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Lateralized cognition: Asymmetrical and complementary strategies of pigeons during discrimination of the "human concept" ☆

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Abstract

This study was aimed at revealing which cognitive processes are lateralized in visual categorizations of "humans" by pigeons. To this end, pigeons were trained to categorize pictures of humans and then tested binocularly or monocularly (left or right eye) on the learned categorization and for transfer to novel exemplars (Experiment 1). Subsequent tests examined whether they relied on memorized features or on a conceptual strategy, using stimuli composed of new combinations of familiar and novel humans and backgrounds (Experiment 2), whether the hemispheres processed global or local information, using pictures with different levels of scrambling (Experiment 3), and whether they attended to configuration, using distorted human figures (Experiment 4). The results suggest that the left hemisphere employs a category strategy and concentrates on local features, while the right hemisphere uses an exemplar strategy and relies on configuration. These cognitive dichotomies of the cerebral hemispheres are

largely shared by humans, suggesting that lateralized cognitive systems already defined the neural architecture of the common ancestor of birds and mammals.

1. Introduction

Nature makes it necessary to visually discriminate between various objects that can be eatable or toxic, predators or prey. Distinctions of that kind are called "concept discriminations" (e.g., Lea, 1984). Such concepts are defined by humans and can be discriminated on perceptual and not functional grounds, since animals sort relevant stimuli not by trial-and-error, but by perceptual cues. The ability to form a conceptually defined picture set enables the formation of invariant reactions to stimuli that display certain variability. Empirical studies support the discrimination of complex stimulus classes in nonhuman animals (e.g., D'Amato & Van Sant, 1988; Herrnstein, 1990; Huber, 1999, 2001; Robert & Mazmanian, 1988; Vonk & MacDonald, 2002). In case of pigeons, the subjects of the present study, many kinds of natural concepts have been evidenced, such as "human" (e.g., Aust & Huber, 2001, 2002, 2003, 2006; Herrnstein & Loveland, 1964), "water," an individual "person" (Herrnstein, Loveland, & Cable, 1976), "tree" (Herrnstein, 1979), "fish" (Herrnstein & DeVilliers, 1980), "human face" (e.g., Huber, Troje, Loidolt, Aust, & Grass, 2000; Jitsumori & Yoshihara, 1997; Troje, Huber, Loidolt, Aust, & Fieder, 1999), and an individual "pigeon" (Nakamura, Croft, & Westbrook, 2003; Poole & Lander, 1971; Watanabe & Ito, 1991). Evidence for successful discriminations is not limited to natural concepts, but also applies to artificial, unnatural concepts like aerial pictures of "man-made objects" (Lubow, 1974), "cartoon pictures" (Cerella, 1980; Matsukawa, Inoue, & Jitsumori, 2004), "styles of paintings" (Watanabe, Sakamoto, & Wakita, 1995), and experimenter-defined "artificial objects" (Lea & Harrison, 1978). These findings indicate that pigeons are capable of concept discriminations with great flexibility, regardless whether the target concept is biologically significant or not.

Successful discrimination and subsequent transfer to novel examples implies that pigeons can attend to the invariant information present in multiple instances of a category. In the case of the "human" concept, at least two different kinds of conceptual information seem to be relevant. These are (1) critical features that are parts of humans like head, body, legs, and arms, and (2) the correct arrangement and thus configuration of these features. In addition to these concept-defining stimulus aspects, pigeons also use non-conceptual cues like color, intensity, and shading if these covary with those relevant to category distinction (Huber et al., 2000). As shown in a series of experiments by Aust and Huber, pigeons use several kinds of information with different priority when having to discriminate between pictures with and without people. Especially stimulus familiarity (Aust & Huber, 2001), but also size, some body parts (Aust & Huber, 2002), and arrangement and orientation of

the body (Aust & Huber, 2003) are critical features. Taken together, these findings suggest that, depending on the availability of information, pigeons are ready to use various conceptually relevant cues as well as unique, non-conceptual features.

Based on these observations, Aust & Huber (2001) identified two strategies of pigeons in concept discrimination experiments which they labeled "item-specific discrimination" and "category-specific discrimination." Item-specific discrimination is defined as a strategy which relies on idiosyncratic stimulus aspects which are used to identify instances but are irrelevant to categorization (Loidolt, Aust, Meran, & Huber, 2003). These features can be rather small since strong scrambling of the original pictures had little effects on discrimination performance (Aust & Huber, 2001). In addition, the pigeons still classified the stimuli as person-present when they were cut into pieces so that they had no biologically correct arrangement anymore (see also Cerella, 1980; Watanabe, 2001). While familiarity is an indispensable prerequisite to the usage of "item-specific discriminations," this is not the case with the second strategy, which is referred to as "category-specific discriminations." Here, the pigeons attend to truly conceptually relevant information (i.e., class-distinguishing stimulus aspects), such as specific body parts as well as their spatial configuration.

It has repeatedly been argued that pigeons have a strong disposition to use local rather than global features (e.g., Cavoto & Cook, 2001). However, there is evidence that they can use both. While Watanabe (2001) showed discrimination by local features in cartoon stimuli, he also found that the pigeons' behavior was impaired when the photographs of real persons were scrambled. Even in case of using cartoons as stimuli, which are apparently of no biological importance for pigeons, they responded on the basis of the global configuration when the target stimuli were embedded into a background (Matsukawa et al., 2004). If pigeons thus indeed use two different strategies simultaneously, it is possible that these are processed in discrete brain areas. If these structures could be dissociated, a disentangling of strategies used during discrimination tasks would be possible. In the present study, we hypothesize that the two hemispheres of pigeons could be engaged in parallel but different analyses of the different pictorial features that define a concept. By temporally restricting visual input to one or the other hemisphere, we were able to disambiguate the possibly different contributions of the left and the right hemispheres to concept learning in pigeons.

For testing this hypothesis, pigeons are ideal subjects. Because the optic nerves of pigeons decussate almost completely (Weidner, Reperant, Miceli, Haby, & Rio, 1985), information from one eye almost exclusively ascends to the contralateral side of the brain. Covering the right eye during a task, for example, is a simple means to analyze the contribution of the left hemisphere. The cognitive lateralization of birds like pigeons and chickens is derived from Manns & Güntürkün (1999), or, at least, modulated by Johnston & Rogers (1999), a prehatch light stimulation asymmetry. Since avian embryos keep their head turned to the right and bend forward such that the left eye is covered by the body, the right eye is stimulated by light shining through the translucent shell, while the left eye remains light deprived (Rogers, 1990; Skiba, Diekamp, & Güntürkün, 2002). In accordance with the stimulation advantage for the right eye, some studies on the cognitive lateralization in birds showed that the right eye/left hemisphere (RE/LH) is dominant in tasks involving object discriminations

(e.g., Diekamp, Prior, & Güntürkün, 1999; Nottelmann, Wohlschläger, & Güntürkün, 2002; Prior, Lingenauber, Nitschke, & Güntürkün, 2002; Rogers, 1982; Vallortigara, Pagni, & Sovrano, 2004), while the left eye/right hemisphere (LE/RH) is specialized for configural or spatial processing, and social recognition (e.g., Güntürkün, 2003; Tommasi & Vallortigara, 2001; Vallortigara, 1992; Vallortigara et al., 2004). On the basis of these findings, it is likely that the RE/LH analyzes objects in detail, whereas the LE/RH attends to broader parts of the stimuli as well as to their configuration.

Here we report that indeed the two hemispheres of pigeons make distinct contributions to concept formation. While the left hemisphere is more able to truly conceptualize the target and uses a non-configural analysis of body parts as defining stimuli, the right hemisphere seems to rely more on a memory-based strategy and additionally uses the correct configuration of the human figure. We believe that our results have implications for general models of hemispheric asymmetries, since many studies seek an understanding on the basis of hemispheric difference during categorization tasks in humans and speculate on the evolutionary roots of these asymmetries (e.g., Burgund & Marsolek, 2000; Jager & Postma, 2003; Koivisto & Laine, 1999; Kosslyn et al., 1989; Laeng, Chabris, & Kosslyn, 2003; Laeng, Shah, & Kosslyn, 1999; Laeng, Zarrinpar, & Kosslyn, 2003; Marsolek, 1995, 1999; Zaidel, 1987).

2. Experiment 1 (monocular and transfer tests)

In the present study, we trained our pigeons to discriminate photographs according to the concept of "human" to examine, for the first time, whether a lateralization in the initial learning speed or in transfer performance was present. To this end, pigeons were first trained to discriminate between pictures with and without people, by means of the same procedure as used by Aust & Huber (2001). After they reached acquisition criterion under binocular conditions, we tested under monocular conditions to see if an asymmetry was observed in initial learning (*monocular test*). Thereafter, the subjects were re-trained under binocular and monocular conditions with the stimulus set that had been used during training. Then, a *transfer test* was conducted by presenting novel stimuli to each eye separately. The *monocular* and the *transfer tests* were used as a first approach to seek for possible asymmetries in the ability to memorize and/or conceptualize a very large pictorial data set that had a certain class of objects in common.

2.1. Method

2.1.1. Subjects
Eight homing pigeons (*Columba livia*) were used. They were housed individually and were kept at 85–90% of their free feeding weight. They were fed a small amount of food (mixed grain) after daily experimental sessions. Grid and water were freely available in their home cages throughout the experimental period. The housing room had a 12/12 h light/dark cycle.

2.1.2. Apparatus

All the experiments of the present study were conducted in two identical operant chambers (33 (w) × 34.5 (d) × 36 (h) cm^3). Each of them was equipped with a transparent glass key (7 × 7 cm^2), which was centered on the front panel, 6.5 cm from the ceiling. The stimuli, which the subjects could see through the key, were presented on a 15-in. TFT LCD monitor (TXA3813MT, iiyama), with a resolution of 1024 × 768 pixels. Two computers controlled the experimental sessions and collected the data. A feeder containing mixed grain was centered at the bottom of the front panel in each chamber and, when activated, a small lamp located above it was lit simultaneously. A house light (on the front panel, 5.5 cm from the ceiling, 6 cm from the right) was lit throughout the experimental sessions except for a 4 s blackout period between the trials. A white key light was used only during autoshaping and the preliminary sessions before discrimination training began. The distance between the surface of the key and the LCD monitor was set at 10 cm.

