The study of hemispheric specialization for categorical and coordinate spatial relations in animals[☆]

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Abstract

This article reviews some of the most representative studies in the animal literature pertaining to the processing of categorical and coordinate spatial relations and of their hemispheric control. Although the processing of coordinate and categorical cognition has been studied directly with nonhuman primates, experiments on cerebral asymmetries in avian spatial orientation are also reviewed. It turns out that Kosslyn's model concerning the existence of two types of spatial representations each with a specific lateralization pattern has received some support in nonhuman primates and is only weakly verified in the avian studies. Procedural differences might explain some but certainly not all of the discrepancies between the human and the animal literature. It is especially the laterality hypothesis of a left hemisphere advantage in relational cognition and a right hemispheric superiority in judging absolute distances that is not supported by the animal data. Studies specifically addressing Kosslyn's hypotheses and bearing on the use of similar stimuli, procedures and methods between the species tested are needed in order to lead to firm conclusions about the existence of coordinate versus categorical processing systems in animals.
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1. Introduction

The current evidence concerning hemispheric specialization for two types of spatial representations (categorical versus coordinate) in humans has been the subject of a recent review (Jager & Postma, 2003). We will thus in this paper not mention the studies that bear upon the demonstrations (or lack) of this phenomenon in humans. Instead, we will directly focus on the available data in the animal literature that can be used and discussed within the distinction of two types of spatial relations and of their hemispheric control. For the time being, it is sufficient to recall that Kosslyn (1987) suggested a dissociation of two kinds of spatial representations: categorical and coordinate,

the former being computed by the left hemisphere and the latter by the right hemisphere. In addition, with practice, a "categorization" of the coordinate computation is likely to appear. This basic dichotomy has been expanded in the last years to cover further processes that can be mapped onto the left and the right hemisphere (Laeng, Shah, & Kosslyn, 1999; Laeng, Chabris, & Kosslyn, 2003).

The rationale of our approach will be first to critically review the (rare) studies that have directly or indirectly investigated coordinate and categorical representations in several animal groups. However, as Jager and Postma (2003) wrote "Apprehending spatial relations serves more purposes than the purely 'spatial'" (p. 513). In effect, as stated by these authors, the categorical/coordinate dichotomy can be extended to two other domains, namely the processing of object identity and the processing of spatial relations involved in performing spatial motor actions, most notably in navigation tasks. These latter fields can offer interesting comparative perspectives with respect to hemispheric specialization in several classes of vertebrates like for example in birds.

Jager and Postma (2003) considered that there are strong empirical and logical grounds to assume hemispheric differentiation in the computation of categorical and coordinate spatial

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relations and that "this division of labor between the two hemispheres may have a firm evolutionary origin" (p. 513). It is thus important to examine the evolutionary roots of the dichotomy. This comparative approach might also contribute to the discussion that language-specific representations in humans have created in our species a special pattern of asymmetries not shared with other vertebrates.

2. Nonhuman primates

Few studies are available in nonhuman primates concerning hemispheric asymmetries for visual spatial abilities in general and to our knowledge, only two studies (Dépy, Fagot, & Vauclair (1998); Hopkins & Morris, 1989) have specifically addressed the question of hemispheric specialization for spatial relations in intact animals. Altogether, four studies are available in the nonhuman primate literature pertaining to the question at hand. To our knowledge, no animal study has specifically assessed both categorical and coordinate relations. This limitation in the availability of animal studies will of course somewhat constrain the theoretical impact of the animal literature.

Jason, Cowey, and Weiskrantz (1984) have investigated visuo-spatial abilities in a group of nine macaques. These authors used a discrimination task between two squares, one square containing a centered dot, while the other square comprising an off-centered dot of varied amplitude. The monkeys were initially trained to locate the on-center dot. Then the splenium was transectioned along with a unilateral ablation of the occipital lobe (the left for four individuals and the right for the remaining five monkeys). Subjects were retested on the discrimination task. Right lesioned monkeys' performance were not affected and even improved. By contrast, monkeys with a left lesion were unable to discriminate small eccentricities. The authors concluded that there was a clear left hemisphere advantage for a task having a strong visuospatial component. In the same line of investigations, Hamilton and Vermeire (1988) showed that split-brain monkeys were better with the left hemisphere than with the right hemisphere to discriminate between tilted lines differing in orientation by 15°. Interestingly, the same split-brain monkeys displayed a clear right hemisphere advantage when they were presented with facial discriminations, indicating the existence of a complementary specialization in this species that depends on the tasks' nature. It should be added that a right hemispheric advantage in individual recognition is not only found in primates but also in sheep (Peirce, Leigh, & Kendrick, 2000) and chicks (Vallortigara & Andrew, 1994). The role of task's demands on hemispheric specialization has also been demonstrated in a study with macaques (Vogels, Saunders, & Orban, 1994). Here, the monkeys showed a left hemisphere advantage in a simultaneous orientation task (deciding which of two gratings was horizontal), while no bias was observed for a successive discrimination of orientations. These data might lend some support for a left hemispheric advantage in categorization.

Visuo-spatial processing was examined by Hopkins and Morris (1989) in two language trained chimpanzees by using a visual half-field paradigm. Initially, the chimpanzees were taught to manipulate a joystick that controlled the movement
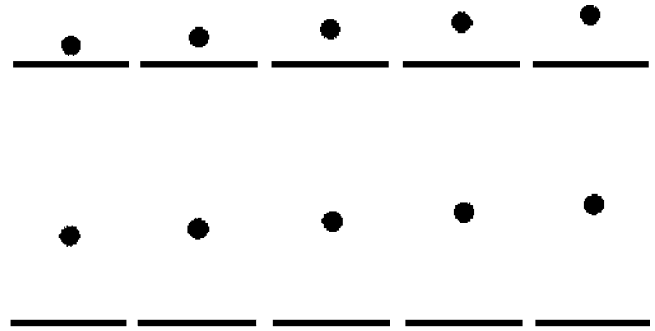

Fig. 1. Example of stimuli of the short- (top) and long-distance categories (bottom) used in the experiment with monkeys and humans by Dépy et al. (1998).

of a cursor on a computer monitor to a central fixation point. Subjects were then taught a visual discrimination based on the location of a short line contained within a geometric form.[1] Testing consisted of systematic presentation rates of 15, 122, and 226 ms to the left and right visual fields. For half of the trials, subjects used their left hand to respond and, alternately, used the right hand for the remaining trials. This task is thus equivalent to a categorical task whereby the ape had to discriminate above/below relations. Reaction time analyses showed that one subject demonstrated significantly faster reaction times to stimuli presented to the left visual field regardless of which hand was used to respond. The other subject demonstrated a significant left visual field bias only when using the left hand. Thus, the data from chimpanzees contrast with those of monkeys and do not support a left hemispheric categorization bias. We must however observe that any conclusion from Hopkins and Morris (1989) study must be taken with great caution given that only two chimpanzees were tested.

