



# It takes two to tango: hemispheric integration in pigeons requires both hemispheres to solve a transitive inference task



Martina Manns<sup>a,\*</sup>, Claudia Krause<sup>b</sup>, Meng Gao<sup>a</sup>

<sup>a</sup> Biopsychology, Institute of Cognitive Neuroscience, Ruhr-University Bochum, Bochum, Germany

<sup>b</sup> Institute of Psychology, FernUniversität Hagen, Hagen, Germany

## ARTICLE INFO

### Article history:

Received 5 September 2016

Initial acceptance 20 October 2016

Final acceptance 30 January 2017

MS. number: 16-00787R

### Keywords:

associative value  
asymmetry  
birds  
lateralization  
relational learning  
visual processing

Cerebral lateralization, the dominance of one brain side for a specific function, is a core feature of the vertebrate brain. Lateralized processing requires complex intra- and interhemispheric interactions mediating exchange, integration or suppression of information. The underlying functional organization of cooperative or independent processing is only basically understood and may differ between vertebrate species depending on the organization of commissural systems and overlap of sensory input. We explored intrahemispheric integration capacities in pigeons, *Columba livia*; although their visual system is primarily crossed and lateralized, it can still integrate interhemispheric information. Pigeons were trained in overlapping colour discriminations in which each hemisphere learned only half the information that represented a linear hierarchy. Therefore, interhemispheric memory about the relational values of the premise stimuli pairs had to be transferred and combined to master a transitive inference task. Pigeons displayed transitive responding under binocular but not under monocular seeing conditions. Hemispheric-specific strategies in accessing the associative values of transfer stimuli resulted in potential conflict with intrahemispheric memory and led to unihemispheric impairment in performance. The response pattern might represent a consequence of neuronal mechanisms avoiding interocular conflicts, and it also indicates that interhemispheric communication in pigeons is an active process that integrates intra- and interhemispheric information in a context-dependent and hemispheric-specific manner.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

A growing number of examples show that the left and right brain halves play differential roles in controlling behaviour not only in humans but also in other vertebrates and even in invertebrates (Concha, Bianco, & Wilson, 2012; Frasnelli, Vallortigara, & Rogers, 2012; Rogers, Vallortigara, & Andrew, 2013; Vallortigara & Rogers, 2005). These cerebral asymmetries are presumably caused by differences in the preferential processing mode of the two brain halves and are based on structural variances between left- and right-hemispheric neuronal circuits (Hervé, Zago, Petit, Mazoyer, & Tzourio-Mazoyer, 2013; Ocklenburg, Friedrich, Güntürkün, & Genç, 2016). Several models suggest general encoding asymmetries that are shared by different vertebrate species and, hence, may have an evolutionary origin (Concha et al., 2012; Vallortigara & Rogers, 2005; Yamazaki, Aust, Huber, Hausmann, & Güntürkün, 2007). Hemispheric asymmetries might be traced back to a left-

hemispheric specialization for routine behaviour and feeding and a right-hemispheric dominance for the detection of unexpected stimuli and control behaviour in emergency situations (Lippolis, Joss, & Rogers, 2009; MacNeilage, Rogers, & Vallortigara, 2009; Vallortigara, 2000). In relation to this basic lateralization pattern, the left hemisphere is specialized to adopt a feature-based strategy by relying on local aspects of stimuli and extracting the common elements of individual stimulus patterns. In contrast, the right hemisphere preferentially encodes global information and responds to novelty, relying on memorized familiarity mechanisms to detect individual variations (Freund et al., 2016; MacNeilage et al., 2009; Manns & Ströckens, 2014; Yamazaki et al., 2007).

Consequently, left- and right-hemispheric networks eventually process information in their specialized relatively independent ways. These differences often result in the dominance of one hemisphere to adopt a specific function but can also lead to conflicts when both hemispheres assess information according to their preferential processing style (Manns & Ströckens, 2014; Turner, Marinsek, Ryhal, & Miller, 2015; Vallortigara, Pagni, & Sovrano, 2004). This conflict entails the dominance of one hemisphere to

\* Correspondence: M. Manns, Biopsychology, Institute of Cognitive Neuroscience, Ruhr-University Bochum, Universitätsstr. 150, 44780 Bochum, Germany.

E-mail address: [martina.manns@ruhr-uni-bochum.de](mailto:martina.manns@ruhr-uni-bochum.de) (M. Manns).

control behavioural output (Van der Knaap & Van der Ham, 2011). In other situations, the hemispheres must work together, for example to acquire a complete representation of the environment, or to combine their expertise for optimal cognition (e.g. Friederici, von Cramon, & Kotz, 2007).

Interhemispheric interactions are accomplished by commissural systems that interconnect the two halves of the nervous systems in all animals (Letzner, Simon, & Güntürkün, 2016). The functional organization of the underlying neuronal processes is still under debate and may depend on the current functional requirements including transfer of information to the specialized hemisphere, inhibition of the subdominant brain side, or combination of left- and right-hemispheric processes (Bloom & Hynd, 2005; Gazzaniga, 2000; Van der Knaap & Van der Ham, 2011) and certainly differs depending on the overlap of sensory input. Thereby, the mode of interhemispheric interactions might be affected by incoming bottom-up information and/or attentional top-down mechanisms mediating current goals or expectations. In the brain of placental mammals, a large body of interhemispheric communication is mediated by the corpus callosum (Bloom & Hynd, 2005; Gazzaniga, 2000; Hervé et al., 2013; Van der Knaap & Van der Ham, 2011) but lateralized interhemispheric processes do not solely depend on this major forebrain commissure (Manns & Güntürkün, 2009). Quick information transfer via the corpus callosum rather impedes the analysis of lateralized interhemispheric processing (e.g. Bergert, Windmann, & Güntürkün, 2006). Thus, an understanding of interhemispheric interactions can profit from model systems lacking a corpus callosum. The avian brain is such a model.

Birds can master complex cognitive tasks (Clayton & Emery, 2015; Güntürkün & Bugnyar, 2016; Jarvis et al., 2005; Vallortigara, 2006, 2012) whereby the two brain halves contribute differently to cognitive challenges. Functional asymmetries in chicks, *Gallus gallus*, and pigeons, *Columba livia*, are related to structural left–right differences that develop in close gene–environment interactions (Güntürkün, Stüttgen, & Manns, 2014; Manns & Güntürkün, 2009; Rogers, 2014; Vallortigara & Rogers, 2005). Hemispheric specializations can be easily tested just by temporarily occluding one eye with an eye cap, i.e. by monocular testing. Since the optic nerves cross virtually completely, information from the left eye is primarily directed to the right brain side and vice versa. Nevertheless, hemispheric-specific information can be exchanged (Letzner, Patzke, Verhaal, & Manns, 2014; Skiba, Diekamp, Prior, & Güntürkün, 2000; Valencia-Alfonso, Verhaal, & Güntürkün, 2009) and combined (Manns & Römling, 2012) via subcortical commissural systems (Letzner et al., 2016). Interhemispheric cooperation is indicated by quantitative advantages of using both eyes compared to monocular performances (Güntürkün et al., 2000; Watanabe, Hodos, & Bessette, 1984).

Hemispheric cooperation in pigeons can be investigated in a transitive inference paradigm (Manns & Römling, 2012). Like several animal species (Vasconcelos, 2008), pigeons are able to infer a relation between two items that have not been presented together before (Lazareva, Kandrav, & Acerbo, 2015; Siemann, Delius, & Wright, 1996). After learning to discriminate overlapping pairs of stimuli (A+B–, B+C–, C+D–, D+E– whereby + indicates rewarded and – unrewarded stimuli), pigeons rank the items by transitive inference logic (A > B > C > D > E). When each hemisphere learned only half of the premise stimulus pairs (i.e. one hemisphere learns A+B–/ B+C– and the other learns C+D–/ D+E–), information from both brain halves must be combined to establish the transitive line. Pigeons can successfully master this problem when seeing with both eyes after monocular learning (Manns & Römling, 2012). How the two brain halves solve this complex problem is still unclear but an answer to this question

helps us understand the functional organization of interhemispheric cooperation. In the present study, we explored hemispheric-specific contributions by training and testing pigeons under monocular seeing conditions. Monocular and therefore hemisphere-specific choices when pigeons are confronted with critical test pairs should indicate whether and which hemisphere responds by transitive inference logic and, hence, is able to integrate interhemispheric information. Superior performances of one hemisphere can result from the dominance in adopting a transitive inference strategy, or from better access to transfer information. Relational learning in chickens indicates a right-hemispheric superiority in transitive reasoning (Daisley, Mascalonzi, Rosa-Salva, Rugani, & Regolin, 2009; Daisley, Vallortigara, & Regolin, 2010). In pigeons, in contrast, the left hemisphere has better access to interhemispheric information (Letzner et al., 2014; Valencia-Alfonso et al., 2009). Moreover, cells within the left visual forebrain differentiate to a higher degree between rewarded and unrewarded stimuli after associative learning, indicating a leading role in reward-associated feedback systems (Verhaal, Kirsch, Vlachos, Manns, & Güntürkün, 2012). The left hemisphere generally dominates visuomotor processing (Manns & Güntürkün, 2009; Manns & Ströckens, 2014), stores memories on sensorimotor integration tasks (Nottelmann, Wohlschläger, & Güntürkün, 2002) and tends to dominate decisions in conflict situations (Adam & Güntürkün, 2009; Freund et al., 2016; Ünver & Güntürkün, 2014). Therefore, the left hemisphere might be better prepared to combine information from both brain sides and/or to control choice behaviour during critical transitive tests. On the other hand, both hemispheres may contribute to the solution of this problem. In this case, unihemispheric performances should differ from bihemispheric ones.

