyrus in the second part. During the categorical task, activation appeared to be stronger within the left angular gyrus at any point of time during the examination, thus, revealing no effects of practice.

In sum, the currently available neuroimaging studies support the idea that processing of the two types of spatial relations activates distinct neural networks in the left and right hemispheres. In particular, the posterior parietal lobes seem involved, although findings are less convincing for categorical than for coordinate spatial processing. It should be mentioned that the amount of research in this area is limited. Much more brain imaging studies are needed.

6. Conclusions

Table 2 presents a weighted overview of the various lines of evidence regarding the categorical-coordinate distinction. Most studies have employed the visual half field technique in normal subjects. On the average, they have resulted in moderate support for the hypothesized lateralization. Five studies have confirmed the hemispheric specialization hypothesis [15,16,26,31,49]. Five other studies have obtained mixed, weakly positive evidence [3,5,37,42,57]. Only one has clearly rejected the hypothesis [50].

It further seems that the lateralization effects are modulated by specific details of the experimental technique. Most importantly, strictly right-handed subjects should be used (with clearest lateralization) and the stimuli should be black targets on white background with limited contrasts and short duration (≤100 ms). Partly, the necessity of these requirements lies in the more elementary mechanisms that account for the lateralization of coordinate and categorical mechanisms. It is suggested that the hemispheres are differentially predisposed to the processing of input from visual neurons with different receptive field sizes (i.e. relative large receptive fields for the right hemisphere and relative small receptive fields for the left hemisphere) and are differentially sensitive to bands of spatial frequencies (i.e. relative high frequencies for the left hemisphere and relative low frequencies for the right hemisphere). Large receptive fields and low spatial frequencies facilitate coordinate processing, whereas categorical relations depend on small receptive fields and high spatial frequencies. Theoretically, the lateralization claim as well as the precise neurocognitive mechanisms involved has been nicely elaborated in computer simulations [2,26]. Amongst other these have indicated that categorical and coordinate computations are best carried out by separate neural networks. In turn, when these networks are equipped with the supposed visual field properties, they indeed selectively tune to either coordinate or categorical relations.

It should be mentioned that the tendency for positive findings in visual half field studies might be troubled by the so called file drawer phenomenon: the fact that many studies which cannot prove a difference or cannot demonstrate clear results, will never be published. Hence, the strength of the support might be somewhat overestimated. On the other hand, it might be mentioned that possible null results might reflect the insensitivity of the visual half field technique rather than really follow from hemispheric equivalence (cf. [4,35]). As such, it is important to notice that two other lines of empirical evidence—patient lesion and brain imaging studies—provide converging evidence for the hypothesized lateralization of the categorical and coordinate processes. Although split-brain research by Sergent [51] did not lead to any convincing outcomes, the unilateral lesion study by Laeng [30] did. One PET-study [29] and one fMRI investigation [1] likewise showed hemispheric differentiation when performing a categorical compared to a coordinate task. Evidence for right hemispheric superiority was most clear. As is also known from the visual half field

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<td>Categorical-coordinate distinction</td>
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+ = support; ± = weak support; ± = no support. A blank is given when no evidence is available or when evidence is not applicable to the human brain.
experiments, left hemispheric specialization for categorical relations seems harder to proof.

In a way, the latter is somewhat surprising in light of the recurrent alternative view, that categorical spatial relations are in fact no more than verbal labels. If so, one naturally would expect a left hemisphere advantage in categorical processing, simply because in general the left hemisphere is dominant for language processing. The difficulty noted above in showing clear-cut left hemispheric specialization for categorical relations counters this view. There are some further arguments against it. Besides assessing the processing of spatial relations in brain-damaged patients, Laeng [30] also directly conducted tests of aphasia. He found that the degree of language impairment did not correlate with performance on the spatial tasks, which is inconsistent with the idea that categorical processing merely reflects upon language-specific representations. Moreover, Kemmerer and Tranel [19] present evidence from two neurological cases for a tripartition between perceptual coordinate spatial codes, perceptual categorical codes and verbal categorical spatial codes. At least, this suggests that perceptual categorical processing is not necessarily always accompanied by verbal labeling.

In sum, it seems that there are both logical and empirical grounds to assume hemispheric differentiation in computing categorical and coordinate spatial relations. This division of labor between the two hemispheres may have a firm evolutionary origin. Engaged in (verbal) categorization from the start predisposed the left hemisphere towards spatial categorization as well. Simultaneously, its dominant role in navigation and attentional orienting favored the right hemisphere for making coordinate computations [21,22,28].

7. Further extensions of the categorical/coordinate dichotomy

Apprehending spatial relations serves more purposes than the purely ‘spatial’. One of them is object processing. Typically, we have to identify objects under a high variation of viewpoints, illuminations, positions and occluding contexts. Essentially, two kinds of variability are noteworthy: First, objects may appear to us from multiple viewpoints, including non-canonical orientations. Second, flexible (e.g. living) objects can take various different poses, in which the precise positions of the individual component parts are highly altered (e.g. when bending, one’s head can be placed between one’s knees), but the abstract relations between the parts remain fixed (e.g. the head is still attached to the trunk). Both situations may require the establishment of general, abstract spatial relations between components—i.e. categorical relations—for efficient processing [26,32].