2.1.3. Stimuli

The stimuli were chosen from those used in Aust & Huber (2001, 2002, 2003). They consisted of photographs of digitized bitmap files of various scenes with a resolution of 72 dpi. Half of them depicted one or more human beings. These were defined as people-present (positive) stimuli, whereas the remaining photographs without people were defined as people-absent (negative) stimuli. The stimuli were 7.7 × 7.7 cm^2 (218 × 218 pixels) on the monitor, and the subjects viewed them with 42° of visual angle both horizontally and vertically, so that viewing conditions were the same as in Aust & Huber (2001, 2002, 2003). A total of 320 pictures, 160 of each class, were used for the training trials. Positive and negative pictures were separately grouped into four sets of 40 pictures each, and 16 pairings of positive and negative sets were made. The selection of the pairings used for baseline trials throughout the experimental sessions was counterbalanced among the subjects.

2.1.4. Procedure

2.1.4.1. Preparation for monocular testing. To prepare the animals for monocular testing, a 3/4 Velcro circle was glued around each eye with the 1/4 gap pointing frontally to enable frontal viewing. During monocular sessions, the eye caps (2.5 cm in diameter) were stuck over one of the eyes to completely prevent light input to this side. To preadapt the animals to the eye caps before using them in the discrimination sessions, they had to wear them in their home cages for 2 h after their daily discrimination training.

2.1.4.2. Initial training. The pigeons were trained in a conventional autoshaping procedure, where a key light was lit for 12 s, followed by 6 s food access and illumination of the feeder. Each autoshaping session consisted of 40 trials. When the subjects started to respond to the key, the autoshaping procedure was terminated and a continuous reinforcement schedule was initiated and continued to the end of the session. Thereafter, the subjects were transferred to a fixed interval (FI) schedule with FI 3 s, and were then progressively trained in FI 5 s, FI 10 s, variable interval (VI) 15 s, and

VI 20 s reinforcement schedules until they continuously responded to the key in each schedule. Each session consisted of 80 trials.

2.1.4.3. Discrimination training. The reinforcement schedule of the discrimination training was identical to that used in Aust & Huber (2003). In a positive (GO) trial, a stimulus showing people was presented for 10 s (FI), followed by VI 10 s. The responses were registered during both phases, but only the responses emitted during the FI period were used for subsequent analysis. After the VI was completed, the subject had to respond twice within 2 s to receive food reinforcement. In a negative (NOGO) trial, a stimulus without people was also presented for FI 10 s and VI 10 s but after the VI, the subject had to refrain from responding for 8 s. A response during this 8 s period prolonged the trial for another 8 s. In both types of trials, stimulus presentation was terminated by the beginning of the inter-trial interval (ITI), a blackout period of 4 s. The pigeons were trained binocularly for at least 12 sessions and then until they reached criterion which was set at $\rho \geqslant 0.8$ (Herrnstein et al., 1976), achieved in three consecutive sessions. Each session consisted of 80 trials, 40 positive and 40 negative ones. The sequence of positive and negative trials was randomized within a session. However, the same type of trial was not presented in more than three consecutive trials. Details of the procedure in each training or test condition are shown in Table 1.

2.1.4.4. Monocular test. The first test after reaching the acquisition criterion was the monocular test, where the subjects had to discriminate between pictures with and without people using only one eye. The test stimuli were 80 familiar instances arbitrarily selected from the training sets. Contingencies were the same as during training. The test sessions were conducted twice, once for each eye condition. Testing the first eye was followed by three consecutive binocular sessions prior to testing the second eye. The sequence of left- and right-sided tests was balanced among the animals.

2.1.4.5. Transfer test. After the subjects completed the monocular test with both eyes, they were re-trained to reach the criterion under binocular and monocular

Table 1
Details of the procedure and the numbers of the trials in each training or test of the present experiment

Condition	Training trials per session (h-present/h-absent)	Total test stimuli (test trials per session)	Test repetition
Initial training	80 (40/40)	–	–
Monocular test	80 (40/40)	80 training stimuli (80)	1×2 monocular condition
Transfer test	60 (30/30)	20 (10 h-present/10 h-absent)	2×3 viewing conditions
Copy and paste test	65 (33/32 or 32/33)	30 (5 ff, 5 fn, and 5nf)	2×3 viewing conditions
Scramble test	60 (30/30)	280 (10 h-present > 1–2 each degree/10 h-absent >1–2 each degree)	3×3 viewing conditions
Element distortion test	60 (30/30)	240 (20 > 1–2 original and seven distorted types > ff, fn, and nf)	5×3 viewing conditions

"h-present" and "h-absent" mean the stimuli with and without human figure, respectively.

conditions in turn. After that, they were tested for transfer of the initial discrimination to new examples of the positive and the negative sets. To this end, 20 pictures of each stimulus set were used, each of which was presented only once within each viewing condition. A test session consisted of 60 training and 20 test trials, 10 from each stimulus set which were randomly dispersed within a session (see Table 1). The test sessions were conducted six times in total, twice for each viewing condition (binocular, monocular left, and monocular right). The schedule of the test trials was identical to that of the training trials, except for the absence of feedback (neither food reinforcement nor timeout) after the VI. Instead, this period was immediately followed by the ITI. The sequence of the three eye condition tests was counterbalanced among subjects throughout all experiments of the present study. Between the three tests, the animals were re-trained to criterion under each condition.

2.1.5. Statistics

The traditional index of ρ (Herrnstein et al., 1976) was used to evaluate discrimination performance. The ρ value is obtained from the U value of the Mann–Whitney U test divided by the number of all compared cases. In addition, we used the standardized response rates (SRRs) as utilized in the series of studies by Aust & Huber (2001, 2002, 2003, 2006). This measure indicates the response rate of the test trials relative to the general response rate on the training trials in a given session. To obtain the SRR, the number of responses emitted to each training and test stimulus in the FI period is divided by the average response rate during the entire session, with only response rates to training stimuli entering the average. Paired t tests were conducted to compare the SRR values of the different viewing conditions. A significance level of $p = .05$ was adjusted for multiple testing using the Bonferroni procedure (Holm, 1979). In addition, ANOVAs with repeated-measures were conducted. In cases of violations of sphericity, α-adjusted degrees of freedom were used according to Greenhouse–Geisser.

2.2. Results

2.2.1. Initial training

Seven out of eight subjects learned the initial discrimination within 12 sessions, as shown in Fig. 1. Such a quick acquisition replicates the results of Aust & Huber (2001), although we used a different strain (Austrian "Strasser" race pigeons had been used in Aust and Huber). The performance of one pigeon was not stable and took 22 sessions to reach criterion.

2.2.2. Monocular test

The ρ values of the monocular test were 0.81 for the left eye and 0.71 for the right eye (averaged means of subjects), as shown in the left panel of Fig. 2. This difference in discrimination performance between eyes was significant, $t(7) = 3.94$, $p = .006$. The SRR values were slightly larger in the left-eye than in the right-eye condition. This difference approached significance, $t(7) = 2.35$, $p = .051$.
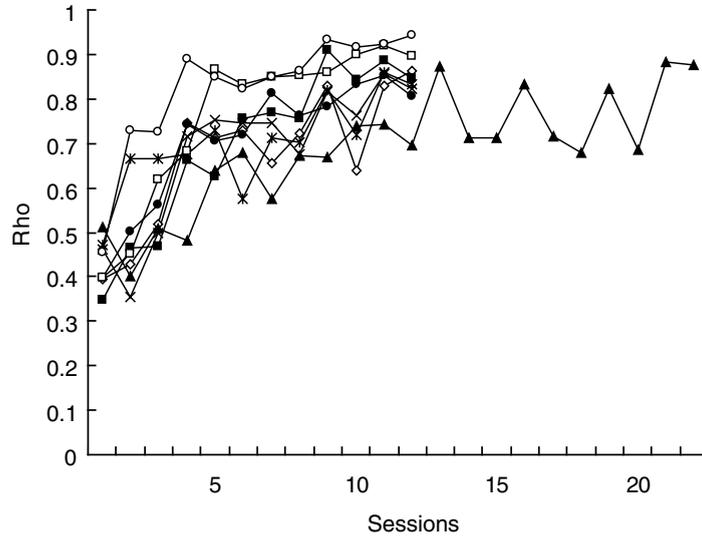
Fig. 1. Acquisition curves of the individual subjects in the initial discrimination training.
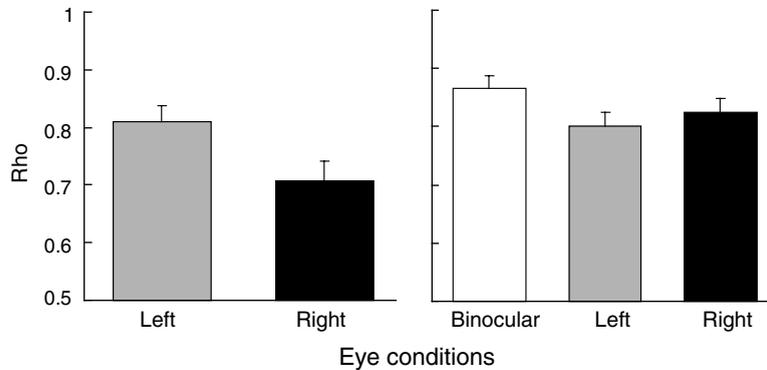

Fig. 2. Performance indicated by the discrimination index, ρ, with each viewing condition of the monocular test (left panel) and the transfer test (right panel).

2.2.3. Transfer test

The ρ values of the transfer test calculated across all subjects were above the training criterion of 0.8 for all the viewing conditions and reached 0.87, 0.83, and 0.84 with the binocular, the left, and the right eye conditions, respectively, as shown in the right panel of Fig. 2. ANOVAs based on SRR values revealed no significant differences between viewing conditions for GO, $F(2,14) = 1.45$, n.s., or NOGO trials, $F(2,14) = .42$, n.s.