2.1. Comparing baboons and humans for processing coordinate spatial relations

The study of hemispheric specialization within the framework initially proposed by Kosslyn (1987) was carried out by Dépy et al. (1998) with Guinea baboons (*Papio papio*). This study will be described in some length because it is the sole of its kinds that explicitly attempted to test Kosslyn's model with regard to the right hemispheric advantage in coordinate cognition. In addition, this study was conducted in a comparative framework as human participants were examined with the same stimuli and tasks.

2.1.1. The task

The task was modeled on Hellige and Michimata's (1989) study with humans. Both monkeys ($n = 6$) and humans ($n = 10$) had to decide whether or not the distance between a line and a dot belonged to a short- or a long-distance category (see Fig. 1).

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[1] In this task, the subject was required to make a decision based on the location of a short line (1.5 cm length) contained within a geometric figure. If the short line was located above a longer parallel line, the subject was required to move the joystick in a upward direction. When the short line appeared below the longer parallel line, movement of the joystick in a downward direction was required.

In order to perform such a task, the monkeys had been previously trained with a setup (computerized apparatus) requiring the manipulation of a joystick (Vauclair & Fagot, 1993). The monkeys had then been tested on different pattern discrimination (e.g. Vauclair, Fagot, & Hopkins, 1993), and categorization problems (e.g. Vauclair & Fagot, 1996).

The same testing procedure was adopted for the two species. It consisted of a conditional matching-to-sample task in which the sample form was briefly displayed in either the left visual field (LVF) or in the right visual field (RVF). The subject initiated the trials by placing one hand on a touch pad. Immediately afterward, a green cursor appeared in the center of the screen along with a white square-shaped fixation stimulus, which was displayed either 1.5 cm above or below the cursor. In response to this display, the subject was required to manipulate the joystick so as to place the cursor for 35 ms on the fixation stimulus. Once the cursor was maintained on the fixation stimulus, a sample stimulus appeared during 120 ms in the left or the right hemi screen.

Subjects of each species first learned the matching rule with four training stimuli. The stimuli were made by combining two line–dot distances (0.1 or 2.7 cm) and two dot locations (above or below the horizontal line). Half of the subjects from each species were requested to select the red square-shaped response stimulus when 0.1 cm separated the dot from the line and the green one when the line–dot distance was equal to 2.7 cm. For the other half, the matching rule was reversed. In order to avoid procedural differences between the two species, human participants were never told what the matching rule was, but had to discover it for themselves. For each subject, either a human or nonhuman primate, the use of left and right hand during training was balanced (see Dépy et al. (1998) for other procedural details).

The main experiment was replicated with the same subjects of both species but with different line–dot distances. A third experiment was conducted with a novel group of human participants who were tested with the line–dot distances used in the second experiment. Finally, a fourth experiment was run (with baboons only) by presenting novel distances.

2.1.2. Summary of the main results

Altogether, (a) Experiments 1 and 2 demonstrated a LH (left hemisphere) instead of the expected RH (right hemisphere) advantage in humans and (b) Experiment 3 showed a RH advantage with naive human subjects, but this effect was restricted to early trials.

As concerns baboons, results of Experiment 1 demonstrated that the monkeys scored better for RVF-LH presentations. However field asymmetries for scores were significant for the distances of 0.7 and 0.9 cm only. Results of Experiment 4 revealed that the baboons categorized distances as they showed an immediate and positive transfer with novel distances rather than the learning of novel stimulus–response associations.[2]

In brief, with respect to lateralization, baboons never presented a RH advantage in our coordinate tasks. However, they presented some evidence: (a) for a LH advantage in Experiment 1 and (b) for the use of categorical strategies (Experiment 4). As for humans (e.g. Chabris & Kosslyn, 1998; Kosslyn et al., 1989), the ephemeral RH advantage in distance processing might have been hidden by practice effects favoring a LH bias. A large number of training trials (on average, 1345 trials; range, 854–2217 trials), were needed for the baboons to meet the training criterion, while humans learned the task in <100 trials. This long training might have facilitated categorical procedures for which the LH appears to be predominant. It can be worth noting that no study in humans has so far employed so many trials and that the practice effect (and it resulting hemispheric shift) can be observed in some of the human studies after just a few dozen trials (e.g. Kosslyn et al., 1989).

2.2. Discussion of the nonhuman primate's studies

The pattern emerging from these studies is far from being clear cut. The dissociation proposed by Kosslyn (1987) of two kinds of spatial representations and of their underlying cerebral control was only partially verified. At first glance, the paradigm used by Jason, Cowey, and Weiskrantz (1984) can be viewed to tap the processing of coordinate relations and thus should lead to a RH advantage. However, the opposite bias was observed. The same rationale can be applied with the distance evaluation task of Dépy et al. (1998). Here again, a LH bias was obtained. A likely explanation for the discrepancy between the primate data and most results reported in human studies (i.e. a RH bias, but see Bruyer, Scailquin, & Coibion, 1997) can be related to procedural differences. Both in Jason et al.'s and Dépy et al.'s studies, the monkeys had to be initially trained on the dimensional cue used for the discrimination, whereas humans are usually not trained on the task. Thus, a training effect due the repetitive presentation of the same distances may have led the monkeys to extract some categorical invariants within the stimuli's dimensions in order to solve the task. Consequently, a coordinate task would have been coded in a categorical fashion by the animal. The results reported by Hopkins and Morris (1989) also contradict Kosslyn's predictions, as a LVF/RH advantage was obtained in chimpanzees for a task that demands the processing of categorical spatial relations. Finally, Hamilton and Vermeire (1988) obtained a LH advantage with split-brain monkeys for discriminating line orientation. This effect is difficult to interpret within a comparative framework, as hemispheric control for line orientation tasks has given contrasting results in humans with some authors reporting RH biases (e.g. Benton, Hannay, & Varney, 1975; Umilta, 1974) and others a LH involvement (e.g.Mehta & Newcombe, 1996; Mehta, Newcombe, & Damasio, 1987). Taken together, the nonhuman primate literature provides a weak support for a left hemispheric bias in categorization but no support for coordinate-type cognition in the right hemisphere.

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[2] The same baboons also succeeded when performing a categorical task requiring the above/below discrimination (Dépy, Fagot, & Vauclair, 1999). However, this latter study did not involve the examination of hemispheric advantages in realizing the discrimination.

3. Birds

3.1. The overall cerebral asymmetry pattern in birds

Birds are a convenient class of vertebrates to study functional asymmetries due to the ease with which each hemisphere can be tested virtually separately. The optic nerves in birds decussate nearly completely and only <0.1% of the fibers proceed to the ipsilateral side (Weidner, Reperant, Miceli, Haby, & Rio, 1985). Since only limited amounts of axons recross via mesencephalic and thalamic commissures, the avian visual system is remarkably crossed. This anatomical condition enables the use of eye caps to study the performance of the animals with sight restricted to one eye and so mainly the contralateral hemisphere. With this procedure, visual lateralization can be demonstrated using a wide range of tasks.

