



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



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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.

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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

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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

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