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Ascending and descending mechanisms of visual lateralization in pigeons

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Brain asymmetries are a widespread phenomenon among vertebrates and show a common behavioural pattern. The right hemisphere mediates more emotional and instinctive reactions, while the left hemisphere deals with elaborated experience-based behaviours. In order to achieve a lateralized behaviour, each hemisphere needs different information and therefore different representations of the world. However, how these representations are accomplished within the brain is still unknown. Based on the pigeon's visual system, we present experimental evidence that lateralized behaviour is the result of the interaction between the subtelencephalic ascending input directing more bilateral visual information towards the left hemisphere and the asymmetrically organized descending telencephalic influence on the tecto-tectal balance. Both the bilateral representation and the forebrain-modulated information processing might explain the left hemispheric dominance for complex learning and discrimination tasks.

Keywords: asymmetry; top–down influence; interhemispheric transfer; tectofugal pathway; thalamofugal pathway; Wulst

1. INTRODUCTION

For more than a century, the scientific community has known about brain asymmetries. Studies with split-brain patients and research on language and further lateralized processes uncovered diverse functional hemispheric specializations and thus differences in the way each hemisphere represents and processes information. However, it took until the late twentieth century to realize that lateralization of brain functions is not exclusively human, but also occurs in other species (Nottebohm 1970). Since then, extensive research has demonstrated that asymmetries are widespread within the animal kingdom, and that lateralized functions across vertebrates follow a common pattern. The right hemisphere is generally related to spatial and instinctive reactions, while the left hemisphere has been linked to experience-based behaviours (Andrew & Rogers 2002). Currently, a significant part of asymmetry research focuses on the common and ancestral characteristics of this phenomenon, and intends to reveal the neurobiological mechanisms underlying this pattern through the use of animal models.

In order to produce these lateralized behaviours, each hemisphere must receive or process information about the outside world differently, and, consequently,

might have an asymmetric representation of it. Therefore, one important issue is how exactly these lateralized representations are achieved in each hemisphere. One possibility is that ascending input is guided in a way that each side of the brain receives a different type or a different amount of information. However, it is also conceivable that higher stations in each hemisphere obtain the same information but process it in a different way or influence the way it is gathered. Therefore, it is possible that functional asymmetries are generated in a bottom–up or in a top–down fashion. Using the birds' visual system as a research model, we extend previous evidences and add new ones, suggesting that lateralized visual functions are related to both ascending and descending pathways. We argue that these two streams shape hemispheric representation of visual information in pigeons. Additionally, we posit that this kind of integration is likely to be the case in many species, including humans.

2. BIRDS AS AN ASYMMETRY MODEL

The visual system of birds constitutes an excellent animal model to investigate brain asymmetries. Their optic nerves decussate nearly completely (Weidner *et al*. 1985), and only limited recrossing commissures at the tectal and diencephalic level allow the necessary interhemispheric communication. As a result of the limited commissural fibres between the two hemispheres, each hemisphere processes mainly visual information from the contralateral eye, but also, to a minor extent, information coming from the ipsilateral eye.