Interestingly, Marsolek and coworkers [6,34] argue that a viewpoint-abstract, category-tuned system is allocated to the left hemisphere, whereas a viewpoint-dependent, exemplar system is situated in the right hemisphere. Burgund and Marsolek [6] contend that the viewpoint-abstract system should pick up features that are relatively invariant across different situations and exemplars. Hence, processing of an object after previous exposure in a different orientation or to a different exemplar out of the same general object category is facilitated with left but not right hemisphere presentation. In turn, the right hemispheric viewpoint-specific system is tuned to novel, unfamiliar objects and less familiar objects. This also applies to familiar objects seen from non-canonical views. The underlying explanation is that initial viewpoint-specific information following from sparse encounters with novel objects or familiar objects in relatively novel-non-canonical poses is stored best in memory by the right hemisphere system. Indeed, various studies have demonstrated that the right hemisphere seems critical for perceiving objects from unusual views [33,35,54–56].

In similar vein, Laeng et al. [32] proposed that different computational mechanisms facilitate the encoding of (flexible) objects seen in unfamiliar contortions compared to conventional poses. When flexible objects non-rigidly transform, the only spatial relations among object parts that remain invariant are abstract, qualitative properties of and between the connections. In other words, only the categorical spatial relations remain invariant. Thus, categorical representations should play an important role in the so-called ‘structural description’ of a flexible object, which is part of its template stored in memory, specifying parts and their connections. Accordingly, Laeng et al. [32] showed a left hemisphere advantage for initial presentation of non-rigid objects in contorted poses. After initial presentation, the right hemisphere took over and became superior in identifying the contorted object. This was accounted for by assuming rapid familiarization of the global object shape contours, with the right hemisphere being superior for encoding familiar overall shapes.

In short, the categorical-coordinate distinction may be fruitfully applied to hemispheric differences in object processing. The question to what extent object processing is lateralized remains elusive. As Kosslyn and coworkers [22,23] point out, object processing is a highly complex process, comprising multiple components, from both left and right, anterior and posterior, and dorsal and ventral brain areas. New insights may arise from closer considering familiarity of the exposed items and the role of categorical relations [32].

A second, important function of processing spatial relations involves the performance of spatial motor actions. As acknowledged in the opening of this paper, coordinate spatial information is highly relevant for navigation and other spatial activities (e.g. pointing towards things or picking them up). In this light, it is worthwhile to consider another eminent distinction in spatial processing as well: that between egocentric and allocentric referencing. Milner and Goodale [38] distinguished egocentric coding of locations (relating a location to a part of one’s body) from allocentric location coding, based on an absolute frame of reference or on the
relations between multiple objects in the environment. As with the coordinate/categorical distinction egocentric and allocentric referencing would recruit different neuroanatomical circuits, but this time involving different intrahemispheric sites, i.e. the dorsal and ventral stream, respectively (cf. [11,12,39,45]). Allocentric processing is supposed to underlie conscious perception of the spatial environment, in particular establishing stable relations between and within objects (the latter was also addressed previously in the context of object processing). As such, allocentric processing clearly resembles categorical coding. Originally, egocentric processing was thought to be exclusively used for direct spatiomotor action, requiring fine-grained positional information. Recent studies have indicated, however, that cognitive judgments of egocentric position also depend on a specific spatial mechanism and neural circuitry, which may differ from the same judgments of allocentric position [13,17,53].

The foregoing raises two theoretical possibilities. One is that allocentric processing more or less equates with categorical coding of spatial relations, whereas egocentric processing is close to coordinate coding. Carey et al. [7] suggest that allocentric processing provides the observer with a sense of ‘space constancy’, an awareness of relative, categorical locations of objects. In turn, metric–coordinate information is used for the egocentric task of performing direct motor actions towards these objects. The second possibility is that the egocentric/allocentric and the categorical/coordinate distinction form orthogonal dimensions, which can be fully combined [40]. That is, while the former defines the point of reference to anchor a location, the latter specifies the grain of the spatial relation. We would thus have four possible situations: (a) egocentric–categorical (the table is in front of your body); (b) egocentric–coordinate (the table is 1 m from yourself); (c) allocentric–categorical (the table is next to the door); (d) allocentric–coordinate (the table is 1 m from the door).

From the above proposal, it seems clearly worthwhile to further consider intrahemispheric differentiations in categorical and coordinate processing. Categorical decisions for within object relations as well as for locations related to object-centered frames might engage the left ventral posterior region. Comparable decisions made towards your own body could activate primarily the left dorsal posterior region. In addition, metric processing of relations between objects might rely most upon right ventral areas, while metric processing of locations with respect to yourself involves the right dorsal area. Admittedly, the foregoing is speculative and has not been tested directly. Some indirect evidence comes from recent studies showing that attenuation of the magnocellular information stream [14,48] selectively diminishes coordinate performance. While this does not allow us to draw any substantial conclusions with respect to the hypothesized marriage between the egocentric/allocentric distinction and the categorical/coordinate dichotomy, it offers a first indication for intrahemispheric modulation of the latter.

References