To summarize, the LE/RH was superior to the RE/LH in the monocular test. There was no evidence for such an asymmetry in the transfer test.

2.3. Discussion

The results of the monocular test revealed a lateralized difference with a higher performance when the left eye was used. However, there was no difference between the two monocular conditions in the transfer test. Thus, the two hemispheres seemed to utilize the pictures in a different way, which affected initial learning performance. Despite this hemispheric difference in strategy or speed, however, both hemispheres might be able to go beyond the memorized patterns to achieve a successful transfer to novel stimuli.

There are, in principle, two possibilities to interpret the result of the monocular test: Either the two hemispheres do the same, but with different efficiency, or they analyze the stimuli in a different way, thereby producing left–right distinctions in learning speed. Diekamp et al. (1999) showed that pigeons were faster in understanding the underlying rule in a serial, reversal learning task using RE/LH. If this could be generalized to categorization learning, it is conceivable that the animals were establishing a concept-based strategy in the left hemisphere and therefore required longer to discriminate among the pictures with their right eye. With the LE/RH, the pigeons might have more relied on "rote learning" and could therefore achieve an initial advantage with the left eye seeing. Indeed, some studies with human subjects indicate that a rote memory strategy by RH results in faster learning than a categorization strategy by LH (e.g., Seger et al., 2000; Silverberg, Gordon, Pollack, & Bentin, 1980).

In summary, we found that the LE/RH mastered the task faster than the RE/LH, but the latter caught up with the former in the transfer test. Although it is possible that the RE/LH is primarily concept-driven, the results of the present experiment are insufficient to prove this. Therefore, we further explored the strategies employed by the two hemispheres in the following experiments.

3. Experiment 2 (copy and paste test)

The results of Experiment 1 showed some hemispheric differences in acquisition and transfer of a large picture set. This data pattern, however, is yet insufficient to deduce the possibly different strategies employed by each hemisphere. For example, if one hemisphere learned a global feature like configuration (e.g., Vallortigara et al., 2004), while the other concentrated on local features like hands, both half brains would be able to successfully generalize to untrained stimuli, despite using different approaches (Aust & Huber, 2002). Therefore, the second experiment was performed to further our understanding of hemisphere-specific strategies by differently probing the impact of target and background information.

To this end, we used stimuli which contained different combinations of familiar (f) or novel (n) targets and/or backgrounds. Three different types of pictures were utilized in the following way: (1) a familiar human figure was pasted on a familiar background from the NOGO stimulus set (ff); (2) a familiar human figure was pasted on a novel background (fn); (3) a novel human figure was pasted on a

familiar background (nf). It should be noted that novel humans on a novel back-ground were, in fact, identical to the transfer stimuli used in the last experiment, so we did not use this type of stimuli. In Aust & Huber (2001, Experiment 3) pigeons were actually able to discriminate ff, fn, and nf pictures according to the presence or absence of people. Furthermore, it was shown that pigeons are able to base their discrimination on very small feature-fragments (Aust & Huber, 2001, Experiment 2). In summary, these results indicated that pigeons can utilize category-specific (i.e., the concept of humans) as well as item-specific (i.e., idiosyncratic stimulus aspects) information to distinguish a large picture-set according to the presence or absence of humans. Indeed, in human subjects, Marsolek (1999) found that the abstract-category subsystem effectively operated in the LH, while the RH employed a specific-exemplar strategy. We assume that nf stimuli constitute the most demanding patterns, since despite a familiar negative background, the pigeons have to decide for GO due to conceptual information provided by the fore-ground.

The transfer test of Experiment 1 had revealed that the LE/RH was to some extent affected by stimulus novelty, suggesting that its decisions were not only based on a conceptual strategy, but also on its pictorial memory that could include learned background information. Thus, we predicted the LE/RH to be more affected by the conflicting information provided by the test stimuli than the RE/LH.

3.1. Method

3.1.1. Subjects and apparatus
Subjects and apparatus were the same as in Experiment 1.

3.1.2. Stimuli
A total of 30 test stimuli were used in the copy and paste test sessions, together with 320 training stimuli, which were the same as in Experiment 1. The training stimuli were utilized to establish a baseline level. The test stimuli were manipulated so as to combine familiarity or novelty of the target (human figure) and/or the back-ground. These stimuli were created by the same protocol as in Experiment 3 in Aust & Huber (2001). Examples are shown in Fig. 3a. There were three types of test stim-uli: ff, fn, and nf. For ff (i.e., familiar people pasted on familiar background) stimuli, the human figures from the training sets were cut out and pasted on background which had been used as negative stimuli during training. For fn (familiar people pasted on novel background), human figures from training stimuli were pasted on backgrounds that the animals had only seen in the transfer test (i.e., without feed-back). For nf (novel people pasted on familiar background), human figures from the transfer test (presented without feedback) were pasted on negative (i.e., non-person) training stimuli. Thus, these copy and paste stimuli were novel for the pigeons although they contained some familiar elements. We used 10 examples of each stimu-lus type and organized them into two sets. Each set contained 15 test stimuli, five of each type.
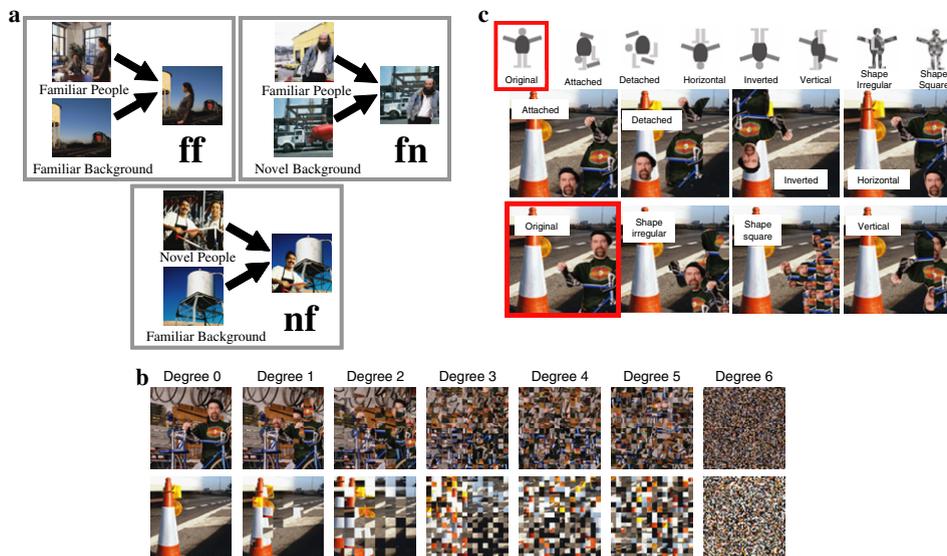
Fig. 3. Test stimuli used in the copy and paste test (a), the scramble test (b), and the element distortion test (c) (modified from Aust and Huber, 2001, 2003).

3.1.3. Procedure

Each test session consisted of 65 training trials (with feedback) and 15 test trials (without feedback). Test trials were interspersed into sequences of 33 and 32 positive or negative trials. Two test sessions, one with each test stimulus set, were conducted for each viewing condition (i.e., six test sessions in total, see Table 1). Test sessions were conducted twice with each eye condition. Between the test sessions, the subjects had to reach criterion once with each eye condition in interspersed training sessions. The orders of eye conditions and sets of test stimuli were balanced among subjects.

3.2. Results

The mean SRRs, relative to the mean SRR in the trained GO trials, are depicted in Fig. 4. The averaged mean SRR values for each viewing condition and stimulus type (baseline GO trials, ff, fn, and nf) were analyzed with an ANOVA, with viewing condition (binocular, left, right) and stimulus type (baseline GO trials, ff, fn, and nf) as repeated-measures. The ANOVA revealed a significant main effect of stimulus type, $F(3,21) = 18.91$, $p < .001$. Neither the main effect of viewing condition, $F(2,14) = 1.01$, n.s., nor the interaction approached significance, $F(6,42) = 1.17$, n.s. As predicted, the nf condition was the most demanding condition. A planned comparison of the left–right difference in the nf condition revealed a trend in favor of the right eye in the nf condition ($M = 1.17$, $SEM = 0.14$), which did not differ significantly from the left eye ($M = 0.86$, $SEM = 0.18$) in this condition, $t(7) = -1.80$, $p = .115$.
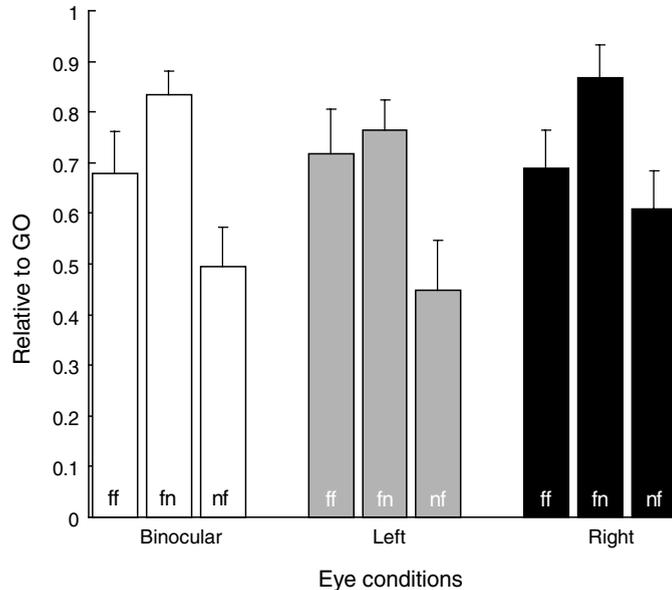
Fig. 4. Performance on each type of test stimuli (ff, fn, and nf), relative to the SRR on trained GO stimuli, with each viewing condition in the copy and paste test.