Different species of birds display a right eye/left hemisphere (RE/LH) superiority when having to distinguish between different visual patterns. This has been shown with various procedures in zebra finches (Alonso, 1998), chicks (Mench & Andrew, 1986), quails (Valenti, Sovrano, Zucca, & Vallortigara, 2003), and pigeons (Güntürkün & Kischkel, 1992). If numerous stimuli are used to induce a memory load, as studied in Fersen and Güntürkün (1990) with 725 abstract patterns, it is again the left hemisphere that is able to memorize most of the patterns over periods of several months. The pigeons of this experiment were able to remember most of the patterns with their RE/LH, but were barely above chance level with their LE/RH. This memory study suggests that visual engrams learned binocularly during training were stored, at least in part, unilaterally in the left hemisphere, although both eyes had equal access to the patterns during acquisition. Similarly Nottelmann, Wohlschläger, and Güntürkün (2002) showed that patterns learned by RE/LH can 'stay' in the left hemisphere without transfer to the other side. Thus, it is likely that the avian left hemisphere stores large amounts of acquired pattern information to which the right hemisphere has only limited access.

In contrast to the left hemispheric superiority in pattern learning, many studies could reveal a right hemispheric advantage in spatial tasks. This was first shown by Rashid and Andrew (1989). They trained chicks to find food buried under sawdust in an arena. When the chicks were tested monocularly, birds under monocular left conditions searched in the areas specified by cues. Chicks in the monocular right condition searched randomly over the complete arena.

The lateralized role of different spatial and non-spatial cues can be elegantly studied in food storing birds during cache localization. Marsh tits store food in large numbers of caches scattered over the home range which they can retrieve many days later with astounding accuracy (Shettleworth, 1990). It is possible to study lateralization of food storing and cache retrieval under controlled conditions using a room with artificial trees, perches, and small holes for caching. In one of these studies (Clayton & Krebs, 1994), four feeders were used which were distinguishable by their specific location and by markings which made them visually unique. Birds were given under monocular conditions parts of a nut in one out of four feeders and were then removed

for 5 min. During this interval, the location of the correct feeder was swapped with an empty one so that spatial and object cues could be dissociated. Then the animals were reentered and were allowed to retrieve the rest of the nut with the same eye cap condition. With the left eye, marsh tits looked for the seed at the correct spatial location, while they relied on object specific cues using the right eye. Thus, the right hemisphere used spatial cues, while the left half of the brain utilized object cues to locate the nut.

Up to now, these studies suggest a pattern that is compatible with a distinction between a categorical (LH) and coordinate (RH) specialization. The RE/LH-superiority in learning to distinguish between visual patterns could be interpreted as a specialized ability to categorize visual images in two clusters that require a dichotomous response. The LE/RH-superiority in spatial tasks could be due to a specialty in computing the precise metric coordinates of objects within a landscape. However, further analyses of avian visual asymmetries do not support such a distinction.

3.2. Asymmetries of avian spatial orientation

In an ingenious series of experiments, Vallortigara and colleagues could uncover further details of the cognitive asymmetry in chicks by using variations of a rather simple design. First, chicks were trained to find food under sawdust by ground-scratching in the center of a square-shaped arena. The position of the food was usually indicated by two different cues: the first was the geometric position of the arena center, which is the only place where the relative distances to all walls are identical. The second were conspicuous landmarks, which could be objects that were placed somewhere in the arena, or came as panels hung to some of the walls. By changing the form or the size of the arena, geometric orientation could be tested. By altering the position of the landmarks and panels, orientation according to visual objects could be analyzed. Among the different mechanisms discovered by these studies, spatial memory seems to depend on at least two sources of information, namely the geometric arrangement of surfaces defining enclosed spaces, and the position of discrete objects (landmarks) located inside or outside such spaces (Gray, Spetch, Kelly, & Nguyen, 2004; Tommasi & Vallortigara, 2004). In addition, it is important to keep in mind that orientation according to the surfaces of an enclosure can incorporate two diverse strategies, one involving a search path at a previously learned position that is at an absolute distance from a wall, and one that is defined by the relative distances of the walls. To make it easy, a verbalized rule for each strategy would be like the following.

Geometric coding (relative distances): "Search at the center of the square-shaped room, where the midpoints of all walls are equidistant".

Absolute distance coding: "Stay 1 m away from the long wall".

Landmark coding: "Search at the red box".

A geometric coding is thus the only strategy where relations of objects (in this case the walls) have to be utilized. Absolute distance coding and landmark coding concentrate

on a conspicuous object and guide the search according to fixed distances or according to a spot that is defined by one object. Now let us look what studies on the asymmetry of these cognitive strategies have revealed in birds.

3.2.1.1. Geometric coding

All studies reveal a predominance of LE/RH in geometric coding, although animals are in principle also able to use to some extent relational information with the RE/LH (Vallortigara, Pagni, & Sovrano, 2004). If the size of the arena is altered (Tommasi & Vallortigara, 2001), or if object and geometric cues contradict each other (Vallortigara et al., 2004), chicks still search in the center with their left eye and therefore rely on the relational properties of the room. This asymmetry seems to be even more prevalent in females (Tommasi and Vallortigara, 2004). If pigeons are tested in complex, very large-scale arenas, alterations of the position of diverse landmarks do not interfere with orientation as long as the animals are using the LE/RH, indicating a right hemispheric geometric processing of major room cues (Prior et al., 2002). Hippocampal lesion studies reveal that encoding of global information actually occurs only in the right hippocampus (Kahn & Bingman, 2004; Tommasi, Gagliardo, Andrew, & Vallortigara, 2003). Since hippocampal lesions are known to interfere with homing performance (Bingman, Hough, Kahn, & Siegel, 2003), it is possible that right hippocampal mechanisms aid homebound flights by using the relational position of stable and reliable sources of information like mountains and lakes to construct a map-like representation (Vargas, Petruso, & Bingman, 2004). Depending on the salience of featural cues, right hemispheric relational orientation seems to dominate search behavior of birds in most studies, resulting in a reliance on geometric cues under binocular conditions (Vallortigara et al., 2004; Vargas et al., 2004).

3.2.1.2. Absolute distance coding

Both chicks (Tommasi and Vallortigara, 2001) and pigeons (Gray et al., 2004) can use absolute distances of objects to localize food. If the animals are tested under monocular conditions, they show a RE/LH prevalence of search patterns at these absolute distance locations (Tommasi and Vallortigara, 2001). Although pigeons can in principle also use geometric information with their RE/LH, they additionally search at locations predicted by fixed distances to major landmarks using their left hemisphere (Prior et al., 2002). Thus, absolute distance coding seems to be in birds a domain of the left hemisphere.

3.2.1.3. Landmark coding

Chicks (Vallortigara et al., 2004) as well as pigeons (Colombo & Broadbent, 2000) can utilize various landmarks to guide their search for food. When geometric and landmark cues are brought into conflict, RE/LH-chicks rely on landmarks (Tommasi and Vallortigara, 2001; Vallortigara et al., 2004), an asymmetry that is especially prevalent in males (Tommasi and Vallortigara, 2004). Similarly, RE/LH-pigeons significantly reduce their searching speed when major landmarks have been removed (Prior et al., 2002). Unilateral forebrain lesions reveal that landmark coding seems to be mainly a property of the left

hemisphere (Tommasi et al., 2003). Although the hippocampus probably plays an important role in landmark utilization (Watanabe & Bischof, 2004), birds are able to guide their search according to landmarks also without a functional hippocampus (Tommasi et al., 2003).