## METHODS

We obtained 28 adult domestic pigeons from local breeders and split them into two groups for two consecutive, independent experiments (first group: 12 birds; second group: 16 birds; one pigeon had to be excluded due to learning impairments). The birds were housed in individual cages (45 × 40 cm and 40 cm high) where they were also trained and tested. They were kept food deprived to approximately 80–90% of their free-feeding weight throughout the experiment. Individual mass was kept within an ecologically relevant level and welfare was not affected by this level of food restriction (e.g. Kangas & Branch, 2006). Water and grit were freely available whereas food was provided daily after training or testing and over the weekend. During the monocular sessions, one eye was temporarily covered with an opaque cardboard cap that was fixed around the eye with Velcro tape. To this end, the hard side of a Velcro ring was glued onto the feathers around the eyes using a nontoxic, solvent-free adhesive (UHU Bastelkleber) while the smooth side was fixed to the cardboard cap.

The study was carried out in compliance with the European Communities Council Directive of November 24, 1986 (86/609/EEC) and the specifications of the German law for the prevention of cruelty to animals, and was approved by the animal ethics committee of the Landesamt für Natur, Umwelt und Verbraucherschutz NRW, Germany. All efforts were made to minimize the number of birds used and to minimize suffering.

### Rationale of the Task

The transitive inference task was designed as simultaneous colour discriminations in which pigeons were first trained to discriminate four overlapping pairs of stimuli, A+B–, B+C–, C+D–, D+E–, that represent a linear hierarchy (A > B > C > D > E). Letters

stand for five varieties of nontoxic aquarium grit differing in particle colour and size. A grain of maize buried under the positive grit (S+) rewarded a correct choice. To achieve hemispheric-specific knowledge, each eye and, hence, the contralateral hemisphere (LH: left hemisphere; RH: right hemisphere) learnt to discriminate only two of the premise pairs that represented the beginning (A+B–, B+C–) or end (C+D–, D+E–) of the transitive line (Manns & Römling, 2012). To consider relational learning, the pigeons were later confronted with stimulus combinations that had not been presented together before (Fig. 1).

We tested two experimental groups: one group learnt the beginning of the transitive line with the left hemisphere (LH-B/RH-D) and the other group with the right hemisphere (RH-B/LH-D, Fig. 1). The first experiment (12 birds: six LH-B/RH-D and six RH-B/LH-D) indicated that some pigeons of the RH-B/LH-D group (and none of the LH-B/RH-D) made choices by transitive inference logic when tested with the left hemisphere. To further explore the critical left-hemispheric performance, we trained a second group of 16 biasing the number of experimental birds (six LH-B/RH-D and 10 RH-B/LH-D). In the Results, we present the combined data of both experiments (compare individual data in Appendix Table A1).

**Colour Discrimination Training**

We conducted only one session per day per bird under one seeing condition. A session consisted of 30 trials while vision was restricted to the left or right eye. Left- and right-eye seeing alternated daily for each bird. The coloured grits were presented in two plastic cups set side-by-side in a plastic trough that was placed below the central opening of the home cages (Manns & Römling, 2012). The trial-to-trial left–right position of the colour stimuli varied quasirandomly. Pecking into the positive grit was classified as a correct choice and the pigeon was allowed to find the hidden grain. Searching among the nonbaited grit represented an error and the plastic boxes were immediately removed. During the early training phase, a pigeon could switch to the positive grit to find the

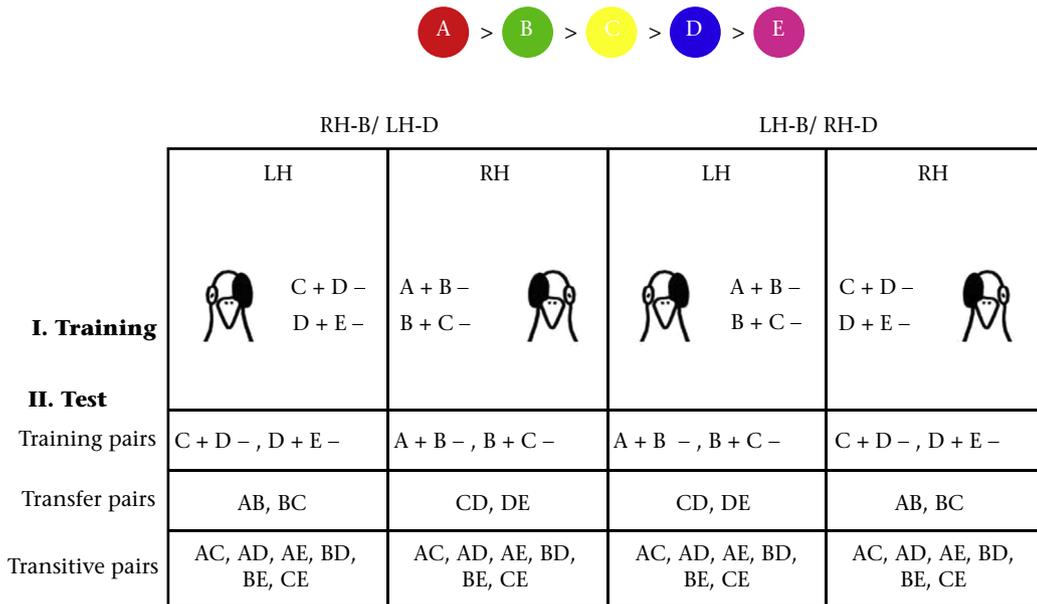
rewarding grain. In accordance with previous experiments, training started with the more difficult overlapping colour pairs B+C– and C+D (Manns & Römling, 2012; Siemann, Delius, & Wright, 1996). After a pigeon reached the learning criterion of 80% correct choices in three consecutive sessions for an individual eye, the second pairs (A+B– or D+E–) were introduced. Colour pairs were presented in runs and presentation frequencies of the training pairs were biased (see Siemann, Delius, & Wright, 1996), first consisting of 20x (B+C–/C+D–) + 10x (A+B–/D+E–), then 2x (10x B+C–/C+D– + 5x A+B–/D+E–) repeated trials. During the last three training sessions, 20% of the training trials remained unrewarded.

**Testing**

After a pigeon reached the learning criterion of 80% correct choices for all colour pairs after six consecutive sessions (three for the left- and three for the right-eye seeing condition), six monocular test sessions with each eye were conducted. Within a session, birds were confronted with a set of three different stimulus types that were randomly mixed. There was again only one session per day and the seeing condition switched daily. One session comprised the following stimulus pairs (Fig. 1): (1) 22 learned colour pairs (rewarded): discrimination was learnt with the tested eye/hemisphere (11x end (A+B–/D+E–) + 11x middle (B+C–/C+D) pairs); (2) two transfer colour pairs (unrewarded): discrimination was learnt with the contralateral eye/hemisphere and, hence, reward contingencies had to be transferred (1x end AB/DE, 1x middle (BC/CD) pair); (3) six transitive colour pairs (unrewarded): discrimination of colour pairs that were not presented during training (AC, AD, AE, BD, BE and CE; 1x each).

After finishing the monocular tests, the birds were retrained to learning criterion and six binocular sessions were conducted whereby learnt colour pairs were interspersed with the six transitive pairs (Manns & Römling, 2012).

Choices were recorded when the pigeon pecked into the grit closest to the beak. Correct responses indicated discrimination



**Figure 1.** Design of the experimental steps. Pigeons learnt to discriminate two colour pairs with each eye. We compared two experimental groups with reversed hemispheric-specific allocation of the premise pairs. We trained pigeons using the five-item transitive inference task (A > B > C > D > E) with four overlapping pairs of stimuli (where pluses represent reinforced stimuli and minuses nonreinforced stimuli). After reaching the learning criterion, pigeons took part in monocular test sessions in which they were confronted with a mixture of training, transfer and transitive pairs. For discrimination of transfer pairs, information about reward contingencies had to be transferred; for discrimination of the transitive pairs, interhemispheric information had to be integrated within the tested hemisphere.

accuracy for the learnt and transfer stimulus pairs. Transitive choices were evaluated by transitive inference logic. Traditionally, test pair BD is regarded as the critical one because the component stimuli are presented equally often as rewarded and as unrewarded stimuli in the premise training pairs (Lazareva et al., 2015; Lazareva & Wasserman, 2012; Vasconcelos, 2008). Thus, their value can only be estimated in relation to the other colours and, hence, after correctly ranking along the transitive line. Accordingly, a correct decision for B indicates successful transitive inference which in turn depends on integration of knowledge from both hemispheres in our paradigm.

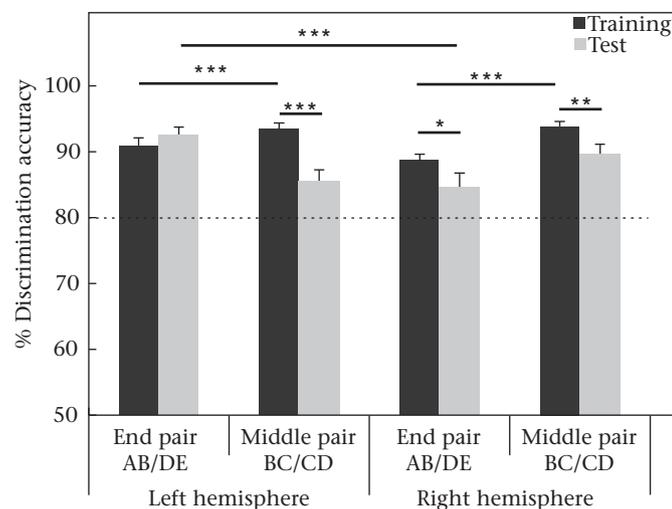
### Data Analysis

Statistical analysis was carried out using the program Statistica 10 (StatSoft, Tulsa, OK, U.S.A.). Normal distribution was evaluated by Kolmogorov–Smirnov and Shapiro–Wilk tests. Then data sets were analysed with mixed repeated measures ANOVA. Dependent and independent *t* tests were conducted when there were significant factor effects. When data were not normally distributed, nonparametric tests were conducted. This was only the case for the analysis of transitive responses.