3.3. Discussion

Independent manipulations of figures and backgrounds, as used in the present experiment, uncovered some hemisphere-specific effects. As a trend, the performance of the LE/RH was negatively affected by the novelty of the human figures (ff vs. nf), but not by the familiarity of the backgrounds (ff vs. fn). This suggests that familiarity, and not the human concept as such, is the main source of information for the LE/RH. Contrary, RE/LH seemed to use conceptual information about humans to a larger degree.

The difference between the monocular conditions, however, was only shown as a trend. One of the reasons of no significant asymmetry might be that both hemispheres are to some extent able to use memory-based as well as category-based information. The aim of the next experiment was therefore to alter our stimulus set further to unrevealing hemisphere-specific strategies in categorization by increasingly scrambling the pictures. This procedure minimizes the size of the relevant pictorial area and thus destroys configuration and limits the source of information.

4. Experiment 3 (scramble test)

In the following two experiments, we investigated the critical cues that are used by the different hemispheres. Experiment 3 examined the effect of stimulus scrambling.

Scrambled stimuli make it possible to dissociate the differential controls exerted by stimulus configuration and local features on discrimination performance. Even a low degree of scrambling destroys stimulus configuration to a considerable extent, while leaving most other features intact. Progressive scrambling reduces pictorial information to increasingly small features. Pigeons are known to be robust against scrambling (e.g., Cerella, 1980). Two pigeons of Aust & Huber (2001) also discriminated significantly between familiar human-present and human-absent stimuli, even when the stimuli were cut into 4096 small squares that were randomly displaced. Thus, in concept discriminations, mere evidence of successful transfer to novel stimuli does not necessarily ensure that pigeons indeed use conceptual properties, because they may use small item-specific features that survived scrambling.

The scrambled stimuli used by Aust & Huber (2001) were dissociated by two factors: the degree of scrambling and the degree of familiarity. Thus, scrambled stimuli were used to disentangle the effects of familiarity and configuration in monocular pigeons. In principle, our stimulus material allowed to specify four different cognitive strategies. (1) If the animals follow a memory-based strategy by recalling local features, their performance should be robust against scrambling of familiar stimuli but should rapidly deteriorate with novel pictures. (2) If the animals utilize conceptual information, but base their decisions on local target features instead of target configuration, performance should be robust in novel and familiar scrambled pictures. (3) If the discrimination strategy of the animals is only memory-based but with the pictures being stored and processed in their correct configuration, even mild scrambling should affect performance. Novel pictures would be especially vulnerable since decisions cannot be based on retrieving item-specific information. (4) If the animals have a conceptual understanding of humans but need to see a human figure in its correct configuration to detect it, even mild scrambling of familiar or novel pictures should deteriorate discrimination performance.

4.1. Method

4.1.1. Subject and apparatus
Subjects and the apparatus were the same as in Experiment 1.

4.1.2. Stimuli
The test stimulus set of the scramble test consisted of intact and of scrambled stimuli, with both of them having familiar (i.e., used in the training sessions) and novel (i.e., used in the transfer test only) subcategories. The detailed protocols of creating the scrambled stimuli can be found in Experiment 2 in Aust & Huber (2001). We will describe them here only briefly. We used six degrees of scrambling, as illustrated in Fig. 3b. For degrees 1 and 2, the pictures were divided into 64 squares (8 × 8). For degree 1, eight squares were arbitrarily displaced, with the 28 marginal squares being kept in their original positions. For degree 2, every second square of every second row changed place with its right diagonal neighbor from the row directly below. For degrees 3, 4, and 5, the pictures were cut into 256 squares (16 × 16), and the squares were rearranged only within each quadrant for degree 3,

and within the upper and the lower halves for degree 4, while all squares were randomly arranged for degree 5. For degree 6, the pictures were cut into 4096 (64×64) squares that were randomly rearranged. We used 20 examples for each degree. Half of them were familiar, whereas the others were novel. A total of 280 stimuli (140 positive and 140 negative) were used.

4.1.3. Procedure

Each session consisted of 60 training and 20 test trials. The stimuli in half of the test trials contained human figures (positive sets), whereas the others did not (negative sets). At least one example from each degree of both sets was presented in a test session. The test session was conducted nine times in total, three times with each viewing condition (see Table 1). Between the test sessions, the birds had to re-achieve the learning criterion with each eye condition in interspersed training sessions. In total, the stimuli from each degree of scrambling were presented for four or five times per subject. Each test stimulus was presented once with each eye condition.

4.2. Results

The averaged differences in the SRR values between the trials with human-present and human-absent stimuli are depicted in Fig. 5, as a function of the degree of scrambling. A degree of 0 corresponds to the original, intact stimuli. To investigate if scrambling had an asymmetric effect on discrimination performance depending on familiarity, we conducted a $2 \times 3 \times 7$ ANOVA with repeated-measures with familiarity (familiar/novel), viewing condition (binocular/left/right), and degree of scrambling (0–6) as within-subject factors. The analysis revealed a significant main effect of degree of scrambling ($F(6, 36) = 19.48$, $p < .001$), pointing to a strong decrease of discrimination as a function of scrambling. The interaction between degree of scrambling and viewing condition approached significance ($F(12, 72) = 1.88$, $p = .051$). This effect suggests that brain hemispheres processed scrambled patterns in a slightly different way. Moreover, the interaction between familiarity and viewing condition
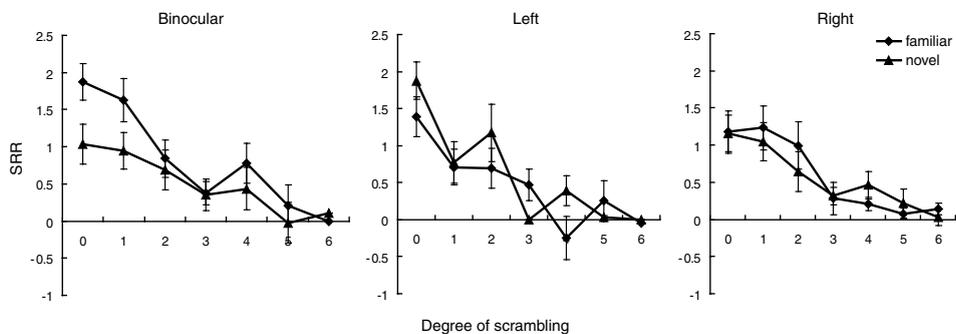

Fig. 5. Performance in the scramble test. Depicted are differences between the SRR of the test trials with (originally) human-present and human-absent stimuli. Degree 0 on the *x*-axis in each panel corresponds to the stimuli without scrambling (original stimuli).

approached significance ($F(2,12) = 3.82$, $p = .052$). No other main effects or interactions approached significance (all $F < 2.34$, n.s.).

According to the tendency for an interaction between viewing condition and scrambling level, we analyzed the scrambling level that results in a significant reduction of SRRs from the original picture (zero-scrambling) using post hoc α-adjusted multiple paired *t* tests for each viewing condition within a sequential testing procedure (adopted from Holm, 1979) (Table 2). According to the logic of our analysis, we defined a threshold (termination criterion) as the level of scrambling beyond which the animals always deviated significantly from discrimination performance at zero-scrambling. To give an example, pigeons that were discriminating familiar stimuli under binocular conditions reached significantly lower SRRs at scrambling levels 6 ($p < .001$) and 5 ($p = .003$), when compared with scrambling level 0. At scrambling level 4, however, the performance did not significantly differ from SRR values at baseline level (no scrambling). Thus, the sequential procedure for this condition was terminated at scrambling level 4.

Using this procedure, the thresholds for discriminating familiar stimuli were scrambling level 3 with the left eye and scrambling level 6 with the right. Thus, with the right eye the pigeons discerned scrambled stimuli up to a much higher degree than with the left eye. For the non-familiar stimuli, the thresholds were scrambling levels 4 for the binocular, level 2 for the left, and level 4 for right eye seeing condition.

4.3. Discussion

The results of the third experiment revealed two additive effects. First, familiar stimuli could be recognized at higher scrambling levels than novel ones. Second, using the RE/LH the animals could successfully reach higher levels of scrambling than with the LE/RH.

The LE/RH seemed to be very sensitive to even small amounts of distortion. Since the configuration of major aspects of the human body is already lost at a scrambling degree of 1, a configural strategy using major figural portions could be an important LE/RH strategy. The fact that the discrimination performance was better with familiar stimuli than with the novel stimuli suggests that a memory-based approach compensated the difficulties of the LE/RH when having to recognize mildly distorted familiar stimuli. However, familiarity did not fully compensate distortions beyond degree 3. Thus, for the LE/RH, an intact configuration might be a very important cue for categorizing pictures.

Table 2
Summary of the α-adjusted multiple paired *t* tests for each viewing condition within a sequential testing procedure adopted from Holm (1979) in scramble test

| | Eye conditions | | |
	Binocular	Left	Right
Familiar	Level 4	Level 3	Level 6
Novel	Level 4	Level 2	Level 4

Scrambling levels indicate the termination criterion at which the SRR values of given distorted stimuli were not significantly lower than that of original intact (i.e., scrambling level 0) stimuli.

The RE/LH seemed to adopt two different strategies depending on familiarity. When faced with novel stimuli, the RE/LH was able to utilize a conceptual strategy based on very small cues that are indicative of a human body. Since these tiny fragments bear no configural information, the RE/LH seems either not to utilize configuration, or is at least able to compensate its absence by exploiting the information within local cues. If stimuli are familiar, the performance of the RE/LH increases considerably. Thus, the RE/LH is also able to use a memory-based approach to detect human figures in familiar scrambled stimuli. This explanation is compatible with the results of Aust & Huber (2002), who found that the categorization performance of pigeons strongly depended on the presence of some human parts like hands, heads, and trunk as target-defining features in the human discrimination task. Thus, it is conceivable that for the RE/LH the presence of local human parts is the most important condition with the correct configuration of these parts only being an accessory variable. The strategy of the LE/RH seems to be complementary to this.