When pigeons home from a distant release site over known territory to the loft, they display a clear RE/LH-advantage (Ulrich et al., 1999), which does not seem to be due to a visual memory-based snapshot tracking that pursues visual features along their pre-learned route (Prior, Wiltschko, Stapput, Güntürkün, & Wiltschko, 2004). Wiltschko, Traudt, Güntürkün, Prior, and Wiltschko (2002) could show a right eye-superiority in magnetic orientation in robins. In birds, magnetic compass orientation is based on intraocular light-dependent processes involving photon absorption to singlet-excited states that forms radical pairs (Ritz, Adem, & Schulten, 2000). As a result, a bird looking into different directions can 'see' the magnetic field vector as a visual modulation pattern on its retina that points into a constant direction. Thus, the magnetic field could be a true landmark that therefore is primarily analyzed by the RE/LH. If this interpretation of the homing asymmetries is correct, the right eye superiority of homeward-bound flights in pigeons could be due to the magnetic field being processed as a conspicuous landmark by the left hemisphere.

To give an interim summary on the lateralization of spatial tasks in birds, it is first important to remind that although the computations of the two hemispheres differ, both are to some degree able to utilize the strategy of the other side. Thus, cerebral asymmetries are always a matter of degree. Within these limitations, the above mentioned papers clearly reveal that the left hemisphere seems to be specialized to orient according to landmarks by using absolute distances of these objects to the goal. The right hemisphere, on the other side, is able to utilize the relation of the position of major objects to each other to locate the goal. Both strategies work and probably both hemispheres complement each other during normal search bouts (Prior & Güntürkün, 2001). But depending on certain circumstances, one strategy can be more useful than the other. In this case we have to assume that a single hemisphere can temporarily be solely in charge to generate spatial orientation.

3.3. Is the asymmetry of spatial orientation special?

Is the distinction between an object-based cognitive strategy that uses absolute distances (LH) and one that computes relational properties of the surrounding enclosure (RH) special for spatial orientation, or is it a general distinction which is also visible in non-spatial tasks? Very likely the asymmetries during spatial cognition are nothing special but just part of a larger cognitive dichotomy.

If chicks are faced with an object that is partly occluded by other opaque items that stand closer to the animal, they are able to 'mentally complete' the partly hidden object. This rather basic cognitive ability is called amodal completion and many species are capable to do so (cf. Regolin, Marconato, & Vallortigara, 2004). Testing chicks under monocular conditions reveals that amodal completion is mainly a specialty of the LE/RH (Regolin
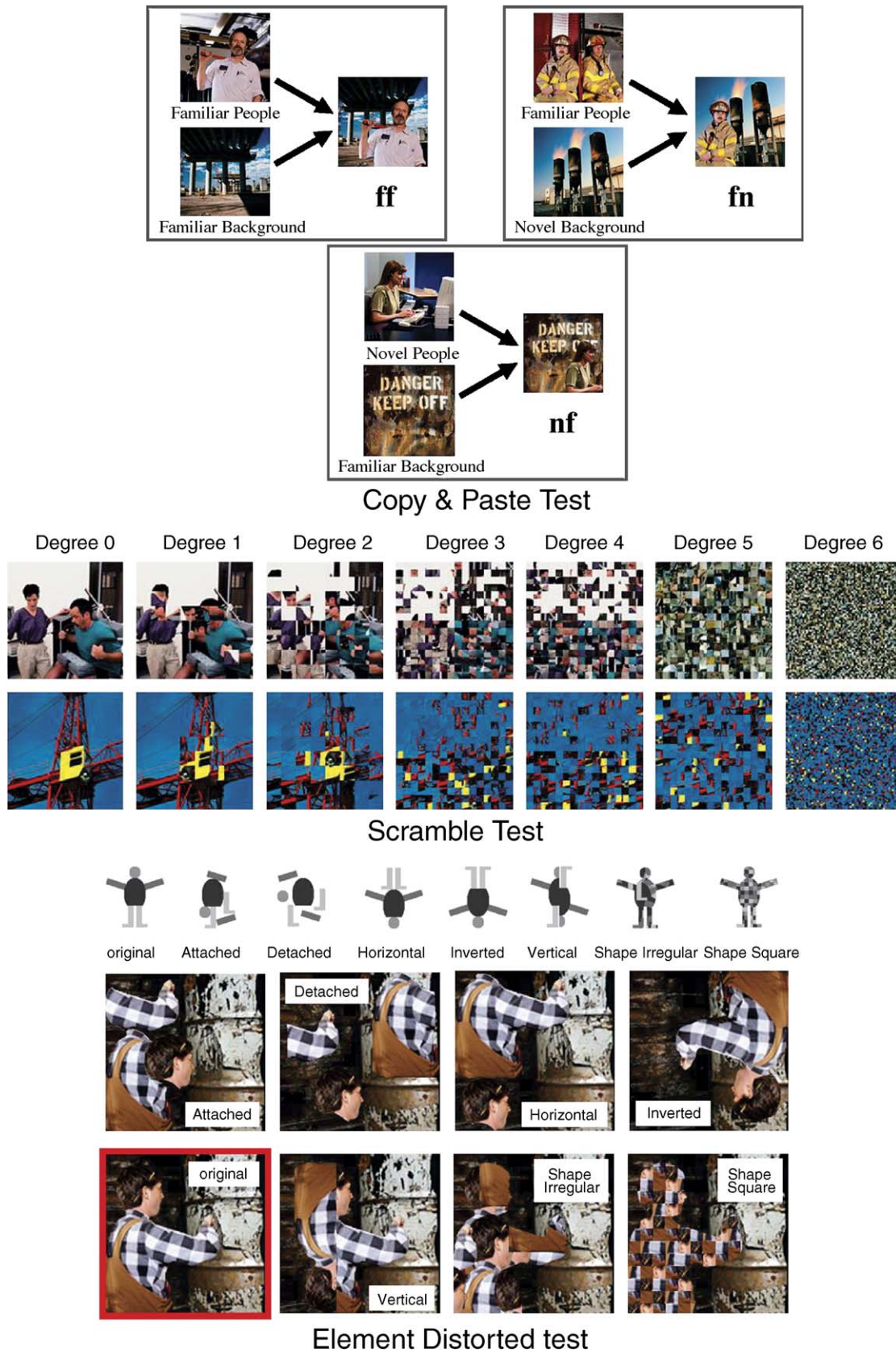
Fig. 2. Synthesized stimuli used in three different tests in the Yamazaki et al. study (2006). Top: Copy and Paste Test. Familiar/novel people and background were combined to make various test stimuli (f = familiar, n = novel). Middle: Scramble Test. The pictures were scrambled in 6° (degree 0 corresponds to the original picture). Bottom: Element Distortion Test. People were detached from the original picture, and were modified in seven manners.

et al., 2004). In order to amodally complete an object, the spatial relationships between the parts of a visual scene must be taken into account. Thus, the superiority of the LE/RH in amodal completion is very likely due to the same cognitive processes that are also responsible for the right hemispheric advantage in geometric spatial coding. Similarly, the ability of various species of birds to achieve higher discrimination scores in pattern discrimination tasks is possibly related to their RE/LH superiority in attending to local features of objects, similar to their ability to utilize local landmarks in spatial orientation (Güntürkün, 2003). Thus, birds probably operate to some degree with an asymmetrical mind that focuses on local features and absolute distances with the left hemisphere and on global objects and relational properties with the right. A new study on the lateralized capabilities of pigeons to learn the categorization of pictures with or without humans is able to illustrate this in detail.