## RESULTS

### Training Performance

The pigeons learned with each eye to discriminate two premise colour pairs representing the beginning or end of the transitive line. They needed a mean  $\pm$  SD of  $82 \pm 24$  days to reach the learning criterion of 80% correct choices for both colour pairs within one session (left-eye and right-eye seeing:  $42 \pm 12$  days each). At the end of training, they achieved a mean discrimination performance of  $92 \pm 4\%$  correct choices during the last three training sessions without any difference between the left- and right-eye seeing conditions (*t* test for dependent samples:  $t_{26} = 0.925$ ,  $P = 0.363$ ). Remarkably, middle (B+C–/C+D–) pairs were significantly better discriminated than end (A+B–/D+E–) pairs (*t* test for dependent samples:  $t_{26} = 4.992$ ,  $P < 0.0001$ ; Fig. 2).



**Figure 2.** Discrimination of learnt colour pairs: monocular discrimination accuracy of learnt end (AB/DE) and middle (BC/CD) colour pairs during the last three training and six test sessions. Bars show mean  $\pm$  SE left- and right-hemispheric discrimination accuracy of transfer end (AB/DE) and middle (BC/CD) colour pairs in the two experimental groups. Dashed line indicates 80% learning criterion. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; *t* tests for dependent samples.

### Monocular Test Performances

During monocular testing, the pigeons were confronted with a mixture of three classes of colour pairs during one session: learnt, transfer and transitive (Fig. 1). Discrimination performances of these stimulus types were analysed separately and indicated intriguing differences in choice strategies between the left and right hemispheres.

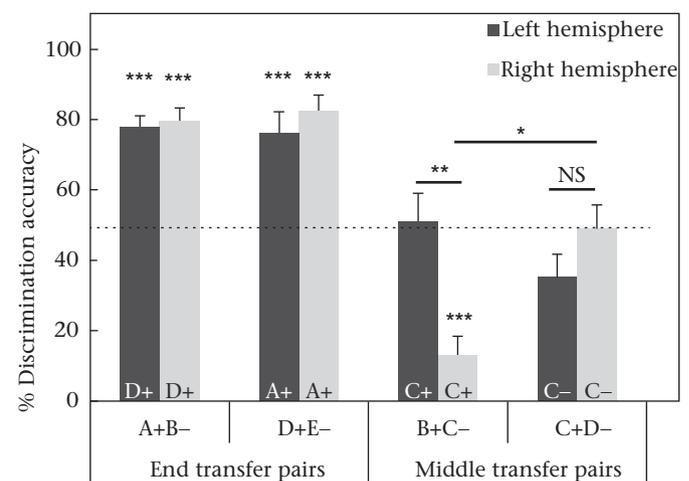
### Learnt Colour Pairs: Reduced Discrimination

Comparing the discrimination performances of learnt colour pairs during training and testing showed differences (Fig. 2) that were analysed by a  $2 \times 2 \times 2$  MANOVA with dependent factors 'time point' (training–test), 'pair type' (end–middle), and 'hemisphere' (left–right). On average, discrimination accuracy was reduced during testing ( $F_{1,26} = 14.90$ ,  $P < 0.001$ , partial eta-squared  $\eta_p^2 = 0.364$ ) but depended on 'pair type' and 'hemisphere' (three-way interaction:  $F_{1,26} = 6.76$ ,  $P < 0.05$ ,  $\eta_p^2 = 0.206$ ). It was intriguing that especially the discrimination accuracy of the middle pairs (B+C–/C+D–) was significantly decreased (left hemisphere:  $t_{26} = 3.992$ ,  $P < 0.001$ ; right hemisphere:  $t_{26} = 3.103$ ,  $P < 0.01$ ) although these pairs were originally better learnt. Concerning the end pairs (A+B–/D+E–), a slight increase in the left- and a decrease in the right-hemispheric discrimination accuracy ( $t_{26} = 2.104$ ,  $P < 0.05$ ) led to an asymmetry that was not present at the end of training (left–right difference:  $t_{26} = 3.880$ ,  $P < 0.001$ ).

### Transfer Colour Pairs

#### Impaired discrimination of ambiguous middle pairs

Differences in the discrimination performances of end and middle pairs were also evident when the pigeons were confronted with the transfer colour pairs (Fig. 3). A  $2 \times 2$  MANOVA with dependent factors 'pair type' (end–middle), and 'hemisphere' (left–right) showed that the mean performances did not differ between the hemispheres ( $F_{1,26} = 0.41$ ,  $P = 0.528$ ,  $\eta_p^2 = 0.016$ ) whereas discrimination accuracy of the end and middle pairs varied remarkably ( $F_{1,26} = 46.007$ ,  $P < 0.0001$ ,  $\eta_p^2 = 0.639$ ). Discrimination of the end pairs (A+B–/D+E–) was significantly above chance level (*t* test for single means against reference value 50%:



**Figure 3.** Discrimination of transfer colour pairs. Bars show mean  $\pm$  SE left- and right-hemispheric discrimination accuracy of transfer end (A+B–/D+E–) and middle (B+C–/C+D–) colour pairs (letters within the columns indicate the directly learnt reward value of the respective critical colour). Dashed line indicates 50% chance level. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; *t* tests for dependent samples.

$t_{26} = 11.77$ ,  $P < 0.0001$ ; Fig. 3) indicating successful access to transfer information. In contrast, discrimination accuracy of the middle pairs (B+C−/C+D−) did not differ from chance level ( $t$  test for single means against reference value 50%:  $t_{26} = -0.238$ ,  $P = 0.815$ ).

The differential discrimination scores of transfer end and middle pairs indicated that associative memory was not simply recalled but evaluated in relation to the hemispheric-specific learning experience (see Discussion). End pairs (A+B−/D+E) combined colours with which the tested hemisphere had no direct experience and, therefore, the transferred reward contingencies did not interfere with intrahemispherically conditioned stimulus values. Middle pairs (B+C−/C+D−), on the other hand included overlapping colour C whose reward value was contrasting between the learnt and transfer stimulus pair. Thus, when the tested hemisphere was confronted with the transfer middle pair, it had to choose the opposite colour to the directly learnt reward contingency. Thereby the two hemispheres differed in weighting conflict information depending on the direction of the conflict.

#### Differential coding of appetitive and aversive stimulus associations

The overlapping colour C could be associated with a positive (appetitive) value (C+D−) or with a negative (aversive) one (B+C−) during learning (see Discussion). This differential encoding affected discrimination of the transfer pairs. The left hemisphere performed at chance level irrespective of whether it was confronted with transfer pair B+C− or C+D− ( $t$  test for single means:  $P > 0.05$ ; Fig. 3). This suggests that the learnt associative values influenced the discrimination accuracy but the performance was independent of the direction of the learnt reward contingency. Right-hemispheric choices, on the other hand, differed depending on the direction of the conflict. When intrahemispheric learning associated C with a negative value (C−), transfer pair C+D− was discriminated at chance level ( $t$  test for single means:  $t_8 = -0.139$ ,  $P = 0.891$ ) and discrimination scores did not differ from left-hemispheric ones ( $t$  test for independent groups:  $t_{25} = 1.32$ ,  $P = 0.200$ ). But when learning experience associated C with a positive value (C+), discrimination scores for B+C− were significantly below 50% ( $t$  test for single means:  $t_8 = -6.860$ ,  $P < 0.001$ ). This means that the right hemisphere clearly chose the stimulus with learnt appetitive association, disregarding information from the contralateral brain side. This was distinct from choices made by the left hemisphere when confronted with B+C− ( $t$  test for independent groups:  $t_{25} = 3.149$ ,  $P < 0.01$ ). Thus, the hemispheres displayed a differential decision pattern when there was a conflict between learnt appetitive and transfer aversive encoding of the conflict stimulus C. This points to a differential relative evaluation of appetitive and aversive stimulus associations when accessing conflicting reward contingencies. These differences also affected transitive responding as described in the following section.

#### Transitive Colour Pairs

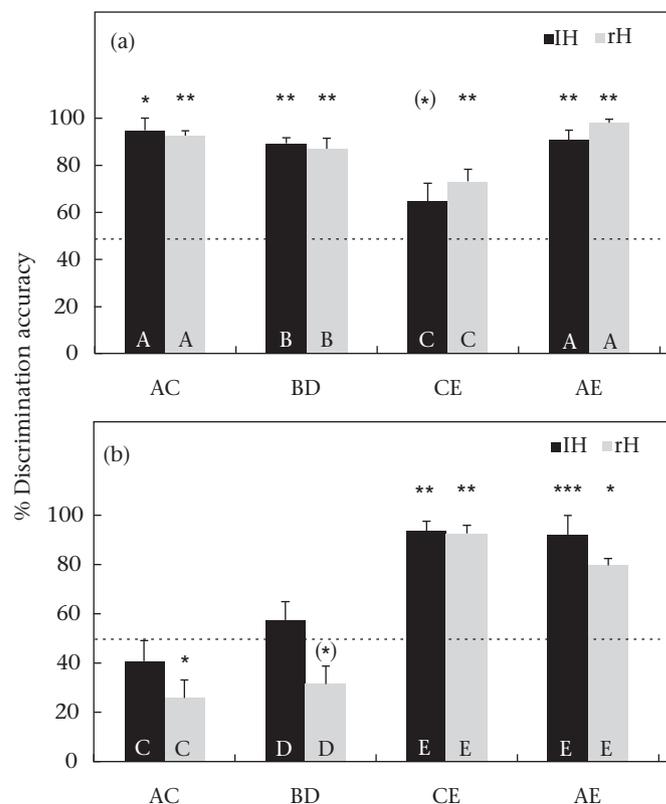
##### Impaired and hemispheric-specific monocular choices

Confronted with the transitive test pairs, the tested hemisphere had only experience with one of the presented colour stimuli; information about the other colour had to be accessed from the contralateral brain side. Therefore, pecking responses could, in principle, be based on two different strategies. On the one hand, the tested hemisphere could choose the known colour with the highest associative value. This 'default' strategy did not require relational encoding and integration of interhemispheric information. It was nevertheless transitive correct when the hemisphere learnt the beginning of the transitive line. When, on the other hand, the tested hemisphere learnt the end of the transitive line; it had to adopt a

'relational' strategy for correct transitive responding. In this case, the hemisphere had to choose the unknown colour of the test pair with which it had no direct experience. This strategy required access and integration of interhemispheric information and thereby relational evaluation of reward contingencies of the learnt and transfer stimuli.