Although the effect of configuration was found mainly for the LE/RH, the fact that not only human figures but also the backgrounds were equally scrambled did not allow us to fully conclude that the right hemisphere was responsible for the configural recognition of the human figure. Additionally, the LE/RH reduced responses to nf pictures in the copy and paste test, suggesting that familiarity affected its discrimination performance more than the intactness of the human figures. Thus, it is quite plausible that the remarkable reduction of the responses with mildly scrambled stimuli would be attributable to a general scrambling effect of the whole picture, and not so much to the loss of configuration of the human figure. Therefore, the next experiment was conducted to test and eventually rule out this interpretation.

5. Experiment 4 (element distortion test)

The experiments so far showed that the LE/RH attends to larger part of the pictures and possibly relies on the familiarity of the trained stimuli, whereas the RE/LH primarily attends to the targeted human figures and analyzes them in detail. Additionally, our results suggest that an intact configuration is for the LE/RH as important as familiarity, whereas the RE/LH primarily attends to local features of the depicted humans without relying on their configuration. However, in Experiment 3, both the figure and the background were scrambled and thus the sole effect of the loss of configuration of the human figure could not be determined. Therefore, the present experiment was conducted to test the role of the configuration of the target only. Additionally, we sought to find out what the defining parts of the human figure were.

Aust & Huber (2003) examined the effects of different types of distortion on the pigeons' performance. They used seven types of test stimuli. One of them was an intact picture, but all others included distorted human figures of a certain type. Fig. 3c shows these distortions. The authors found that the pigeons used local features as well as relational information to discriminate human-present and human-absent stimuli. This is exactly what we would predict if both hemispheres contributed to these kinds of challenges with their differential strategies. According

to Aust & Huber (2003), none of the distortions reduced the response rates down to the level shown with negative stimuli, and the reduction was only significant in case of novel pictures. Thus, the pigeons probably used some very elemental features that survived all distortions when classifying familiar stimuli. Although pigeons obviously use both feature- and category-based strategies, the critical determinants of the discriminative cues still remain to be defined.

In Experiment 4, we examined the possibility that the two hemispheres contributed with different strategies to solving the distortion task. To this end, we presented several kinds of distorted stimuli as used in Aust & Huber (2003) to only one hemisphere. Distortions were applied to the same types of stimuli (ff, fn, and nf) as presented in the copy and paste test of Experiment 2. The advantage of using these stimuli was that it was possible to investigate not only the effects of distortion, but also those of familiarity and novelty.

5.1. Method

5.1.1. Subject and apparatus
Subjects and the apparatus were the same as in Experiment 1.

5.1.2. Stimuli
The stimuli were derived from those used in the copy and paste test in Experiment 2 (ff, fn, and nf), and they were distorted in seven different ways. Note that only the human figures were distorted while the background was always kept intact. These seven types of distortion were the same as those in Aust & Huber (2003): *attached* (the human figure was cut into parts which were then attached to each other in randomized positions), *detached* (the human figure was cut into parts which were scattered on the background), *horizontal* (the human figure was horizontally cut into three parts and these were re-ordered randomly), *vertical* (the human figure was cut vertically into two halves and one of them was attached to the other upside-down; inverted sides were balanced), *inverted* (the human figure was placed upside-down), *shape square* (the interior of the human figure was cut into randomly re-arranged squares of 17×17 pixels, with the contour remaining intact), *shape irregular* (the interior of the human figure was cut into randomly re-arranged irregular parts, with contour remaining intact). There were 10 examples for each type of stimulus (i.e., each ten for ff, fn, and nf), thus a total of 240 stimuli (30×7 types of distortion, and 30 original stimuli) were used in the element distortion test. An example of the stimuli used in the present experiment is shown in Fig. 3c.

5.1.3. Procedure
The schedules of training and test trials were the same as those of the preceding experiments. Each session consisted of 60 training (30 positive and 30 negative) and 20 test trials. No feedback was given at the end of a test trial. The test session was conducted five times with each viewing condition (see Table 1). In each test session, the test stimuli from each distorted type were presented for four or five times in total.

Between the test sessions, the subjects had to reach to the criterion with each viewing condition in interspersed training sessions.

5.2. Results

Response rates on the distorted stimuli were compared to the *original* ones. The $3 \times 3 \times 8$ ANOVA with repeated-measures, with viewing condition (binocular, left, and right), combination (ff, fn, and nf), and distortion types as repeated-measures factors revealed a significant main effect for novelty/familiar combinations, $F(2,14) = 21.54$, $p < .001$, and distortion types, $F(7,49) = 5.07$, $p < .001$. Moreover, the three-way interaction between viewing condition, combination, and distortion type was significant, $F(28,196) = 1.54$, $p = .05$. Neither the main effect of viewing condition nor any other two-way interaction approached significance (all $F < 1.78$, n.s.). Based on the significant triple interaction, we analyzed the eye-condition-by-distortion-type-interactions separately for ff, fn, and nf. The analysis revealed that only for the fn condition the interaction approached significance ($F(14,98) = 1.65$, $p = .08$). This interaction did not approach significance for the ff ($F(14,98) = .79$, $p = .68$) and nf ($F(14,98) = 1.14$, $p = .33$) conditions. Although, neither of these interactions was significant, the relation between eye condition and distortion type was strongest in the fn condition. To understand this relation, we analyzed the difference between distortions relative to the original depiction for each eye and novelty/familiar combinations with α-adjusted multiple paired *t* tests (Holm, 1979). Seven comparisons ("original" compared with seven distortion types) were made within each combination type (ff, fn, and nf) and with each viewing condition. Because it is reasonable to assume that the responses to the distorted stimuli would be fewer than those to the intact stimuli, we conducted one-tailed analysis. Table 3 shows the results in comparison with those of Experiment 3 of Aust & Huber (2003). In the ff condition, no comparison between distorted types and the original SRR approached significance for all viewing conditions. Besides a significant difference between *shape square* type and the original SRR in the binocular viewing condition

Table 3
SRR scores for all distorted types for each eye condition and novelty/familiar combination

Eye condition	Aust and Huber (2003)					Present experiment					
	Binocular					Left eye			Right eye		
	Familiar	Novel	ff	fn	nf	ff	fn	nf	ff	fn	nf
Original			1.154	1.437	0.941	0.851	1.544	0.800	0.862	0.962	0.958
Attached	ns	**	1.055	1.014	0.543	0.682	**1.059**	0.539	0.850	1.009	0.625
Detached	ns	**	0.932	1.221	0.656	1.161	**0.831**	0.542	0.859	0.971	0.375
Horizontal	ns	**	0.758	**0.670**	0.553	0.779	**0.837**	0.615	0.517	1.256	0.516
Inverted	ns	**	0.902	1.291	0.457	0.853	**0.933**	0.851	0.760	1.259	0.748
Shape irregular	ns	**	0.748	0.889	0.683	0.666	**0.735**	0.320	0.649	0.653	0.439
Shape square	ns	**	0.563	1.016	**0.360**	0.536	**0.467**	0.424	0.871	0.642	0.484
Vertical	ns	**	0.844	0.988	0.757	0.878	**0.873**	0.747	0.834	0.935	0.462

SRRs in bold letters represent significant differences between distorted types and original SRR (one-tailed, α-adjusted for multiple testing, Holm, 1979). In the left column, the comparable results (**significant, ns: not significant) from Aust and Huber (2003) are shown.

($p = .003$), no further comparison approached significance in the nf condition. In the fn combination, however, all distorted stimuli differed significantly from the original in the LE/RH condition. No such difference appeared in the RE/LH condition. Moreover, the difference between *horizontal* and the original SRR was significant in the binocular/fn condition ($p = .001$).

5.3. Discussion

The results of Experiments 1–3 indicated that the LE/RH seems to rely on the correct configuration of the human figure, whereas the RE/LH has a tendency to base its decisions on figural parts that are able to define a category. Thus we had expected that the distorted stimuli, due to the loss of target configuration, would deteriorate right hemisphere performance more strongly than that of the left hemisphere.

Table 3 shows the degree to which discrimination by the LE/RH was configuration-dependent. It is obvious that performance of the LE/RH suffered severely from distortion. Significant results were obtained only for fn. Since the stimuli were to some extent known from previous exposure and since the LE/RH utilizes both foreground and background, the lack of a familiar background possibly let the animals in the fn condition to decide on the basis of human figures only. As a consequence, performance was significantly reduced in all of the seven distortion types.

It is, however, important to note that these conclusions rest on indirect evidences, based on the presence of significant distortion-related reductions of SRRs relative to the undistorted condition for the left, but not for the right eye. A direct analysis for eye-condition-by-distortion-type-interaction in the fn condition had revealed only weak support for this conclusion.

The failure of showing significant differences between *original* and each type of distorted stimuli clearly indicated that the human features did matter for the RE/LH, regardless of their configuration. Obviously, feature size and shape did not matter as the subjects did not seem to care whether the human figures were cut into square pieces or into biological parts. In addition, the RE/LH does not care about the orientation of the human figures, because the performance on *inverted* stimuli showed no significant difference from the original performance, regardless of the stimulus types (ff, fn, and nf). The data indicate that orientation invariance in pigeons (e.g., Delius & Hollard, 1995; Hollard & Delius, 1982) may be supported primarily by the RE/LH, even when the stimuli are not familiar.

6. General discussion

6.1. Summary of the results

In a series of experiments, we found that pigeons that were trained to categorize hundreds of pictures according to the presence or absence of a human being showed performances that depended on the eye in use (binocular, left, and right). Due to the virtually complete decussation of the optic nerves in birds, the left eye reveals right

hemispheric mechanisms (LE/RH), whereas right eye performance indicates left hemispheric processes (RE/LH). In the monocular test (Experiment 1), it was revealed that in the initial training phase the animals discriminated more accurately using the LE/RH and not the RE/LH. In the transfer test, however, they performed equally well under all three viewing conditions when faced with novel stimuli. In the copy and paste test (Experiment 2) stimuli with new combinations of familiar and novel human figures as well as familiar and novel backgrounds were used. This experiment revealed a trend towards a higher amount of difficulties of the LE/RH in recognizing novel human figures on a familiar background, compared with the RE/LH. In the scramble test (Experiment 3), the LE/RH had a tendency to lose its discriminatory capacity even when faced with only mildly scrambled stimuli, whereas the performance of the RE/LH was more robust to even extensive scrambling. The element distortion test (Experiment 4) showed weak evidence for higher resistance of the RE/LH against distortions of the human figure.