In pigeons, it has been widely accepted that they can categorize various visual stimuli on the basis of concepts, such as 'people' (e.g. Aust & Huber, 2003) and 'fish' (Herrnstein & DeVilliers, 1980), to mention a few. To form a concept, it is necessary to ignore the local differences among the members of the stimuli, and to attend to the invariant information that defines that concept. If lateralized brain mechanisms similar to those observed in spatial tasks also operate during visual concept discriminations, it could be predicted that the LE/RH would be responsible for the processing by concept, whereas the RE/LH would be responsible for the processing of local, learned memories. Yamazaki et al. (2006) examined this issue by using a human concept discrimination task in pigeons. The subjects were trained in a GO/NOGO discrimination training, and were tested with eye caps to test for a lateralization of discrimination capability. Initially, the discrimination performance of the LE/RH was superior to that of the RE/LH. After a short period, the RE/LH caught up with the LE/RH, and in the following transfer test to the novel stimuli, there was no difference between the two hemispheres. This suggests that both hemispheres could in principle use categorically relevant cues. However, in further tests, it was found that when the subjects were presented with synthetic pictures containing familiar or novel human figures pasted on a novel or a familiar background (see "Copy and Paste Test" in Fig. 2), the LE/RH had difficulty to recognize novel human figures on familiar backgrounds, whereas the RE/LH did not. This suggests that the LE/RH relied less on conceptual cognition but more on its memory store of familiar humans and had difficulty when faced with a new person. When the pictures were increasingly scrambled to force the animals to use smaller and smaller pieces of pictorial information (see "Scramble Test" in Fig. 2), the LE/RH gave up rather quickly, while the RE/LH could follow up to higher scrambling levels. This showed that the LE/RH needed larger cues to recognize the pattern than the RE/LH. In a final test, pictures of humans were cut in pieces or distorted in various ways and assembled in wrong configurations (see "Element Distorted Test" in Fig. 2). Again the LE/RH was more affected, showing that the right hemisphere was using configurational information to recognize stimuli, while the left hemisphere based its decisions on the presence or absence of critical components, irrespective of their relative position.

Together these findings indicate that in principle both hemispheres are able to use conceptual cognition, albeit with different strategies and efficiencies. The left hemisphere seems to focus on smaller portions of a pattern, does not care of the configuration of these portions, and is rather effective in acquiring a category that can be transferred to novel pictures. Contrary, the right hemisphere is more globally driven, uses relational information and is less effective in transferring to new exemplars. Thus, in pigeons, categorical information was more supported by the left hemisphere, which is consistent to the theory by Kosslyn and colleagues. Note, however, that the categorical information used by the left hemisphere did not need to be correctly configured, which is contrary to the prediction of the theory.

4. Categorical versus coordinate asymmetry in nonhuman animals

4.1. Kosslyn's early theoretical position

Studies on cerebral asymmetries in nonhuman animals do not provide strong support for a categorical and a coordinate superiority of the left and the right hemisphere, respectively. We herein use these labels in sensu Kosslyn (1987) and Laeng et al. (1999). However, we have to distinguish between the early assumptions of Kosslyn (1987) and the extension of this theory by subsequent studies (e.g. Laeng et al., 2003). While the early assumptions receive some support from the animal literature, the latter does not.

Based on computational considerations, Kosslyn (1987) posited a "snowball" mechanism that biases the left hemisphere to specialize for a categorical and the right hemisphere for a coordinate mode of spatial code. Such a category/coordinate-dichotomy that is mapped onto a left–right division of labor is partly substantiated by monkey and bird studies. Dépy et al. (1998), Jason et al. (1984) and Vogels et al. (1994) provided data that are compatible with a view that monkeys switched to a categorical mode of processing after extensive training with stimuli between which the animals had to dichotomously decide. Yamazaki, Aust, Huber, and Güntürkün (2006) showed that also pigeons that learned a human versus nonhuman discrimination task were able to grasp and categorize the essential invariant properties of humans significantly faster with the left hemisphere. Thus, a left hemispheric advantage in categorization can be shown in monkeys and pigeons. This is a very important finding since it is always possible that participants that perform a categorization task are influenced by internal verbal cues which have their roots in the left cerebral hemisphere. Indeed, Parrot, Doyon, Démonet, and Cardebat (1999) showed that language areas of the brain are also activated when performing categorizations. The finding that monkeys and pigeons possibly excel in categorization with their left hemisphere demonstrates that a left hemispheric advantage in categorization does not necessarily result from verbal codes.

There is, however, no direct evidence for a coordinate superiority of the right hemisphere in monkeys and birds. This conclusion especially rests on the results of Dépy et al. (1998) that were crafted according to paradigms used with human participants

and that did not reveal a corresponding lateralization in baboons. Similarly, both in chicks (Tommasi & Vallortigara, 2001) and in pigeons (Prior, Lingenauber, Nitschke, & Güntürkün, 2002) distance coding was a domain of the left hemisphere. There is, however, some indirect evidence for an asymmetry resembling the position of Kosslyn's original theory. Kosslyn and Jacobs (1994), see also Laeng et al. (2003) have proposed that the biases that may work to constrain categorical and coordinate encodings to the left and right hemispheres, respectively, are to be found at an early organization of the visual system. Specifically, the receptive fields of visual neurons in the LH specialize for small and non-overlapping receptive fields (or high spatial frequency processing), whereas the same neurons in the RH would have large and overlapping receptive fields (low spatial frequency). This arrangement would in turn favor the development of lateralization for different types of spatial relations. A good deal of empirical evidence from human studies has confirmed this division of labour of the two hemispheres for processing low versus high spatial frequencies (cf. Laeng et al., 2003). In addition, differing hemispheric biases for attention to "global" and "local" levels of visual stimuli (Navon, 1977) have been observed and these attention biases seem closely connected with the spatial frequency biases (e.g. Hughes, Fendrich, & Reuter-Lorenz, 1990). Typically, the RH is faster and more accurate to identify global components of the input and the LH is faster and more accurate to identify local components (e.g. Fink et al., 1996; Van Kleek, 1989).