On average, response patterns indicated that neither hemisphere successfully adopted a transitive strategy but there were intriguing differences between the hemispheres. For a better understanding of the complex data sets, we confine the description of results to test pairs that combine eventually conflicting reward values most clearly (AC = combining the two colours with the highest reward value for the two hemispheres, BD = critical transitive test pair, CE = combining the two colours with the lowest reward value for the two hemispheres, AE = combining the colour with the highest (A) and the lowest (E) reward value). For an overview of all data, see Fig. A1, and of individual data see Table A1.

When the tested hemisphere learnt the beginning of the transitive line (i.e. the left hemisphere of the LH-B/RH-D group and the right hemisphere of the RH-B/LH-D group), left- as well as right-hemispheric discrimination scores were well above chance for all colour pairs (Fig. 4a) as indicated by a comparison between correct and false decisions (Fig. 4a, Fig. A1). All responses could be explained by a choice for the known colour with the higher conditioned stimulus (except for CE) and, hence, by the adoption of the default strategy.



**Figure 4.** Left- (IH) and right-hemispheric (rH) transitive responding expressed as the mean + SE choice percentage for the transitively correct colour. Dependent on the learnt stimulus pairs, the hemisphere can respond successfully with different strategies: (a) when the tested hemisphere learnt the beginning of the transitive line, decisions for the known colour are correct (default strategy), (b) when the tested hemisphere learnt the end of the transitive line, decisions for the transfer colour are correct (relational strategy). Letters within the columns indicate the learnt (=known) colour. Dashed lines indicate 50% chance level. (\* $P = 0.07$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; Wilcoxon signed-rank tests.

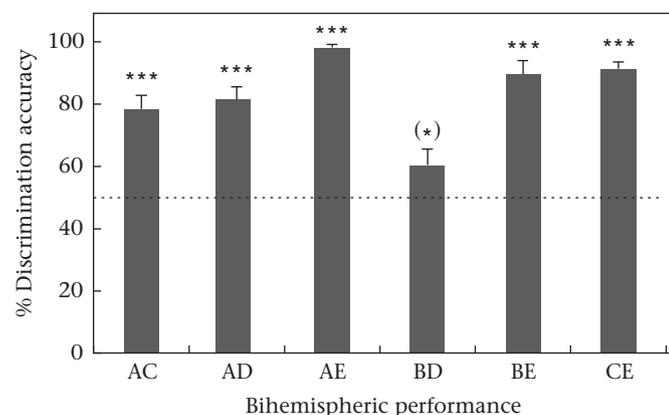
When the tested hemisphere learnt the end of the transitive line (i.e. the left hemisphere of the RH-B/LH-D and the right hemisphere of the LH-B/RH-D group), left- as well as right-hemispheric discrimination scores differed profoundly (Fig. 4b). The left hemisphere responded transitively correct when confronted with pairs AE and CE (Fig. 4b, Fig. A1), simply avoiding the most negative stimulus E. In contrast, choices for pairs AC and BD (Fig. 4b, Fig. A1) were at chance level. Unclear choices indicated interference between intra- and interhemispheric information preventing a definite transitive response. The right hemisphere also responded correctly when confronted with AE and CE (Fig. 4b, Fig. A1). When confronted with pairs AC and BD (Fig. 4b, Fig. A1), the pigeons chose the transitively incorrect but known colours C and D, respectively. Thus, the right hemisphere clearly used the 'default' and not the 'relational' strategy.

#### Relational responding during binocular discrimination

Monocular performances indicated that neither the left nor the right hemisphere alone adopted a transitive strategy. This response pattern differed profoundly from binocular choices. When pigeons used both hemispheres, discrimination scores differed between the transitive colour pairs (Friedman's ANOVA:  $\chi^2_5 = 46.225$ ,  $N = 27$ ,  $P < 0.000$ ; Fig. 5). Comparison between correct and false decisions yielded a well above chance transitive responding for colour pairs AC, AD, AE, BE, CE (Wilcoxon signed-ranks test:  $P < 0.0001$  for all colour pairs), a nonsignificant tendency to peck on B in test pair BD (Wilcoxon:  $Z = 1.810$ ,  $P = 0.07$ ) and no significant difference in binocular performances between the two experimental groups.

## DISCUSSION

The present study shows that pigeons do not integrate hemisphere-specific knowledge to adopt a transitive inference strategy when using only one hemisphere. This is presumably caused by a differential encoding of conflicting stimulus values whereby the two hemispheres differ in the evaluation of associative information. Since the birds, on the other hand, display transitive responding when seeing with both eyes, efficient interhemispheric cooperation seems to depend on the simultaneous activation of both brain sides. This suggests that pigeons use flexible intra- and interhemispheric encoding strategies depending on the seeing conditions to generate a pecking response. This flexibility might be a consequence of neuronal mechanisms avoiding interocular conflicts in birds with laterally placed eyes.



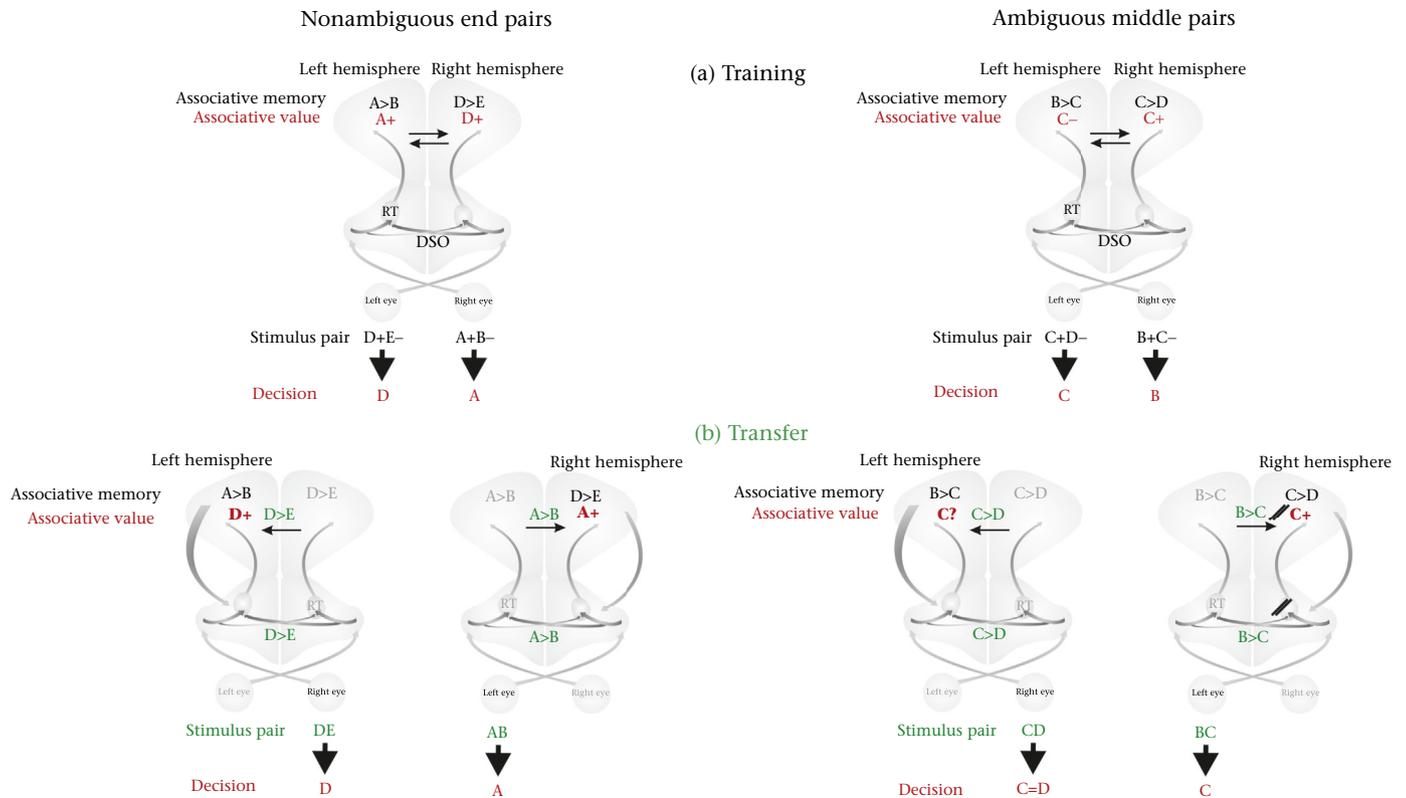
**Figure 5.** Transitive responding expressed as the mean + SE choice percentage for the transitively correct colour when using both hemispheres. Dashed line indicates 50% chance level. (\*) $P = 0.07$ ; \*\*\* $P < 0.001$ ; Wilcoxon signed-rank tests.

Response patterns during the critical monocular tests suggest that the relative reward values of each stimulus are differentially evaluated by an active process comparing intra- and interhemispheric information. We work out the details of this conclusion step by step in the following discussion. Here, we take the perspective of the hemispheres so that contralateral input means afferents from the contralateral eye while ipsilateral input represents transfer information from the ipsilateral eye and/or contralateral hemisphere. Accordingly, intrahemispheric information is directly learnt while interhemispheric information requires transfer from the ipsilateral eye/contralateral hemisphere.

Even discrimination accuracy of learnt colour pairs changed during critical testing as also observed in previous experiments (e.g. Letzner et al., 2014; Manns & Römling, 2012). Diminished performances might be caused by the more complex test situation; it was however, intriguing that especially discrimination of the overlapping middle pairs was decreased. This was particularly surprising since these pairs were significantly better learnt at the end of training presumably due to overtraining (Siemann, Delius, & Wright, 1996). Middle pairs included colour C, which had two opposite associative values because of its different reward contingencies in the two trained colour combinations (B+C-/C+D-; Fig. 6a). Although discrimination of the intrahemispherically learnt reward contingencies should be unaffected by information from the contralateral brain side, the decreased performance points to a distracting influence and provides a first hint that associative memory is not just passively accessed, at least when contralateral experience provides divergent information. Interhemispheric interference, however, was more obvious when the pigeons were discriminating transfer colour pairs.