In sum, the data indicate that the LE/RH is likely to be responsible for decisions by familiarity and configuration, whereas the RE/LH is responsible for decisions by category-defining features with an emphasis on local cues. Note that conceptual decisions made by the RE/LH did not necessarily imply a correct configuration of the human figures. In the following, we will discuss the implications of these data and will search for an integrated explanation from a comparative, and neurocognitive point of view.

6.2. Monocular and transfer tests

In the monocular test, the left eye performed better than the right eye in the discrimination of human figures. Such a left-eye superiority is contrary to the findings of a previous study by Fersen & Güntürkün (1990) in which pigeons had to memorize 725 abstract patterns that were arbitrarily divided into a group of 100 positive and one of 625 negative patterns. This visual memory study had evinced a clear right-eye dominance. The difference between the present study and that of Fersen & Güntürkün (1990) is, though, obvious. The positive patterns in the study of Fersen & Güntürkün (1990) had nothing in common that could be used to distinguish them from the negative ones but had to be discriminated one-by-one on the basis of item-specific features. Therefore, the animals had to rely on their visual memory for pattern details. In the present study, however, a common set of category-relevant features (i.e., features confounded with the human figure) defined the positive pictures. Thus, the difference of eye-dominance between these two seemingly similar experiments makes it likely that the pigeons in the present experiment were not solely relying on a memory-based strategy.

We found that the LE/RH was superior in performance at the time of the monocular test, but that the RE/LH caught up during transfer. Interestingly, there are similar findings with human subjects in categorical tasks (e.g., Dépy, Fagot, & Vauclair, 1998; Kallman & Corballis, 1975; Kosslyn et al., 1989; Seger et al., 2000; Silverberg, Bentin, Gaziel, Obler, & Albert, 1979; Silverberg et al., 1980). Silverberg et al. (1980), using auditory–visual word matching, suggested that the initial

dominance of the right hemisphere was due to pattern recognition, not to verbal analysis (e.g., sound analysis or serial ordering). Seger et al. (2000) suggested the right hemisphere to be involved in visual pattern processing that is independent of learning. Laeng et al. (1999) showed advantages by the left hemisphere when contoured stimuli were first presented and by the right hemisphere after the stimuli were well familiarized. These and similar data make it conceivable that in humans and pigeons the hemispheric dominance changes concomitantly with a shift of cognitive strategy. In pigeons, we assume the LE/RH to be initially faster due to a memory-based strategy that pays in the beginning, but is less efficient in the long run than a conceptual strategy.

6.3. Copy and paste, scramble, and element distortion tests

In the copy and paste test, there seemed to be a trend for the decreased LE/RH responses to the nf stimuli (pictures with novel people on a familiar background). In the scramble test, the analyses suggest that the RE/LH was more robust against extensive scrambling when dealing with novel stimuli. In the element distortion test, the LE/RH was more affected by several distortions in the fn condition, while this was less pronounced for the RE/LH. Together, these results indicate the presence of different strategies used by the two hemispheres. For the LE/RH, in general, matching to memory (familiarity) seems to be the most dominant strategy. In case of novel human figures, the intact configuration of the human figure is a necessary attribute to compensate for lack of familiarity. The dramatic decrease in performance in the scramble test suggests that the configuration-based strategy goes along with a reliance on global features. On the other hand, the RE/LH depends on category-defining local features abstracted during training. The response rule does not necessarily require correct configuration of the body parts but goes along with utilization of local features.

Now it is possible to better explain the performance in the monocular and transfer tests which were somewhat contradictory. At the beginning of training, the LE/RH possibly tried to memorize the stimuli including foreground and background, while the RE/LH tried to abstract the category-relevant information which was common to all positive stimuli. Such "rule-abstraction" by the left hemisphere is consistent with the findings of Diekamp et al. (1999), who used repeated color reversals and found faster learning and a steeper asymptotic function for rule extraction by the left hemisphere. Since abstraction of the class rule by the RE/LH is possibly more time-consuming than a merely memory-dependent strategy as applied by the LE/RH (Cook, Wright, & Kendrick, 1990), the animals would have learned faster with their left eye seeing before the monocular test.

Although the LE/RH was found to depend on memory in recognizing human figures, successful transfer to the novel pictures in the transfer test suggests that this memory dependency is not an exclusive, but a dominant strategy. This idea is supported by the facts that performance on the novel original stimuli by the LE/RH was higher than that by the RE/LH in the scramble test and that the LH/RH was attending to both the human figures and the backgrounds.

In the element distortion test, one possible solution to the problem of discriminating the test stimuli of *shape irregular* and *shape square* was to use contours of the human figure and ignoring the scrambled interior. The LE/RH, however, was unable to discriminate both the test stimulus types in case of the fn stimuli, and the binocular pigeons failed to discriminate the *shape square* cases of nf stimuli. In case of *shape square*, the size of the squares corresponded to that of degree 2 or 3 in the scramble test in Experiment 3, so the lower SRR values could be interpreted in terms of failure to recognize human figures in such small fragments. However, the fact that the subjects were reluctant to respond to *shape irregular* stimuli suggests that the loss of information about the inner parts of the human figure was sufficient for the LE/RH to reduce responses, even when the human contour was kept intact. In a preceding study, Aust & Huber (2002) reported that the binocular pigeons had difficulty in the silhouette stimuli test in Group P (reinforcement was contingent on the responses to the human-present stimuli). The test stimuli of *shape irregular* and *shape square* in our element distortion test contain distorted human figure, whereas the silhouette stimuli in Aust & Huber (2002) contain no human-like features. However, the pigeons' failure to discriminate was a common result of both studies, despite the use of different stimuli. This fact further suggests that the LE/RH could not use very small features. Pigeons, however, have proved able of learning stimuli by their contours, as shown by their ability to transfer from silhouettes to outline stimuli, regardless of inner color (Lombardi & Delius, 1988). However, the study by Lombardi & Delius (1988) used black-and-white two-dimensional shapes, whereas our experiment employed natural pictures. Information about target-outline shape would be one of the major features in the former case, but not in the latter case. We employed human figures with various postures. Therefore, a more reliable strategy for successful discrimination in our task would be the utilization of conceptual information of body parts and similar features. Thus, the poor performance of the LE/RH on shape irregular and shape square in case of fn stimuli further supports the idea that the LE/RH is reluctant to use small features for the discrimination.

Finally, we would like to add a more phenomenological example to our evidence for a configuration-based strategy by the LE/RH. In the transfer test, we examined if certain NOGO stimuli were especially prone to producing mistakes (i.e., were treated as people-present pictures). This was done for each viewing condition and the resulting stimuli were listed according to their response rates in descending order. Because most non-people stimuli produced few responses, five pictures on which the pigeons made the most erroneous responses were selected for each viewing condition. Interestingly, these five pictures produced false alarms under all viewing conditions, albeit with different ranks. Using the rank orders of the SRR values on each of the five pictures to compare performance, a Wilcoxon's rank sum test revealed a significant eye difference ($p = .008$, significance level was set at $p = .01$ by Bonferroni's correction) only for stimulus NP9 (Fig. 6). That is, the subjects responded to NP9 erroneously more often with the left eye compared with the right. NP9 is a picture showing differently colored reels of cotton in a basket. It is suggestive to conceive these elongated reels with their differently colored top as a group of humans. Apart from overall configuration, however, no detailed features resembling humans are present in this

Fig. 6. The people-absent picture (NP9) where there was a significant difference among viewing conditions in number of erroneous responses.

photograph (at least to the human eye). It is possible that the presence of a human-like configuration and the absence of human features in NP9 allowed for a good dissociation of hemispheric strategies: the LE/RH would have focused on overall shape while ignoring elemental features, whereas the RE/LH would have rejected the stimulus by searching for the constituting elements of the human figure.

It is important to express a word of caution at the end of the discussion of the present results. Some of the effects reported in this study could only be revealed as a trend and thus missed significance. However, as discussed in the following, the results are in agreement with previous studies using human subjects and therefore provide an evolutionary perspective. Such a perspective allows integrating various findings from the animal literature into a broader theoretical framework.

6.4. Cognitive asymmetries—An evolutionary perspective

In Table 4, we have tentatively condensed our findings. The left hemisphere seems to rely on local features and is able to extract categorical information from the presentation of various exemplars that belong to two distinct groups. The right hemisphere seems to utilize a configuration-based and thus relational analysis of visual

Table 4
Overview of the lateralized visuocognitive operations found in the pigeons of the present study

Left hemisphere	Right hemisphere
Local features	Configuration (global?)
Categorical information	Familiarity/exemplars

patterns. This necessarily goes along with an attention to larger chunks of the visual scenery and might include a global coding. In addition, the right hemisphere operates on an exemplar-based mode and therefore relies heavily on memorized familiarity mechanisms. As discussed in the following sections, these cognitive asymmetries strongly resemble the pattern found in humans and some other animals.

6.4.1. Local features vs. configural coding

Studies on spatial orientation in birds revealed a predominance of the RE/LH in the utilization of local features like landmarks to find the way (Prior et al., 2002; Vallortigara et al., 2004). When landmark positions are brought into conflict with configural cues of the surrounding, RE/LH chicks rely on landmarks (Tommasi & Vallortigara, 2001; Vallortigara et al., 2004), an asymmetry that is especially prevalent in males (Tommasi & 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, Gagliardo, Andrew, & Vallortigara, 2003).