Few but conclusive studies are available concerning the processing of global versus local information and its lateralization in nonhuman primates. The first study was conducted by Horel (1994) who showed that cooling the dorsal inferotemporal cortex of macaques inhibited their ability to perceive the local level of forms, but had no effect for the global level. Three researches investigated laterality for processing Navon's type compound stimuli with behavioral procedures. Thus, Deruelle and Fagot (1997) and Fagot and Deruelle (1997) conducted several experiments with Guinea baboons and humans, tested in parallel. Both baboons and humans showed a RH advantage for global trials and a reversed but not significant left-hemisphere advantage for local trials. Hopkins (1997) found similar results in chimpanzees. In this study, compound stimuli made of letters at both the local and global levels were presented to chimpanzees in a divided field setup. There was no significant effect of lateralization for accuracy scores. For the speed of the response, however, there was a significant LH advantage for local processing, but no significant advantage for global processing.

The data of Yamazaki et al. (in prep.) in pigeons also show that pigeons rely on local features with their left hemisphere and on more larger configurations with their right. Therefore, a local- versus global-distinction that results from left- and right-hemispheric mechanisms, respectively, can be found in nonhuman primates and pigeons. It can thus be concluded that there is some support from the animal literature for a left hemispheric advantage in categorical cognition. Although there is no support for a right hemispheric bias in coordinate processing, a local/global distinction, as also assumed by Kosslyn and Jacobs (1994) to result from a basic dichotomy

of spatial processing, can be shown in nonhuman primates and birds.

4.2. Subsequent additions to the early theoretical position

Over the years the original theory of Kosslyn was extended as a result of new data emerging from subsequent studies (e.g. Laeng et al., 1999), although many of these additions had already been anticipated in Kosslyn (1987). Along the line of argumentation of these more recent studies that follow the original proposal, we would require the left hemisphere to be superior in: (i) recognizing altered images of known objects, and in (ii) the utilization of relational properties between parts of objects. In contrast, we would expect the right hemisphere to: (iii) achieve higher scores in recognizing known objects in their previously learned form. These three assumptions were up to now not tested in monkeys but they were in birds.

The first assumption of Laeng et al. (1999) is that the left hemisphere excels in encoding objects in unfamiliar contortions. This has not been tested in birds in a way similar to the procedures used by Laeng et al. (1999), but in general avian lateralization studies reveal that image alterations can be compensated by both left and right hemispheric processes, but with different algorithms. While the left hemisphere seems able to recognize the match between the distorted pattern and the previous image by concentrating on local features, the right hemisphere operates with a special ability to perceive the configurational arrangement of object's parts and memorizes whole scenes. Thus, both hemispheres are able to identify a known form in a contorted form, albeit with different means. The second assumption is that the left hemisphere is superior in seeing relational properties between parts. This is contradicted by experiments with birds which demonstrate that it is the right hemisphere which excels in this task. The third proposal assumes that the right hemisphere achieves higher scores in image recognition, once they become familiar. This is contrary to experiments with birds showing that it is the left hemisphere that is superior in recognition of familiar patterns. In summary, there is no support for the theoretical position of Laeng et al. (1999) from avian studies.

4.3. Summary

Only few comparative studies support an ancient heritage of the cerebral dichotomies as proposed by Kosslyn and colleagues. The strongest support comes from a local versus global differentiation in left- and right-hemispheric processing, respectively. Mammals and birds separated nearly 300 millions years ago with birds having evolved between 50 and 100 million years after mammals. Thus, an asymmetric local/global distinction could be a very old feature of vertebrate brains.

Some, albeit weak support exists for a left hemispheric advantage in categorical coding. With important reinterpretations of the data, the results of Dépy et al. (1998), Jason et al. (1984), and Vogels et al. (1994) might be seen as pointing to such a kind of functional asymmetry. The findings in pigeons (Yamazaki et al., in prep.) go into the same direction. However, the study of Hopkins and Morris (1989) in language trained chimpanzees

shows a right hemisphere advantage in a task that is of clearly categorical nature. If indeed the supporting experiments tap a categorical cognition similar to the one proposed by Kosslyn and colleagues, this asymmetry would not necessarily be based on verbal codes. Language might then be correlate of categorical thinking but not a prerequisite.

There is no support for a right hemispheric advantage in coordinate coding in animal studies. And there is equally no support from the animal literature for the subsequent additions to Kosslyn's initial theory. This checkered pattern with comparable and different results between human and nonhuman studies bears several theoretically important conclusions: the local/global distinction was seen as a computational result from an architectural design of the visual system that also produces incompatible algorithms of categorical versus coordinate processing. However, the animal literature shows that a local/global asymmetry can exist independently from a categorical/coordinate lateralization. Thus, the animal literature shows that a local versus global distinction does not necessarily imply the emergence of categorical and coordinate dichotomies. It would probably be more compatible with the existence of more basic input variables like those associated with the theory on lateralized processing of spatial frequencies (Sergent, 1982). It is however likely that the spatial frequency factor might serve as a bridge between global/local processing lateralization and lateralization of spatial processing. As demonstrated by Jacobs and Kosslyn (1994, see also Jager and Postma, 2003), the left hemisphere is predisposed to input from visual neurons with smaller receptive fields, and thus would be tuned to high frequency spatial information as well as be superior in categorical tasks. By contrast, the right hemisphere, is predisposed to input from visual neurons with relative large receptive fields, and thus would be sensitive to low frequency spatial information and be superior in coordinate spatial tasks. This opens the interesting possibility that the global/local hemispheric processing would have, more or less automatically, lead to a spatial relation lateralization.

There are, in principle, two possibilities to interpret these sobering results. One interpretation could be that the evolutionary line leading to humans resulted in a lateralized architecture that is not comparable to other vertebrates. Although this conclusion could be defended, a number of arguments make it unlikely. Most importantly, a very large number of studies show human asymmetries as being largely comparable to those of other vertebrates (Rogers & Andrew, 2002). This makes it unlikely that the asymmetrical mechanisms of spatial orientation in humans have taken a completely different phylogenetic path. But if so, we should see at least in our closest relatives glimpses of our organization. However, even the study of Hopkins and Morris (1989) in language trained chimpanzees shows a right hemisphere advantage in a task that is of clearly categorical nature. As it was stated above, this study with only two chimpanzees is of limited impact for drawing any firm or definitive conclusion.

The second possibility is that the theory of the lateralized distinction between categorical and coordinate cognition has to be altered at least in some aspects. This could result not only in an explanatory system that clarifies the results with nonhuman animals, but would also be able to incorporate the contradictions within the human literature. Laeng et al. (1999) showed that human participants were superior with the left hemisphere in recognizing known objects in contorted poses. They interpreted this as an indication for the superior ability of the left hemisphere to understand the relative positions of limbs that are attached to trunks even when seeing from unusual perspectives. In fact, the pigeons in the study of Yamazaki et al. (2006) did the very same: they recognized new examples of human subjects in various circumstances as part of the category 'human' more reliably with the left hemisphere. However, as outlined above, this was not due to the ability of the left hemisphere to understand relational properties, but due to the left hemispheric specialization to extract invariant properties out of multiple examples. Similarly, the proposal of Laeng et al. (1999) that the right hemisphere achieves higher scores in the recognition of images, once they become familiar, could simply be related to the primarily global strategy of pattern recognition in humans (e.g. Navon, 1977). The fact that pigeons continue to excel with their left hemisphere in such tasks is compatible with their tendency to use a local strategy (e.g. Covato & Cook, 2001). Thus, the camps between Kosslyn and colleagues and the animal asymmetry groups might differ less if the assumption of a left hemispheric relational superiority is abandoned and if the local precedence of pigeons and baboons is incorporated as an important variable into the framework of interpretation.