#### Differential Encoding of Ambiguous Intra- and Interhemispheric Memory

In principle, transfer of conditioned colour discriminations was possible, as indicated by the well above chance performance of all pigeons when they were confronted with the transfer end pairs. This was in line with previous data, although we did not observe the reported left-hemispheric superiority (Letzner et al., 2014; Valencia-Alfonso et al., 2009). End pairs (A+B-/D+E-) were composed of colours with which the tested hemisphere had no direct experience so that no conflict with intrahemispheric memory arose. This was different when pigeons were confronted with a middle pair (B+C-/C+D-). Owing to the two opposite reward values of C, intrahemispheric learning experience contrasted with the transfer information. Accordingly, the tested hemisphere had to ignore the directly conditioned reward value of C when discriminating the transfer pair. But the poor performances suggest that intrahemispheric memory affected the discrimination. Thereby the hemispheres differentially dealt with the ambiguous intra- and interhemispheric information (Fig. 6). The left hemisphere performed at chance level when confronted with transfer middle pairs supporting the hypothesis that there was interference between directly experienced and transferred associative memory. The right hemisphere displayed differential response patterns depending on the directly experienced reward value of C. As already discussed in the Results, association with a negative value (i.e. after learning B+C-) led to uncertain choices when pigeons were confronted with the transfer pair C+D-. Positive association of C (i.e. after learning C+D-) resulted in pigeons choosing C when discriminating transfer pair B+C-. Thus, when associative learning led to an appetitive coding of a stimulus within the right hemisphere, neuronal processes comparing intra- and interhemispheric information weighted the intrahemispheric information more strongly or even inhibited information from the contralateral side (Fig. 6b).



**Figure 6.** Schematic model indicating lateralized intra- and interhemispheric interactions in the pigeon brain involved in choice selection when confronted with learnt and transfer colour discriminations (for details see text). (a) After monocular learning, associative memory is primarily stored within the contralateral hemisphere. (b) When the bird is confronted with transfer stimulus pairs, information can be accessed by both hemispheres if there is no conflict with intrahemispheric memory (nonambiguous end pairs AB/DE). When there is conflict between intra- and interhemispheric information (ambiguous middle pairs BC/CD), the hemispheres differ in encoding and choice selection. The left hemisphere accesses transfer information and the ambiguous associative value of C leads to uncertain pecking decisions. The right hemisphere blocks transfer information when intrahemispheric memory ascribes ambiguous stimulus C a positive associative value and therefore clearly chooses C. Commissural and top-down projections may regulate interhemispheric information processing (DSO = supraoptic decussation, RT = nucleus rotundus).

In sum, impaired discrimination of the ambiguous middle pairs indicates that transfer information is differentially processed depending on the kind of conflict between intra- and interhemispheric reward values. This means that access to associative memory is the result of an active process whereby the two hemispheres differ in their strategies to integrate conflicting information. Poor performances might be related to neuronal mechanisms avoiding conflicts between the hemispheres in animals with laterally placed eyes (see below). As discussed in the following section, the underlying encoding strategies prevent relational encoding of interhemispheric stimulus values and therefore impair transitive responding.

#### *Hemispheric-specific Evaluation of Conflicting Information and Transitive Responding*

Since the discrimination of middle transfer pairs was impaired, it was not surprising that neither the left nor the right hemisphere displayed relational responding during monocular tests. Aligning stimuli along a transitive line is based on considering relational reward values of the premise stimulus combinations (Lazareva & Wasserman, 2012; Vasconcelos, 2008) and requires integration of intra- and interhemispheric knowledge in our paradigm. Thereby C is the critical stimulus linking left- and right-hemispheric knowledge but representing ambiguous associative values for the left and right hemispheres (highest value for one, lowest value for the other hemisphere; Manns & Römmling, 2012). Therefore, only relational not associative encoding (Lazareva & Wasserman, 2012; Vasconcelos, 2008) of intra- and interhemispheric stimulus

values allows the establishment of a complete transitive line. Response patterns during monocular tests in our experiment show that neither the left nor the right hemisphere based its choices clearly on relational computations. Stimulus pairs were rather considered pair by pair relying on a differential relative evaluation of conflicting intra- and interhemispheric stimulus values. As described in the Results, the hemispheric choices can, in principle, be explained by two strategies that require a different degree of interhemispheric interaction. When the tested hemisphere (the left hemisphere of the LH-B/RH-D group and the right hemisphere of the RH-B/LH-D group) learnt the beginning of the transitive line ( $A+B-$ ,  $B+C-$ ), responses were transitively correct when the hemisphere chose simply according to its direct learning experience and, hence, according to a default strategy. This means that the observed superior performances can be explained by an associative reinforcement-driven mechanism that does not require relational encoding of associative values (Lazareva & Wasserman, 2012; Wynne, 1997). An associative mechanism even explains responding to BD, the generally accepted critical test pair indicative of transitive reasoning (Lazareva & Wasserman, 2012; Vasconcelos, 2008). The tested hemisphere had only direct experience with B and it clearly chose this stimulus although B was reinforced in one ( $B+C-$ ) and not in the other ( $A+B-$ ) training pair. Owing to the overtraining of  $B+C-$ , B was presumably associated with a positive reward (Lazareva et al., 2015; Lazareva & Wasserman, 2012) and therefore was chosen. The hemispheres also successfully discriminated pairs that included colour E and, hence, the colour with the lowest reward value that was, however, not directly experienced. This is especially remarkable for stimulus pair CE since it combined

E with C, the stimulus with the lowest reward value for the tested hemisphere. This choice pattern supports the hypothesis that each hemisphere can integrate interhemispheric reward information when no conflict with intrahemispheric learning experience arises.

When the tested hemisphere (the left hemisphere of the RH-B/LH-D group and the right hemisphere of the LH-B/RH-D group) learnt the end of the transitive line (C+D–, D+E–), a transitively correct response had to be a choice for the unknown and against the appetitively encoded colour. Only responses against intrahemispheric associative experience indicate adoption of a relational strategy that evaluates learnt and transfer stimulus values and establishes an interhemispheric transitive line. In this respect, choices were critical when pigeons were confronted with the test pairs AC and BD. Neither of these test pairs was discriminated transitively correct suggesting that the hemispheres did not base their decisions on an ordered transitive series. Thereby, the hemispheres displayed intriguing differences in their response pattern. Ambiguous choices made by the left hemisphere indicate interference between intra- and interhemispheric information preventing a definite transitive response. Right-hemispheric choices support the hypothesis that this brain side preferentially chooses the stimulus with which it has direct positive experience (see above). This is particularly illustrated in the discrimination of AC. A relational response required a choice for A although C had the highest reward value for the tested hemisphere. The right hemisphere chose C and, hence, according to its appetitive associative memory. Interference or even suppression of interhemispheric information presumably prevented relational encoding of interhemispheric stimulus values and therefore also prevented the hemispheres combining information to adopt a transitive strategy.

The monocular response patterns were, however, in stark contrast to the binocular performances. Responses when discriminating AC and BD indicate that transitively correct decisions relied on mechanisms that detect an ordered hierarchy after combination of hemispheric-specific knowledge (Manns & Römling, 2012). Thus, our results clearly show that pigeons only integrate information of the two hemispheres to solve a complex cognitive task when both hemispheres are simultaneously activated by visual input. This supports the hypothesis that mono- and binocular visuomotor processing differ profoundly, as already indicated, at the behavioural (e.g. Wilzeck, Prior, & Kelly, 2009) and physiological level (Folta, Diekamp, & Güntürkün, 2004; Schmidt & Bischof, 2001; Voss & Bischof, 2003). This also implies that associative and relational strategies are not mutually exclusive and depend not only on the trained relational rules and reinforcement history (Lazareva et al., 2015) but also on the integration of intra- and interhemispheric learning experience. Thereby, the two hemispheres obviously differ in the underlying encoding strategies.

We cannot conclude which neuronal areas mediate the neuronal processes but a recent study indicates the involvement of the hippocampus to create a representation of an ordered series of the stimuli instead of maintaining the reinforcement history of each stimulus (Lazareva et al., 2015). Impaired monocular performance indicates that the hippocampus is not able to integrate contralateral information or does not receive appropriate interhemispheric information, for example from striatal or neopallial areas that are involved in decisions between differentially valued options in mammals (Strait, Sleezer, & Hayden, 2015) and pigeons (Rose, Schiffer, & Güntürkün, 2012; Starosta, Güntürkün, & Stüttgen, 2013).

#### *Functional Organization of Interhemispheric Visual Information Processing*

Evaluation and combination of information from the left and right brain sides may emerge from differential hemispheric-specific

interactions of intra- and interhemispheric visual networks. It is intriguing that recall and integration of conditioned memory were only affected in situations when intra- and interhemispheric information were at odds in our experiment. This might be related to general mechanisms avoiding processing of discrepant information from the laterally positioned eyes of pigeons. Owing to the limited binocular visual fields, the eyes mediate virtually different input to the brain. This in turn requires mechanisms that control the interhemispheric attention switch and suppression of input from one eye to avoid interocular conflicts (Güntürkün, 2000; Stacho, Letzner, Theiss, Manns, & Güntürkün, 2016). As indicated by the results of our experiments, these processes may also regulate access to interhemispheric associative memory. After monocular training, unihemispheric discrimination performance was influenced by conflicting intra- and interhemispheric memory in a hemispheric-specific manner (Fig. 6). Ambiguous choices of the left hemisphere suggest that transfer information is accessed in principle, and it points to interference in the encoding of intra- and interhemispheric information about the associative values of single stimuli. The right-hemispheric response pattern, on the other hand, indicates that conflicting transfer information is ignored or even blocked when this input contrasts with intrahemispheric appetitive memory. These differences might be related to the differential functional role of the hemispheres. The left hemisphere dominates routine behaviour (MacNeilage et al., 2009; Vallortigara, 2000) based on categorization and the integration of experience into visual analysis (Freund et al., 2016). This processing style may also consider information from the contralateral brain side. Since the right hemisphere, on the other hand, controls quick responses in emergency situations (MacNeilage et al., 2009; Vallortigara, 2000), information processing should not be compromised by eventually conflicting information from the contralateral brain side.