Similar spatial orientation studies reveal a predominance of the LE/RH in geometric coding (Prior et al., 2002; Vallortigara et al., 2004). If the size of the testing room is altered (Tommasi & Vallortigara, 2001), or if object and geometric cues contradict each other (Vallortigara et al., 2004), chicks search with their left eye according to the relational properties of the room. 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 et al., 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 using the relational position of stable and reliable sources of information like mountains or odor-sources to construct a map-like representation (Vargas, Petruso, & Bingman, 2004).

As also shown in the present study, the right-hemispheric relational coding is not bound to spatial tasks. 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—a cognitive ability that is called amodal completion (Regolin, Marconato, & Vallortigara, 2004). Testing chicks under monocular conditions reveal that amodal completion is mainly a specialty of the LE/RH (Regolin 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. Thus, birds probably operate to some degree with an asymmetrical mind that focuses on local features with the left hemisphere and on global objects and relational properties with the right (Vauclair, Yamazaki, & Güntürkün, 2006).

Since the landmark study of Navon (1977), a very large number of studies with human subjects have confirmed a division of labor of the two hemispheres with a local bias for the left and a global bias for the right hemisphere. These studies revealed that, for example, the LH is faster and more accurate in identifying local components, while the RH is usually faster and more accurate in identifying global components of the input (e.g., Evert & Kmen, 2003; Fink, Marshall, Halligan, & Dolan, 1999; Van Kleeck, 1989). While some experiments with healthy subjects could not reveal such a lateralized distinction (e.g., Blanca & Alarcon, 2002; Yovel, Yovel, & Levy, 2001), a local-left and global-right dichotomy is mostly more apparent in brain-damaged patients (Ferman, Primeau, Delis, & Jampala, 1999; Schatz, Ballantyne, & Trauner, 2000). More and more studies using fMRI, PET, and event-related potentials (Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Lux et al., 2004) reveal the neural stages of processing where an asymmetrical analysis of local and global features takes place. In addition, there is a longstanding debate if a local/global dichotomy goes along with or even results from a precedence of the left and the right hemispheres for the analysis of low versus high spatial frequencies, respectively (Hughes, Fendrich, & Reuter-Lorenz, 1990; but see Delis, Robertson, & Efron, 1986; Fink et al., 1999; Robertson & Delis, 1986; Robertson & Lamb, 1991; Van Kleeck, 1989). We will not deal with this discussion here. But it is important for us to state that cerebral asymmetries that favor a left hemispheric strategy for attending to local features and a right hemispheric bias to use global and possibly relational cues is firmly founded in studies with human subjects. Thus, this cognitive asymmetry seems to be shared by birds and humans and might have a long phylogenetic history.

6.4.2. Categorical vs. exemplar coding

One of the most influential theories on cognitive lateralization of human subjects has been developed by Kosslyn and colleagues and posits that spatial cognition is represented by two different relations, categorical and coordinate, with each of them being encoded in the left and the right hemispheres, respectively (e.g., Kosslyn et al., 1989; Laeng, Chabris, et al., 2003; for a review see Jager & Postma, 2003). In their view, categorization refers to stored information about principal ("canonical") spatial arrangements that preserve invariant spatial information by ignoring distance measures ("above," "behind," etc.), whereas coordinate relations refer to precise metric information like distance, size, etc. We will especially discuss the categorization aspect of this theory (for a detailed discussion on the possible comparative aspects of coordinate asymmetries, see Vauclair et al., 2006).

Several empirical studies have supported a categorization superiority of the left hemisphere (Laeng et al., 1999; Laeng, Chabris, et al., 2003; Laeng, Zarrinpar, et al., 2003; Seger et al., 2000; but see Sergent, 1991 for contradictory results). In addition, there is evidence for a memory-based strategy of the right hemisphere (Laeng et al., 1999). Zaidel (1987) & Koivisto & Laine (1999) found that the typicality effect was stronger in the right hemisphere than in the left, suggesting that the right hemispheric strategy was to match the presented stimuli with the stored information, whereas that of left hemisphere was to analyze the pictures truly categorically. In split-brain patients, Levy & Trevarthen (1976) found that the right hemisphere is specialized in

detecting the visuo-structural similarity, while the left hemisphere is in detecting the functional or conceptual familiarity. An elegant series of studies of Burgund & Marsolek (2000) & Marsolek (1999) revealed that the human left hemisphere utilizes an abstract-category mode, while the right hemisphere operates more effectively on a specific-exemplar subsystem. According to Marsolek (1999), such an asymmetry requires a neural architecture in which the left hemisphere maps dissimilar input channels to the same output representation, while the right hemisphere has the ability to map similar input to different output representations. Indeed, an fMRI study revealed that human subjects showed a left hemispheric view-invariant object representation, but a right hemispheric view-dependent object processing mode (Vuilleumier, Henson, Driver, & Dolan, 2002). Together, these studies substantiate a category-based vs. exemplar-based mode of processing in the left and the right hemisphere of humans, respectively. This essentially covers an important part of some of our results with pigeons. The parallel nature of the findings in humans and pigeons not only makes a common evolution likely, it also shows that the left hemispheric categorical coding precedence as proposed by studies with human subjects is not based on verbal codes. Language might be a correlate of categorical thinking but not a prerequisite (see Aust, Apfalter, & Huber, 2005).

One evolutionary driving force for the establishment of a dichotomous mind could be the problem of a functional incompatibility (Vallortigara, Rogers, & Bisazza, 1999). When assessing novel stimuli, organisms have to carry out two different types of analyses. On the one side, they have to assign a stimulus to a certain category and to thus treat it in a way that was successful on previous encounters. Categorization necessarily implies an ignorance of idiosyncratic features in favor of invariant ones. On the other side, organisms also have to detect individual variations to eventually respond in an unusual way. Animals which are able to perform these seemingly incompatible operations simultaneously have the potential for both without losing time. Perhaps, cognitive asymmetries may derive from such evolutionary pressures (Vallortigara & Andrew, 1991).

Our data reveal that cerebral asymmetries seem to have a long and common evolutionary history (Rogers & Andrew, 2002). This view on asymmetries is also supported by a recent paradigm shift in the understanding of the organization of the vertebrate brain that shows that the pallial entities comprising the mammalian and the avian forebrains are truly homologous with a common phyletic history (Jarvis et al., 2005; Reiner et al., 2004). Mammals and birds separated about 300 million years ago with a member of the stem amniotes as their last common ancestor. If our finding that pigeons display an asymmetrical cognitive architecture that strongly resembles that of humans is not the result of convergent evolutionary events, it must reflect a lateralized way of information processing that already existed 300 million years ago.

References

Aust, U., Apfalter, W., & Huber, L. (2005). Pigeon categorization: Classification strategies in a non-linguistic species. In P. Grialou, G. Longo, & M. Okada (Eds.), *Images and reasoning* (Vol. 1, pp. 183–204). Interdisciplinary Conference Series on Reasoning Studies. Keio University Press.

Aust, U., & Huber, L. (2001). The role of item- and category-specific information in the discrimination of people- versus non-people images by pigeons. *Animal Learning and Behavior, 29*, 107–119.

Aust, U., & Huber, L. (2002). Target-defining features in a "people-present/people-absent" discrimination by pigeons. *Animal Learning and Behavior, 30*, 165–176.

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.

Aust, U., & Huber, L. (2006). Picture-object recognition in pigeons: Evidence of representational insight in a visual categorization task using a Complementary Information Procedure. *Journal of Experimental Psychology: Animal Behavior Processes, 32*, 190–195.

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, and Evolution, 62*, 117–127.

Blanca, M. J., & Alarcon, R. (2002). Hemispheric differences in global and local processing with orientation classification tasks. *Neuropsychologia, 40*, 957–963.

Burgund, E. D., & Marsolek, C. J. (2000). Viewpoint-invariant and viewpoint-dependent object recognition in dissociable neural subsystems. *Psychonomic Bulletin & Review, 7*, 480–489.

Cavoto, 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.

Cerella, J. (1980). The pigeon's analysis of pictures. *Pattern Recognition, 12*, 1–6.

Cook, R. G., Wright, A., & Kendrick, D. F. (1990). Visual categorization in pigeons. In M. L. Commons, R. J. Herrnstein, S. M. Kosslyn, & D. B. Mumford (Eds.), *Quantitative analyses of behavior: Behavioral approaches to pattern recognition and concept formation* (pp. 187–214). Hillsdale, NJ: Erlbaum.

D'Amato, M. R., & Van Sant, P. (1988). The person concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes, 14*, 43–55.

Delis, D. C., Robertson, L. C., & Efron, R. (1986). Hemispheric specialization of memory for visual hierarchical stimuli. *Neuropsychologia, 24*, 205–214.

Delius, J. D., & Hollard, V. D. (1995). Orientation invariant pattern recognition by pigeons (*Columba livia*) and humans (*Homo sapiens*). *Journal of Comparative Psychology, 109*, 276–290.

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

Diekamp, B., Prior, H., & Güntürkün, O. (1999). Functional lateralization, interhemispheric transfer, and position bias in serial reversal learning in pigeons (*Columba livia*). *Animal Cognition, 2*, 187–196.

Evert, D. L., & Kmen, M. (2003). Hemispheric asymmetries for global and local processing as a function of stimulus exposure duration. *Brain and Cognition, 51*, 115–142.

Ferman, T. J., Primeau, M., Delis, D., & Jampala, C. V. (1999). Global–local processing in schizophrenia: Hemispheric asymmetry and symptom-specific interference. *Journal of International Neuropsychological Society, 5*, 957–963.

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

Fink, G. R., Marshall, J. C., Halligan, P. W., & Dolan, R. J. (1999). Hemispheric asymmetries in global/local processing are modulated by perceptual salience. *Neuropsychologia, 37*, 31–40.

Güntürkün, O. (2003). Hemispheric asymmetry in the visual systems of birds. In K. Hugdahl & R. J. Davidson (Eds.), *The asymmetrical brain* (pp. 3–36). London: The MIT Press.

Heinze, H. J., Hinrichs, H., Scholz, M., Burchert, W., & Mangun, G. R. (1998). Neural mechanisms of global and local processing: A combined PET and ERP study. *Journal of Cognitive Neuroscience, 10*, 485–498.