A last factor of course needs to be mentioned as it concerns the original notion proposed by Kosslyn (e.g. 1987) that the specialization for speech control and language processing in the left hemisphere might have been the antecedent for the development of a left hemispheric bias for categorical spatial relation processing. The data reported in this review and the animal literature clearly shows that language was not a decisive factor in the shaping of left hemispheric lateralization patterns. It is thus presumed that instead of being primarily linked to language, lateralization actually emerged as a solution to larger perceptual and/or motor demands (Vauclair, Fagot, & Dépy, 1999).

References

Alonso, Y. (1998). Lateralization of visual guided behaviour during feeding in zebra finches (*Taeniopygia guttata*). *Behavioural Processes*, *43*, 257–263.

Aust, U., & Huber, L. (2003). Elemental versus configural perception in a people-present/ people-absent discrimination task by pigeons. *Learning and Behavior*, *31*, 213–224.

Benton, A., Hannay, H. J., & Varney, N. R. (1975). Visual perception of line direction in patients with unilateral brain disease. *Neurology*, *25*, 907–910.

Bingman, V. P., Hough, G. E., II, Kahn, M. C., & Siegel, J. J. (2003). The homing pigeon hippocampus and space: in search of adaptive specialization. *Brain, Behavior, Evolution*, *62*, 117–127.

Bruyer, R., Scailquin, J. C., & Coibion, P. (1997). Dissociation between categorical and coordinate spatial computations: modulation by cerebral hemispheres, task properties, mode of response, and age. *Brain and Cognition*, *33*, 245–277.

Chabris, C. F., & Kosslyn, S. M. (1998). How do the cerebral hemispheres contribute to encoding spatial relations? *Current Directions in Psychological Science*, *7*, 8–14.

Clayton, N. S., & Krebs, J. R. (1994). Memory for spatial and object-specific cues in food-storing and non-storing birds. *Journal of Comparative Physiology A*, *174*, 371–379.

Colombo, M., & Broadbent, N. (2000). Is the avian hippocampus a functional homologue of the mammalian hippocampus? *Neuroscience and Biobehavioral Reviews*, *24*, 465–484.

Covato, K. K., & Cook, R. G. (2001). Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 3–16.

Dépy, D., Fagot, J., & Vauclair, J. (1998). Comparative assessment of distance processing and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*). *Brain and Cognition*, *38*, 165–182.

Dépy, D., Fagot, J., & Vauclair, J. (1999). Processing of above/below categorical spatial relations by baboons (*Papio papio*). *Behavioural Processes*, *48*, 1–9.

Deruelle, C., & Fagot, J. (1997). Hemispheric lateralization and global precedence effects in the processing of visual stimuli by humans and baboons (*Papio papio*). *Laterality*, *2*, 233–246.

Fagot, J., & Deruelle, C. (1997). Processing of global and local visual information and hemispheric specialization in humans (Homo sapiens) and baboons (*Papio papio*). *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 429–442.

Fersen, L., & Güntürkün, O. (1990). Visual memory lateralization in pigeons. *Neuropsychologia*, *28*, 1–7.

Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees? *Nature*, *382*, 626–628.

Gray, E. R., Spetch, M. L., Kelly, D. M., & Nguyen, A. (2004). Searching in the center: Pigeons (Columba livia) encode relative distance from walls of an enclosure. *Journal of Comparative Psychology*, *118*, 113–117.

Güntürkün, O. (2003). Hemispheric asymmetry in the visual system of birds. In K. Hugdahl & R. J. Davidson (Eds.), *Brain asymmetry* (2nd Ed.). (pp. 3–36). Cambridge, MA: MIT Press.

Güntürkün, O., & Kischkel, K.-F. (1992). Is visual lateralization sex-dependent in pigeons? *Behavioural Brain Research*, *47*, 83–87.

Hamilton, C. R., & Vermeire, B. A. (1988). Complementary hemispheric specialization in monkeys. *Science*, *242*, 1691–1694.

Hellige, J. B., & Michimata, C. (1989). Categorization versus distance: hemispheric differences for processing spatial information. *Memory & Cognition*, *17*, 770–776.

Herrnstein, R. J., & DeVilliers, P. A. (1980). Fish as a natural category for people and pigeons. In G. H. Bower (Ed.), *The psychology of learning and motivation: Vol. 14* (pp. 60–97). San Diego: Academic Press.

Hopkins, W. D. (1997). Hemispheric specialization for local and global processing of hierarchical visual stimuli in chimpanzees (*Pan troglodytes*). *Neuropsychologia*, *35*, 343–348.

Hopkins, W. D., & Morris, R. D. (1989). Laterality for visual-spatial processing in two language trained chimpanzees (*Pan troglodytes*). *Behavioral Neuroscience*, *103*, 227–234.

Horel, J. A. (1994). Local and global perception examined by reversible suppression of temporal cortex with cold. *Behavioural Brain Research*, *65*, 157–164.

Hughes, H. C., Fendrich, R., & Reuter-Lorenz, P. A. (1990). Global versus local processing in the absence of low spatial frequencies. *Journal of Cognitive Neuroscience*, *2*, 272–282.

Jacobs, R. A., & Kosslyn, S. M. (1994). Encoding shape and spatial relations: The role of receptive field size in coordinating complementary representations. *Cognitive Science*, *18*, 361–386.

Jager, G., & Postma, A. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: a review of the current evidence. *Neuropsychologia*, *41*, 504–515.

Jason, G. W., Cowey, A., & Weiskrantz, L. (1984). Hemispheric asymmetry for a visuo-spatial task in monkeys. *Neuropsychologia*, *22*, 777–784.

Kahn, M. C., & Bingman, V. P. (2004). Lateralization of spatial learning in the avian hippocampal formation. *Behavioral Neuroscience*, *118*, 333–344.

Kosslyn, S. M. (1987). Seeing and imagining in the cerebral hemispheres: A computational approach. *Psychological Review*, *94*, 148–175.

Kosslyn, S. M., & Jacobs, R. (1994). Encoding shape and spatial relations: A simple mechanism for coordinating complementary representations. In L. U. Honavar (Ed.), *Artificial intelligence and neural networks: Steps toward principled integration* (pp. 373–385). New York: Academic Press.

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. E. (1989). Evidence for two types of spatial representations: hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 723–735.