The observed flexible regulation of information transfer may depend on lateralized intra- and/or interhemispheric interactions (Fig. 6). Thereby, interhemispheric mechanisms are primarily implemented within the ascending visual processing stream (Fig. 6). In pigeons, visual information is critically transferred within the tectofugal system projecting from the retina to the contralateral optic tectum from where fibres ascend to the thalamic nucleus rotundus and then to the telencephalic entopallium (Güntürkün et al., 2014; Manns & Güntürkün, 2009). Although the tectorotundal projection is largely ipsilaterally organized, a considerable number of fibres recross within the supraoptic decussation (DSO) whereby more fibres project from the right tectum to the left rotundus than vice versa (Güntürkün, Hellmann, Melsbach, & Prior, 1998). Integrity of the DSO is a prerequisite for successful transfer of pattern, brightness or colour discrimination (e.g. Watanabe, 1985; Watanabe, Hodos, Bessette, & Shimizu, 1986), which indicates that ascending projections mediate interhemispheric exchange of associative memory. Nevertheless, transfer of colour discriminations requires at least 1 h after acquisition, suggesting that accessing transfer information does not occur automatically (Skiba et al., 2000). Electrophysiological recordings show that input from the ipsilateral eye is primarily suppressed at the rotundal (Engelage & Bischof, 1988; Folta, et al., 2004; Schmidt & Bischof, 2001) and entopallial level (Voss & Bischof, 2003). Inhibition is mediated by a tectofugal side pathway via the subpretectal nuclei (Mpodozis et al., 1996; Theiss, Hellmann, & Güntürkün, 2003; Voss & Bischof, 2003) or via an interhemispheric network between the left and right tectum comprising pretectal and thalamic structures (Stacho et al., 2016). At forebrain level, context-dependent interhemispheric interactions (Schmidt & Bischof, 2001) can be regulated via the anterior commissure which is the major commissural projection of the avian forebrain (Letzner et al., 2016). This commissure does not directly mediate information

transfer but is presumably part of an active filter (Skiba et al., 2000) controlling exchange and integration of interhemispheric information (Letzner et al., 2016).

A second mechanism comprises descending projections that arise from the visual Wulst in the forebrain and exert top-down control onto tectofugal processing (Folta et al., 2004; Freund et al., 2016; Manns, Freund, Patzke, & Güntürkün, 2007; Fig. 6b). The Wulst mediates attentional processes in accordance with experience or current goals but is also relevant when changing or ambiguous stimulus values have to be considered (Freund et al., 2016; Pasternak, 1977; Shimizu & Hodos, 1989). This top-down control is primarily ipsilaterally organized and has strong impact on the left but not the right tectofugal system (Freund et al., 2016; Manns, Freund, Patzke, & Güntürkün, 2007) which is in accordance with the more top-down regulated processing style of the left hemisphere dominating routine behaviour (MacNeilage et al., 2009; Vallortigara, 2000). In relation to this (although speculative), enhanced top-down control may facilitate access to transfer information within the left hemisphere while contralateral input is blocked within the right brain side (Fig. 6b).

In sum, our results show that exchange and combination of intra- and interhemispheric associative memory is an active and flexible process that critically depends on the seeing conditions and differs between the two hemispheres. Our results provide some of the first evidence for behavioural consequences of neuronal mechanisms that avoid interocular conflicts in animals with laterally placed eyes. They illustrate the complex intra- and interhemispheric processes in a lateralized brain (Hervé et al., 2013; Manns & Ströckens, 2014; Ocklenburg & Güntürkün, 2012).

## Acknowledgments

We thank Gina Rüger and Elisa Kulewki for their help with data collection. This research was supported by grants from the German Science Foundation DFG to M.M.

## References

- Adam, R., & Güntürkün, O. (2009). When one hemisphere takes control: Meta-control in pigeons (*Columba livia*). *PLoS One*, 4(4), e5307. <http://dx.doi.org/10.1371/journal.pone.0005307>.
- Bergert, S., Windmann, S., & Güntürkün, O. (2006). Is interhemispheric communication disturbed when the two hemispheres perform on separate tasks? *Neuropsychologia*, 44(8), 1457–1467.
- Bloom, J. S., & Hynd, G. W. (2005). The role of the corpus callosum in interhemispheric transfer of information: Excitation or inhibition? *Neuropsychology Review*, 15(2), 59–71.
- Clayton, N. S., & Emery, N. J. (2015). Avian models for human cognitive neuroscience: A proposal. *Neuron*, 86(6), 1330–1342. <http://dx.doi.org/10.1016/j.neuron.2015.04.024>.
- Concha, M. L., Bianco, I. H., & Wilson, S. W. (2012). Encoding asymmetry within neural circuits. *Nature Review Neuroscience*, 13(12), 832–843. <http://dx.doi.org/10.1038/nrn3371>.
- Daisley, J. N., Mascalonzi, E., Rosa-Salva, O., Rugani, R., & Regolin, L. (2009). Lateralization of social cognition in the domestic chicken (*Gallus gallus*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1519), 965–981.
- Daisley, J. N., Vallortigara, G., & Regolin, L. (2010). Logic in an asymmetrical (social) brain: Transitive inference in the young domestic chick. *Social Neuroscience*, 5(3), 309–319.
- Engelage, J., & Bischof, H. J. (1988). Enuclation enhances ipsilateral flash evoked responses in the ectostriatum of the zebra finch (*Taeniopygia guttata castanotis* Gould). *Experimental Brain Research*, 70(1), 79–89.
- Folta, K., Diekamp, B., & Güntürkün, O. (2004). Asymmetrical modes of visual bottom-up and top-down integration in the thalamic nucleus rotundus of pigeons. *Journal of Neuroscience*, 24(43), 9475–9485.
- Frasnelli, E., Vallortigara, G., & Rogers, L. J. (2012). Left-right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience and Biobehavioural Review*, 36(4), 1273–1291. <http://dx.doi.org/10.1016/j.neubiorev.2012.02.006>.
- Freund, N., Valencia-Alfonso, C. E., Kirsch, J., Brodmann, K., Manns, M., & Güntürkün, O. (2016). Asymmetric top-down modulation of ascending visual pathways in pigeons. *Neuropsychologia*, 83, 37–47. <http://dx.doi.org/10.1016/j.neuropsychologia.2015.08.014>.
- Friederici, A. D., von Cramon, D. Y., & Kotz, S. A. (2007). Role of the corpus callosum in speech comprehension: Interfacing syntax and prosody. *Neuron*, 53(1), 135–145.
- Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition? *Brain*, 123(Pt 7), 1293–1326.
- Güntürkün, O. (2000). Sensory physiology: Vision. In G. Causey Whittow (Ed.), *Sturkie's avian physiology* (5th ed., pp. 1–19). San Diego, CA: Academic Press.
- Güntürkün, O., & Bugnyar, T. (2016). Cognition without cortex. *Trends in Cognitive Sciences*, 20(4), 291–303. <http://dx.doi.org/10.1016/j.tics.2016.02.001>.
- Güntürkün, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A., et al. (2000). Asymmetry pays: Visual lateralization improves discrimination success in pigeons. *Current Biology*, 10(17), 1079–1081.
- Güntürkün, O., Hellmann, B., Melsbach, G., & Prior, H. (1998). Asymmetries of representation in the visual system of pigeons. *Neuroreport*, 9(18), 4127–4130.
- Güntürkün, O., Stüttgen, M. C., & Manns, M. (2014). Pigeons as model systems in cognitive neuroscience. *e-Neuroforum*, 5(4), 86–92. <http://dx.doi.org/10.1007/s13295-014-0057-5>.
- Hervé, P. Y., Zago, L., Petit, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2013). Revisiting human hemispheric specialization with neuroimaging. *Trends in Cognitive Sciences*, 17(2), 69–80. <http://dx.doi.org/10.1016/j.tics.2012.12.004>.
- Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., et al. (2005). Avian Brain Nomenclature Consortium. Avian brains and a new understanding of vertebrate brain evolution. *Nature Review Neuroscience*, 6(2), 151–159.
- Kangas, B. D., & Branch, M. N. (2006). Stability of pigeon body weight under free-feeding conditions. *Journal of Experimental Analysis of Behaviour*, 86(3), 393–396.
- Lazareva, O. F., Kandray, K., & Acerbo, M. J. (2015). Hippocampal lesion and transitive inference: Dissociation of inference-based and reinforcement-based strategies in pigeons. *Hippocampus*, 25(2), 219–226. <http://dx.doi.org/10.1002/hipo.22366>.
- Lazareva, O. F., & Wasserman, E. A. (2012). Transitive inference in pigeons: Measuring the associative values of Stimuli B and D. *Behavioural Processes*, 89(3), 244–255. <http://dx.doi.org/10.1016/j.beproc.2011.12.001>.
- Letzner, S., Patzke, N., Verhaal, J., & Manns, M. (2014). Shaping a lateralized brain: Asymmetrical light experience modulates access to visual interhemispheric information in pigeons. *Scientific Reports*, 4, 4253. <http://dx.doi.org/10.1038/srep04253>.
- Letzner, S., Simon, A., & Güntürkün, O. (2016). Connectivity and neurochemistry of the commissura anterior of the pigeon (*Columba livia*). *Journal of Comparative Neurology*, 524(2), 343–361. <http://dx.doi.org/10.1002/cne.23858>.
- Lippolis, G., Joss, J. M., & Rogers, L. J. (2009). Australian lungfish (*Neoceratodus forsteri*): A missing link in the evolution of complementary side biases for predator avoidance and prey capture. *Brain, Behavior and Evolution*, 73(4), 295–303. <http://dx.doi.org/10.1159/000230674>.
- MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left & right brain. *Scientific American*, 301(1), 60–67.
- Manns, M., Freund, N., Patzke, N., & Güntürkün, O. (2007). Organization of telencephalotectal projections in pigeons: Impact for lateralized top-down control. *Neuroscience*, 144(2), 645–653.
- Manns, M., & Güntürkün, O. (2009). Dual coding of visual asymmetries in the pigeon brain: The interaction of bottom-up and top-down systems. *Experimental Brain Research*, 199(3–4), 323–332.
- Manns, M., & Römling, J. (2012). The impact of asymmetrical light input on cerebral hemispheric specialization and interhemispheric cooperation. *Nature Communications*, 3, 696. <http://dx.doi.org/10.1038/ncomms1699>.
- Manns, M., & Ströckens, F. (2014). Functional and structural comparison of visual lateralization in birds—similar but still different. *Frontiers in Psychology*, 5, 206. <http://dx.doi.org/10.3389/fpsyg.2014.00206>.
- Mpodozis, J., Cox, K., Shimizu, T., Bischof, H. J., Woodson, W., & Karten, H. J. (1996). GABAergic inputs to the nucleus rotundus (pulvinar inferior) of the pigeon (*Columba livia*). *Journal of Comparative Neurology*, 374(2), 204–222.
- Nottelmann, F., Wohlschläger, A., & Güntürkün, O. (2002). Unihemispheric memory in pigeons—knowledge, the left hemisphere is reluctant to share. *Behavioural Brain Research*, 133(2), 309–315.
- Ocklenburg, S., Friedrich, P., Güntürkün, O., & Genç, E. (2016). Intrahemispheric white matter asymmetries: The missing link between brain structure and functional lateralization? *Reviews in the Neuroscience*, 27(5), 465–480. <http://dx.doi.org/10.1515/revneuro-2015-0052>.
- Ocklenburg, S., & Güntürkün, O. (2012). Hemispheric asymmetries: The comparative view. *Frontiers in Psychology*, 3, 5. <http://dx.doi.org/10.3389/fpsyg.2012.00005>.
- Pasternak, T. (1977). Delayed matching performance after visual Wulst lesions in pigeons. *Journal of Comparative and Physiological Psychology*, 91(3), 472–484.
- Rogers, L. J. (2014). Asymmetry of brain and behavior in animals: Its development, function, and human relevance. *Genesis*, 52(6), 555–571. <http://dx.doi.org/10.1002/dvg.22741>.
- Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided brains: The biology and behaviour of brain asymmetries*. New York, NY: Cambridge University Press.
- Rose, J., Schiffer, A. M., & Güntürkün, O. (2012). Striatal dopamine D1 receptors are involved in the dissociation of learning based on reward-magnitude. *Neuroscience*, 230, 132–138. <http://dx.doi.org/10.1016/j.neuroscience.2012.10.064>.
- Schmidt, A., & Bischof, H. J. (2001). Integration of information from both eyes by single neurons of nucleus rotundus, ectostriatum and lateral neostriatum in the zebra finch (*Taeniopygia guttata castanotis* Gould). *Brain Research*, 923(1–2), 20–31.