Herrnstein, R. J. (1979). Acquisition, generalization, and discrimination reversal of a natural concept. *Journal of Experimental Psychology: Animal Behavior Processes, 5*, 116–129.

Herrnstein, R. J. (1990). Levels of stimulus control: A functional approach. *Cognition, 37*, 1–22.

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. 59–95). New York: Academic Press.

Herrnstein, R. J., & Loveland, D. H. (1964). Complex visual concept in the pigeon. *Science, 146*, 549–551.

Herrnstein, R. J., Loveland, D. H., & Cable, C. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 2*, 285–311.

Hollard, V. D., & Delius, J. D. (1982). Rotational invariance in visual pattern recognition in pigeons and humans. *Science, 218*, 804–806.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6*, 65–70.

Huber, L. (1999). Generic perception: Open-ended categorization of natural classes. *Cahiers de Psychologie Cognitive—Current Psychology of Cognition, 18*, 845–888.

Huber, L. (2001). Visual categorization in pigeons. In Avian visual cognition [on-line]. Available at http:// www.pigeon.psy.tufts.edu/avc/.

Huber, L., Troje, N. F., Loidolt, M., Aust, U., & Grass, D. (2000). Natural categorization through multiple feature learning in pigeons. *The Quarterly Journal of Experimental Psychology, 53*(B), 341–357.

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.

Iidaka, T., Yamashita, K., Kashikura, K., & Yonekura, Y. (2004). Spatial frequency of visual image modulates neural responses in the temporo-occipital lobe: An investigation with event-related fMRI. *Cognitive Brain Research, 18*, 196–204.

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.

Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience, 6*, 151–159.

Jitsumori, M., & Yoshihara, M. (1997). Categorical discrimination of human facial expressions by pigeons: A test of the linear feature model. *The Quarterly Journal of Experimental Psychology, 50*(B), 253–268.

Johnston, A. N., & Rogers, L. J. (1999). Light exposure of chick embryo influences lateralized recall of imprinting memory. *Behavioral Neuroscience, 113*, 1267–1273.

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

Kallman, H., & Corballis, M. C. (1975). Ear asymmetry in reaction time to musical sounds. *Perception and Psychophysics, 17*, 368–370.

Koivisto, M., & Laine, M. (1999). Strategies of semantic categorization in the cerebral hemispheres. *Brain and Language, 66*, 341–357.

Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. E. (1989). Evidence of 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. J. Davidson (Eds.), *The asymmetrical brain* (pp. 303–339). London: The MIT Press.

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

Laeng, B., Zarrinpar, A., & Kosslyn, S. M. (2003). Do separate processes identify objects as exemplars versus members of basic-level categories? Evidence from hemispheric specialization. *Brain and Cognition, 53*, 15–27.

Lea, S. E. G. (1984). In what sense do pigeons learn concepts? In H. S. Terrace, T. G. Bever, & H. L. Roitblat (Eds.), *Animal cognition* (pp. 263–276). Hillsdale, NJ: Lawrence Erlbaum.

Lea, S. E. G., & Harrison, S. N. (1978). Discrimination of polymorphous stimulus sets by pigeons. *Quarterly Journal of Experimental Psychology, 30*, 521–537.

Levy, J., & Trevarthen, C. (1976). Metacontrol of hemispheric function in human split-brain patients. *Journal of Experimental Psychology: Human Perception and Performance, 2*, 299–312.

Loidolt, M., Aust, U., Meran, I., & Huber, L. (2003). Pigeons use item-specific and category-level information in the identification and categorization of human faces. *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 261–276.

Lombardi, C. M., & Delius, J. D. (1988). Pattern recognition invariance in pigeons (*Columba livia*): Outline, color and contrast. *The International Journal of Comparative Psychology, 2*, 83–102.

Lubow, R. E. (1974). High-order concept formation in the pigeon. *Journal of the Experimental Analysis of Behavior, 21*, 475–483.

Lux, S., Marshall, J. C., Ritzl, A., Weiss, P. H., Pietrzyk, U., Shah, N. J., et al. (2004). A functional magnetic resonance imaging study of local/global processing with stimulus presentation in the peripheral visual hemifields. *Neuroscience, 124*, 113–120.

Manns, M., & Güntürkün, O. (1999). Monocular deprivation alters the direction of functional and morphological asymmetries in the pigeon's visual system. *Behavioral Neuroscience, 113*, 1–10.

Marsolek, C. J. (1995). Abstract visual-form representations in the left cerebral hemisphere. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 375–386.

Marsolek, C. J. (1999). Dissociable neural subsystems underlie abstract and specific object recognition. *Psychological Science, 10*, 111–118.

Matsukawa, A., Inoue, S., & Jitsumori, M. (2004). Pigeon's recognition of cartoons: Effects of fragmentation, scrambling, and deletion of elements. *Behavioural Processes, 65*, 25–34.

Nakamura, T., Croft, D. B., & Westbrook, R. F. (2003). Domestic pigeons (*Columba livia*) discriminate between photographs of individual pigeons. *Learning and Behavior, 31*, 307–317.

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.

Poole, J., & Lander, D. G. (1971). The pigeon's concept of pigeon. *Psychonomic Science, 25*, 157–158.

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

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.

Reiner, A., Perkel, D. J., Bruce, L. L., Butler, A. B., Csillag, A., Kuenzel, W., et al. (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *The Journal of comparative Neurology, 473*, 377–414.

Robert, W. A., & Mazmanian, D. S. (1988). Concept learning at different levels of abstraction by pigeons, monkey, and people. *Journal of Experimental Psychology: Animal Behavior Processes, 14*, 247–260.

Robertson, L. C., & Delis, D. C. (1986). "Part-whole" processing in unilateral brain-damaged patients: Dysfunctions of hierarchical organization. *Neuropsychologia, 24*, 363–370.

Robertson, L. C., & Lamb, M. R. (1991). Neuropsychological contributions to theories of part–whole organization. *Cognitive Psychology, 24*, 363–370.

Rogers, L. J. (1982). Light experience and asymmetry of brain function in chickens. *Nature, 297*, 223–225.

Rogers, L. J. (1990). Light input and the reversal of functional lateralization in the chicken brain. *Behavioural Brain Research, 38*, 211–221.

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

Schatz, A. M., Ballantyne, A. O., & Trauner, D. A. (2000). A hierarchical analysis of block design errors in children with early focal brain damage. *Developmental Neuropsychology, 17*, 75–83.

Seger, C. A., Poldrack, R. A., Prabhakaran, V., Zhao, M., Glover, G. H., & Gabrieli, J. D. E. (2000). Hemispheric asymmetries and individual differences in visual concept learning as measured by functional MRI. *Neuropsychologia, 38*, 1316–1324.

Sergent, J. (1991). Judgments of relative position and distance on representations of spatial relations. *Journal of Experimental Psychology: Human Perceptual Performance, 91*, 762–780.

Silverberg, R., Bentin, S., Gaziel, T., Obler, L. K., & Albert, M. L. (1979). Shift of visual field preference for English words in native Hebrew speakers. *Brain and Language, 8*, 184–190.

Silverberg, R., Gordon, H. W., Pollack, S., & Bentin, S. (1980). Shift of visual field preference of Hebrew words in native speakers learning to read. *Brain and Language, 11*, 99–105.

Skiba, M., Diekamp, B., & Güntürkün, O. (2002). Embryonic light stimulation induces different asymmetries in visuoperceptual and visuomotor pathways of pigeons. *Behavioural Brain Research, 134*, 149–156.

Tommasi, L., Gagliardo, A., Andrew, R. J., & Vallortigara, G. (2003). Separate processing mechanisms for encoding of geometric and landmark information in the avian hippocampus. *The 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.

Troje, N. F., Huber, L., Loidolt, M., Aust, U., & Fieder, M. (1999). Categorical learning in pigeons: The role of texture and shape in complex static stimuli. *Vision Research, 39*, 353–366.

Vallortigara, G. (1992). Right hemisphere advantage for social recognition in the chick. *Neuropsychologia, 30*, 761–768.

Vallortigara, G., & Andrew, R. J. (1991). Lateralization of response to change in a model partner by chicks. *Animal Behaviour, 41*, 187–194.

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.

Vallortigara, G., Rogers, L. J., & Bisazza, A. (1999). Possible evolutionary origins of cognitive brain lateralization. *Brain Research Reviews, 30*, 164–175.

Van Kleeck, M. H. (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, 27*, 1165–1178.

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

Vauclair, J., Yamazaki, Y., & Güntürkün, O. (2006). The study of hemispheric specialization for categorical and coordinate spatial relations in animals. *Neuropsychologia, 44*, 1524–1534.

Vonk, J., & MacDonald, S. E. (2002). Natural concepts in a juvenile gorilla (*Gorilla gorilla gorilla*) at three levels of abstraction. *Journal of the Experimental Analysis of Behavior, 78*, 315–332.

Vuilleumier, P., Henson, R. N., Driver, J., & Dolan, R. J. (2002). Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nature Neuroscience, 5*, 491–499.

Watanabe, S. (2001). Discrimination of cartoons and photographs in pigeons: Effects of scrambling of elements. *Behavioural Processes, 53*, 3–9.

Watanabe, S., & Ito, Y. (1991). Discrimination of individuals in pigeons. *Bird Behavior, 9*, 20–29.

Watanabe, S., Sakamoto, J., & Wakita, M. (1995). Pigeons' discrimination of painting by Monet and Picasso. *Journal of the Experimental Analysis of Behavior, 63*, 165–174.

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.

Yovel, G., Yovel, I., & Levy, J. (2001). Hemispheric asymmetries for global and local visual perception: Effects of stimulus and task factors. *Journal of Experimental Psychology: Human Perceptual Performance, 27*, 1369–1385.

Zaidel, D. (1987). Hemispheric asymmetry in long-term semantic relationships. *Cognitive Neuropsychology, 4*, 321–332.