Laeng, B., Chabris, C. F., & Kosslyn, S. M. (2003). Asymmetries in encoding spatial relations. In K. Hugdahl & R. Davidson (Eds.), *The asymmetrical brain* (pp. 303–339). Cambridge, MA: MIT Press.

Laeng, B., Shah, J., & Kosslyn, S. (1999). Identifying objects in conventional and controrted poses: Contributions of hemisphere-specific mechanisms. *Cognition*, *70*, 53–85.

Mehta, Z., & Newcombe, F. (1996). Dissociable contributions of the two cerebral hemispheres to judgments of line orientation. *Journal of the International Neuropsychological Society*, *2*, 335–339.

Mehta, Z., Newcombe, F., & Damasio, H. (1987). A left hemisphere contribution to visuospatial processing. *Cortex*, *23*, 447–461.

Mench, J. A., & Andrew, R. J. (1986). Lateralization of a food search task in the domestic chick. *Behavioral and Neural Biology*, *46*, 107–114.

Navon, D. (1977). Forest before trees: the precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353–383.

Nottelmann, F., Wohlschläger, A., & Güntürkün, O. (2002). Unihemispheric memory in pigeons—knowledge, the left hemisphere is reluctant to share. *Behavioural Brain Research*, *133*, 309–315.

Parrot, M., Doyon, B., Démonet, J. F., & Cardebat, D. (1999). Hemispheric preponderance in categorical and coordinate visual processes. *Neuropsychologia*, *37*, 1215–1225.

Peirce, J. W., Leigh, K. M., & Kendrick, K. M. (2000). Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. *Neuropsychologia*, *38*, 475–483.

Prior, H., & Güntürkün, O. (2001). Parallel working memory for spatial location and object-cues in foraging pigeons Binocular and lateralized monocular performance. *Learning and Memory*, *8*, 44–51.

Prior, H., Lingenauber, F., Nitschke, J., & Güntürkün, O. (2002). Orientation and lateralized cue use in pigeons navigating a large indoor environment. *Journal of Experimental Biology*, *205*, 1795–1805.

Prior, H., Wiltschko, R., Stapput, K., Güntürkün, O., & Wiltschko, W. (2004). Visual lateralization and homing in pigeons. *Behavioural Brain Research*, *154*, 301–310.

Rashid, N., & Andrew, R. J. (1989). Right hemisphere advantage for topographic orientation in the domestic chick. *Neuropsychologia*, *27*, 937–948.

Regolin, L., Marconato, F., & Vallortigara, G. (2004). Hemispheric differences in the recognition of partly occluded objects by newly hatched domestic chicks (*Gallus gallus*). *Animal Cognition*, *7*, 162–170.

Ritz, T., Adem, S., & Schulten, K. (2000). A model for photoreceptor-based magnetoreception in birds. *Biophysical Journal*, *78*, 707–718.

Rogers, L. J., & Andrew, R. (Eds.). (2002). *Comparative vertebrate lateralization*. Cambridge, UK: Cambridge University Press.

Sergent, J. (1982). The cerebral balance of power: confrontation or cooperation? *Journal of Experimental Psychology: Human Perception and Performance*, *8*, 253–272.

Shettleworth, S. J. (1990). Spatial memory in food-storing birds. *Philosophical Transactions of the Royal Society of London B*, *329*, 143–151.

Tommasi, L., Gagliardo, A., Andrew, R. J., & Vallortigara, G. (2003). Separate processing mechanisms for encoding of geometric and landmark information in the avian hippocampus. *European Journal of Neuroscience*, *17*, 1695–1702.

Tommasi, L., & Vallortigara, G. (2001). Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. *Behavioral Neuroscience*, *115*, 602–613.

Tommasi, L., & Vallortigara, G. (2004). Hemispheric processing of landmark and geometric information in male and female domestic chicks (*Gallus gallus*). *Behavioural Brain Research*, *155*, 85–96.

Ulrich, C., Prior, H., Duka, T., Leshchins'ka, I., Valenti, P., Güntürkün, O., et al. (1999). Left-hemispheric superiority for visuospatial orientation in homing pigeons. *Behavioural Brain Research*, *104*, 169–178.

Umilta, C. (1974). Hemispheric differences in the discrimination of line orientation. *Neuropsychologia*, *12*, 165–174.

Valenti, A., Sovrano, V. A., Zucca, P., & Vallortigara, G. (2003). Visual lateralisation in quails (*Coturnix coturnix*). *Laterality*, *8*, 67–78.

Vallortigara, G., & Andrew, R. J. (1994). Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behavioural Processes*, *33*, 41–58.

Vallortigara, G., Pagni, P., & Sovrano, V. A. (2004). Separate geometric and non-geometric modules for spatial reorientation: evidence from a lopsided animal brain. *Journal of Cognitive Neuroscience*, *16*, 390–400.

Van Kleek, M. (1989). Hemispheric differences in global versus local processing of hierarchical visual stimuli by normal subjects: New data and a meta-analysis of previous studies. *Neuropsychologia*, *28*, 1165–1178.

Vargas, J. P., Petruso, E. J., & Bingman, V. P. (2004). Hippocampal formation is required for geometric navigation in pigeons. *European Journal of Neuroscience*, *20*, 1937–1944.

Vauclair, J., & Fagot, J. (1993). Manual and hemispheric specialization in the manipulation of a joystick by baboons (*Papio papio*). *Behavioral Neuroscience*, *107*, 210–214.

Vauclair, J., & Fagot, J. (1996). Categorization of alphanumeric characters by Guinea baboons: Within- and between-class stimulus discrimination. *Current Psychology of Cognition*, *15*, 449–462.

Vauclair, J., Fagot, J., & Dépy, D. (1999). Nonhuman primates as models of hemispheric specialization. In M. Haug & R. E. Whalen (Eds.), *Animal models of human emotion and cognition* (pp. 247–256). New York: APA Books.

Vauclair, J., Fagot, J., & Hopkins, W. H. (1993). Rotation of mental images in baboons when the visual input is directed to the left cerebral hemisphere. *Psychological Science*, *4*, 99–103.

Vogels, R., Saunders, R. C., & Orban, G. A. (1994). Hemispheric lateralization in rhesus monkeys can be task-dependent. *Neuropsychologia*, *32*, 425–438.

Watanabe, S., & Bischof, H.-J. (2004). Effects of hippocampal lesions on acquisition and retention of spatial learning in zebra finches. *Behavioural Brain Research*, *155*, 147–152.

Weidner, C., Reperant, J., Miceli, D., Haby, M., & Rio, J. P. (1985). An anatomical study of ipsilateral retinal projections in the quail using radioautographic, horseradish peroxidase, fluorescence and degeneration techniques. *Brain Research*, *340*, 99–108.

Wiltschko, W., Traudt, J., Güntürkün, O., Prior, H., & Wiltschko, R. (2002). Lateralization of magnetic compass orientation in a migratory bird. *Nature*, *419*, 467–470.

Yamazaki, Y., Aust, U., Huber, L., & Güntürkün, O. (2006). Lateralized cognition: Asymmetrical and complementary strategies of pigeons during discrimination of the "human concept, submitted for publication.