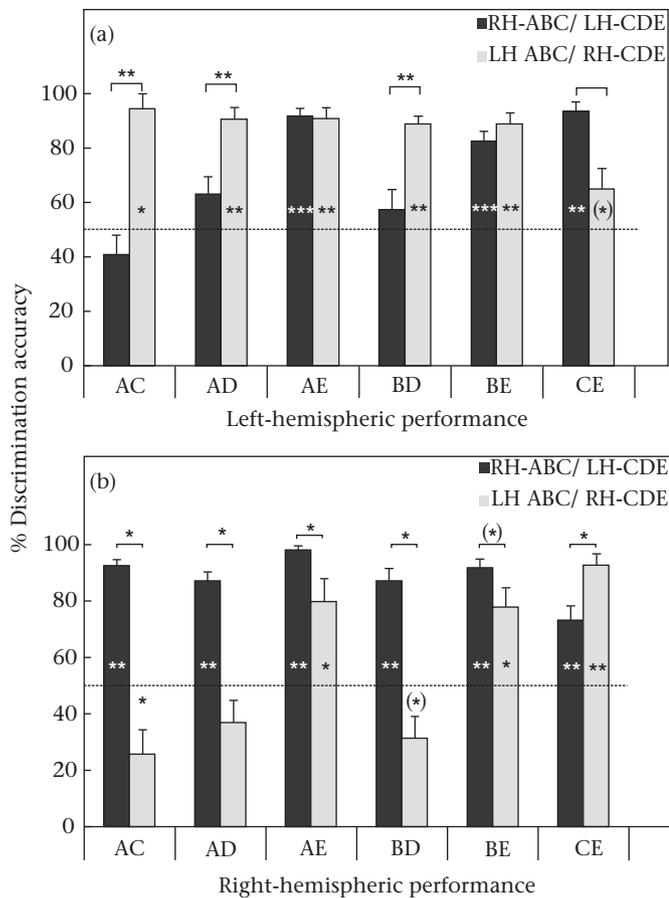
- Shimizu, T., & Hodos, W. (1989). Reversal learning in pigeons: Effects of selective lesions of the Wulst. *Behavioural Neuroscience*, *103*(2), 262–272.
- Siemann, M., Delius, J. D., & Wright, A. A. (1996). Transitive responding in pigeons: Influences of stimulus frequency and reinforcement history. *Behavioral Processes*, *37*(2–3), 185–195.
- Skiba, M., Diekamp, B., Prior, H., & Güntürkün, O. (2000). Lateralized interhemispheric transfer of color cues: Evidence for dynamic coding principles of visual lateralization in pigeons. *Brain and Language*, *73*(2), 254–273.
- Stacho, M., Letzner, S., Theiss, C., Manns, M., & Güntürkün, O. (2016). A GABAergic tecto-tegmento-tectal pathway in pigeons. *Journal of Comparative Neurology*, *524*(14), 2886–2913. <http://dx.doi.org/10.1002/cne.23999>.
- Starosta, S., Güntürkün, O., & Stüttgen, M. C. (2013). Stimulus-response-outcome coding in the pigeon nidopallium caudolaterale. *PLoS One*, *8*(2), e57407. <http://dx.doi.org/10.1371/journal.pone.0057407>.
- Strait, C. E., Sleezer, B. J., & Hayden, B. Y. (2015). Signatures of value comparison in ventral striatum neurons. *PLoS Biology*, *13*(6), e1002173. <http://dx.doi.org/10.1371/journal.pbio.1002173>.
- Theiss, M. P., Hellmann, B., & Güntürkün, O. (2003). The architecture of an inhibitory sidepath within the avian tectofugal system. *Neuroreport*, *14*(6), 879–882.
- Turner, B. O., Marinsek, N., Ryhal, E., & Miller, M. B. (2015). Hemispheric lateralization in reasoning. *Annals of the New York Academy of Science*, *1359*, 47–64. <http://dx.doi.org/10.1111/nyas.12940>.
- Ünver, E., & Güntürkün, O. (2014). Evidence for interhemispheric conflict during meta-control in pigeons. *Behavioral Brain Research*, *270*, 146–150. <http://dx.doi.org/10.1016/j.bbr.2014.05.016>.
- Valencia-Alfonso, C. E., Verhaal, J., & Güntürkün, O. (2009). Ascending and descending mechanisms of visual lateralization in pigeons. *Philosophical Transactions of the Royal Society B: Biology Science*, *364*(1519), 955–963. <http://dx.doi.org/10.1098/rstb.2008.0240>.
- Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: A stroll through left and right animals' perceptual worlds. *Brain and Language*, *73*(2), 189–219.
- Vallortigara, G. (2006). The cognitive chicken: Visual and spatial cognition in a non-mammalian brain. In E. A. Wasserman, & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 41–58). Oxford, U.K.: Oxford University Press.
- Vallortigara, G. (2012). Core knowledge of object, number, and geometry: A comparative and neural approach. *Cognitive Neuropsychology*, *29*(1–2), 213–236.
- 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*(3), 390–400.
- Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioural and Brain Sciences*, *28*(4), 575–589.
- Van der Knaap, L. J., & Van der Ham, I. J. (2011). How does the corpus callosum mediate interhemispheric transfer? A review. *Behavioural Brain Research*, *223*(1), 211–221. <http://dx.doi.org/10.1016/j.bbr.2011.04.018>.
- Vasconcelos, M. (2008). Transitive inference in non-human animals: An empirical and theoretical analysis. *Behavioural Processes*, *78*(3), 313–334. <http://dx.doi.org/10.1016/j.beproc.2008.02.017>.
- Verhaal, J., Kirsch, J. A., Vlachos, I., Manns, M., & Güntürkün, O. (2012). Lateralized reward-related visual discrimination in the avian entopallium. *European Journal of Neuroscience*, *35*(8), 1337–1343. <http://dx.doi.org/10.1111/j.1460-9568.2012.08049.x>.
- Voss, J., & Bischof, H. J. (2003). Regulation of ipsilateral visual information within the tectofugal visual system in zebra finches. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioural Physiology*, *189*(7), 545–553.
- Watanabe, S., Hodos, W., & Bessette, B. B. (1984). Two eyes are better than one: Superior binocular discrimination learning in pigeons. *Physiology & Behaviour*, *32*(5), 847–850.
- Watanabe, S. (1985). Interhemispheric transfer of visual discrimination in pigeons with supraoptic decussation (DSO) lesions before and after monocular learning. *Behavioral Brain Research*, *17*(3), 163–170.
- Watanabe, S., Hodos, W., Bessette, B. B., & Shimizu, T. (1986). Interocular transfer in parallel visual pathways in pigeons. *Brain, Behaviour and Evolution*, *29*(3–4), 184–195.
- Wilzeck, C., Prior, H., & Kelly, D. M. (2009). Geometry and landmark representation by pigeons: Evidence for species-differences in the hemispheric organization of spatial information processing? *European Journal of Neuroscience*, *29*(4), 813–822. <http://dx.doi.org/10.1111/j.1460-9568.2009.06626.x>.
- Wynne, C. D. (1997). Pigeon transitive inference: Tests of simple accounts of a complex performance. *Behavioural Processes*, *39*(1), 95–112.
- Yamazaki, Y., Aust, U., Huber, L., Hausmann, M., & Güntürkün, O. (2007). Lateralized cognition: Asymmetrical and complementary strategies of pigeons during discrimination of the 'human concept'. *Cognition*, *104*(2), 315–344.

## Appendix

**Table A1**  
Individual transitive performance of left and right hemispheres

Group	Bird	Left hemisphere						Right hemisphere						
		AC	AD	AE	BD	BE	CE	AC	AD	AE	BD	BE	CE	
RH-ABC/LH-CDE	T893	<b>100.00</b>	<b>83.33</b>	<b>100.00</b>	<b>16.67</b>	<b>100.00</b>	<b>100.00</b>	83.33	83.33	100.00	100.00	100.00	100.00	100.00
	T890	<b>83.33</b>	<b>83.33</b>	<b>100.00</b>	<b>50.00</b>	<b>83.33</b>	<b>100.00</b>	100.00	66.67	100.00	100.00	100.00	100.00	100.00
	T879	<b>83.33</b>	<b>83.33</b>	<b>100.00</b>	<b>100.00</b>	<b>83.33</b>	<b>100.00</b>	83.33	100.00	100.00	83.33	83.33	100.00	100.00
	T860	<b>16.67</b>	<b>66.67</b>	<b>83.33</b>	<b>66.67</b>	<b>100.00</b>	<b>100.00</b>	83.33	83.33	100.00	83.33	100.00	83.33	100.00
	T857	<b>66.67</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	<b>100.00</b>	83.33	83.33	100.00	100.00	100.00	100.00	100.00
	T856	<b>66.67</b>	<b>50.00</b>	<b>100.00</b>	<b>100.00</b>	<b>83.33</b>	<b>100.00</b>	83.33	83.33	100.00	100.00	100.00	100.00	100.00
	T844	<b>50.00</b>	<b>66.67</b>	<b>100.00</b>	<b>66.67</b>	<b>100.00</b>	<b>50.00</b>	100.00	66.67	100.00	66.67	66.67	66.67	66.67
	T843	<b>50.00</b>	<b>100.00</b>	<b>83.33</b>	<b>66.67</b>	<b>83.33</b>	<b>83.33</b>	100.00	83.33	100.00	100.00	83.33	66.67	66.67
	T711	<b>0.00</b>	<b>0.00</b>	<b>100.00</b>	<b>0.00</b>	<b>83.33</b>	<b>100.00</b>	100.00	100.00	100.00	100.00	100.00	100.00	66.67
	T634	<b>33.33</b>	<b>16.67</b>	<b>83.33</b>	<b>66.67</b>	<b>50.00</b>	<b>66.67</b>	83.33	100.00	100.00	66.67	66.67	33.33	33.33
	T704	<b>33.33</b>	<b>33.33</b>	<b>83.33</b>	<b>33.30</b>	<b>50.00</b>	<b>100.00</b>	100.00	100.00	100.00	100.00	100.00	100.00	66.67
	T708	<b>50.00</b>	<b>50.00</b>	<b>100.00</b>	<b>83.33</b>	<b>83.33</b>	<b>100.00</b>	83.33	100.00	100.00	100.00	100.00	100.00	83.33
	T701	<b>0.00</b>	<b>83.33</b>	<b>100.00</b>	<b>0.00</b>	<b>83.33</b>	<b>83.33</b>	100.00	100.00	100.00	100.00	100.00	100.00	66.67
	T961	<b>16.67</b>	<b>83.33</b>	<b>66.67</b>	<b>66.67</b>	<b>83.33</b>	<b>100.00</b>	100.00	66.67	83.33	50.00	66.67	50.00	50.00
	T657	<b>33.33</b>	<b>50.00</b>	<b>83.33</b>	<b>33.33</b>	<b>83.33</b>	<b>100.00</b>	100.00	100.00	83.33	100.00	100.00	100.00	50.00
	T969	<b>16.67</b>	<b>50.00</b>	<b>100.00</b>	<b>66.67</b>	<b>66.67</b>	<b>100.00</b>	100.00	100.00	100.00	100.00	100.00	100.00	83.33
T010	<b>33.33</b>	<b>66.67</b>	<b>66.67</b>	<b>50.00</b>	<b>100.00</b>	<b>100.00</b>	83.33	66.67	100.00	66.67	100.00	50.00	50.00	
T014	<b>0.00</b>	<b>66.67</b>	<b>100.00</b>	<b>66.67</b>	<b>66.67</b>	<b>100.00</b>	100.00	83.33	100.00	50.00	83.33	50.00	50.00	
LH-ABC/RH-CDE	T633	100.00	100.00	83.33	83.33	100.00	33.33	<b>0.00</b>	<b>16.67</b>	<b>50.00</b>	<b>0.00</b>	<b>33.33</b>	<b>83.33</b>	
	T700	100.00	66.67	83.33	83.33	83.33	66.67	<b>0.00</b>	<b>33.33</b>	<b>33.33</b>	<b>33.33</b>	<b>83.33</b>	<b>83.33</b>	
	T710	50.00	83.33	66.67	100.00	100.00	100.00	<b>16.67</b>	<b>16.67</b>	<b>66.67</b>	<b>33.33</b>	<b>66.67</b>	<b>100.00</b>	
	T649	100.00	83.33	83.33	83.33	83.33	33.33	<b>16.67</b>	<b>33.33</b>	<b>100.00</b>	<b>33.33</b>	<b>100.00</b>	<b>100.00</b>	
	T696	100.00	83.33	100.00	83.33	83.33	66.67	<b>0.00</b>	<b>16.67</b>	<b>100.00</b>	<b>16.67</b>	<b>83.33</b>	<b>100.00</b>	
	T702	100.00	100.00	100.00	83.33	100.00	83.33	<b>66.67</b>	<b>16.67</b>	<b>83.33</b>	<b>33.33</b>	<b>100.00</b>	<b>66.67</b>	
	T043	100.00	100.00	100.00	100.00	83.33	50.00	<b>50.00</b>	<b>66.67</b>	<b>100.00</b>	<b>33.33</b>	<b>66.67</b>	<b>100.00</b>	
	T044	100.00	100.00	100.00	100.00	66.67	66.67	<b>33.33</b>	<b>66.67</b>	<b>83.33</b>	<b>83.33</b>	<b>83.33</b>	<b>100.00</b>	
	T045	100.00	100.00	100.00	83.33	100.00	83.33	<b>50.00</b>	<b>66.67</b>	<b>100.00</b>	<b>16.67</b>	<b>83.33</b>	<b>100.00</b>	

RH = right hemisphere; LH = left hemisphere; A, B, C, D and E are colour stimuli presented in pairs. Bold type indicates hemispheric performances that required relational and, hence, interhemispheric encoding.



**Figure A1.** Transitive responding expressed as the mean + SE choice percentage for the transitivity correct colour in test pairs when pigeons used (a) the left or (b) the right hemisphere. Dashed lines indicate 50% chance level. (\*) $P = 0.07$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; Wilcoxon signed-rank tests. Left-hemispheric discrimination scores of the LH-B/RH-D group (grey bars in (a)) differed between the transitive colour pairs (Friedman's ANOVA:  $\chi^2_5 = 17.253$ ,  $N = 9$ ,  $P < 0.01$ ). Comparisons between correct and false decisions were significant for colour pairs AC, AE, BD (Wilcoxon signed-ranks test:  $N = 8$ ,  $P < 0.05$  for AC,  $N = 9$ ,  $P < 0.01$  for AE, BD) or approached significance for CE (Wilcoxon signed-ranks test:  $N = 8$ ,  $P = 0.07$ ). Left-hemispheric discrimination scores of the RH-B/LH-D group (black bars in (a)) varied between the transitive test pairs (Friedman's ANOVA:  $\chi^2_5 = 49.029$ ,  $N = 18$ ,  $P < 0.0001$ ). Transitivity correct responses were significant for pairs AE, BE and CE (Wilcoxon signed-ranks test:  $P < 0.01$  for all colour pairs). Choices for pairs AC ( $Z = 1.562$ ,  $P = 0.118$ ) and BD ( $Z = 0.724$ ,  $P = 0.469$ ) were at chance level. Left-hemispheric discrimination scores differed significantly between the experimental groups for AC, AD, BD and CE (Mann–Whitney  $U$  test:  $P < 0.01$  for all pairs). Right-hemispheric discrimination scores of the RH-B/LH-D group (black bars in (b)) varied significantly between the transitive colour pairs (Friedman's ANOVA:  $\chi^2_5 = 22.859$ ,  $N = 18$ ,  $P < 0.001$ ); the birds chose the transitivity correct colours significantly more often (Wilcoxon signed-ranks test:  $P < 0.01$  for all colour pairs). Right-hemispheric discrimination scores of the LH-B/RH-D group (black bars in (b)) varied between the test pairs (Friedman's ANOVA:  $\chi^2_5 = 35.522$ ,  $N = 9$ ,  $P < 0.0001$ ). Transitivity correct responses were significant for pairs AE ( $Z = 2.240$ ,  $P < 0.05$ ), BE ( $Z = 2.547$ ,  $P < 0.05$ ) and CE ( $Z = 2.666$ ,  $P < 0.01$ ) while discrimination of AD was at chance level ( $Z = 1.422$ ,  $P = 0.155$ ). When confronted with pairs AC ( $Z = 2.197$ ,  $P < 0.05$ ) and BD ( $Z = 1.836$ ,  $P = 0.06$ ), the pigeons chose the transitivity incorrect colours C and D. Right-hemispheric discrimination scores differed significantly between the experimental groups for all colour pairs (Mann–Whitney  $U$  test:  $P < 0.05$ ) except BE ( $Z = 1.800$ ,  $P = 0.07$ ).