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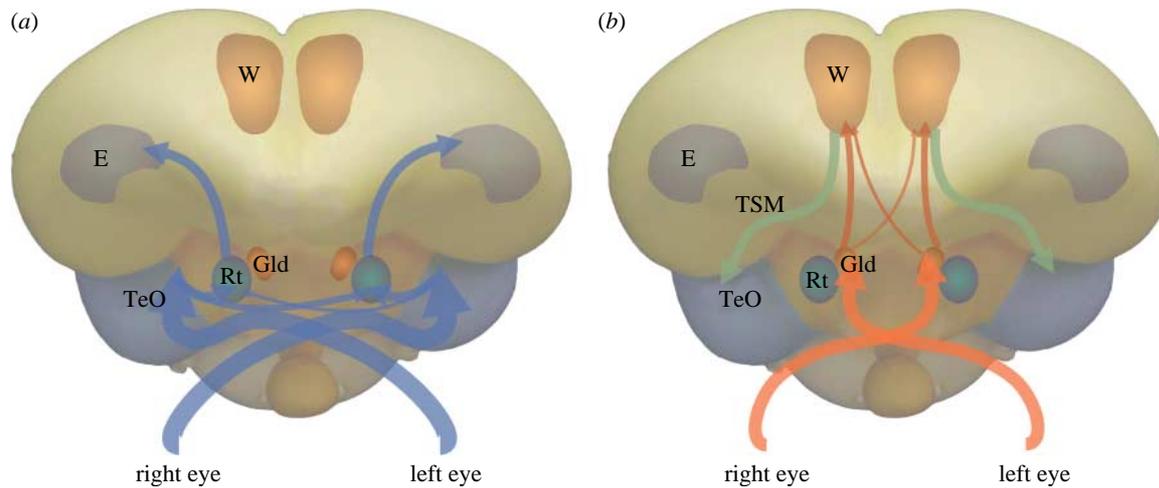† These authors contributed equally to this work.

Figure 1. Schematic of the main ascending and descending pathways in the pigeon's visual system as seen when looking from an anterior position onto the brain; dorsal is at the top. (*a*) In the tectofugal pathway (blue arrows), optic nerve fibres project to the contralateral optic tectum (TeO), from where fibres lead bilaterally to the thalamic nucleus rotundus (Rt), which then projects to the ipsilateral entopallium (E) of the forebrain. (*b*) The thalamofugal pathway (orange arrows) projects from the retina via the contralateral nucleus geniculatus lateralis, par dorsalis (Gld) bilaterally to the visual Wulst in the telencephalon (Güntürkün 2000). From the Wulst, a massive forebrain projection, the tractus septomesencephalicus (TSM, green arrows) projects to the tectum. The structures are not all normally visible within a single plain because of their different positions in the anterior–posterior axis, but, for explanatory purposes, they are showed here as seeing through a glass brain.

Besides, chicks and pigeons, two of the most popular bird models, show the same basic behavioural dichotomy described above for vertebrates. In these birds, there is a left hemisphere dominance for experience-based object manipulation (Andrew *et al.* 2000) and visual discrimination (Güntürkün 1985; Zappia & Rogers 1987). In addition, the left side of the brain is related to complex cognitive abilities such as discrimination of two-dimensional artificial patterns (Güntürkün 1985), three-dimensional natural objects (Güntürkün & Kesch 1987), geometrical optic illusions (Güntürkün 1997*b*), reversal learning (Diekamp *et al.* 1999) and concept learning (Yamazaki *et al.* 2007). By contrast, their right hemisphere is associated with spatial orientation tasks (Tommasi & Vallortigara 2001) and species-typical or instinct-based reactions such as social discrimination and attack (Vallortigara & Andrew 1991, 1994), fear responses (Phillips & Youngren 1986; Rogers *et al.* 1998) and sexual behaviour (Rogers *et al.* 1985). These studies clearly show why the visual system of birds constitutes a very useful tool for investigating the neuronal mechanisms of brain lateralization.

In birds, visual representation is processed by two parallel pathways within the brain: the tectofugal and the thalamofugal systems (figure 1). These are suggested to be equivalent to the extrageniculocortical and the geniculocortical visual pathways of mammals, respectively (Shimizu & Karten 1993; Hellmann & Güntürkün 1999). The avian tectofugal pathway is composed of optic nerve fibres projecting to the contralateral optic tectum. From the optic tectum, fibres lead bilaterally to the thalamic nucleus rotundus (Güntürkün *et al.* 1993), which then project to the ipsilateral entopallium of the forebrain (figure 1*a*). The thalamofugal pathway projects from the retina to the contralateral nucleus geniculatus lateralis, pars dorsalis. From here, fibres project bilaterally to the visual Wulst in the telencephalon (figure 1*b*). In spite of the anatomical and functional

separation between the thalamofugal and tectofugal systems, they have been shown to interact extensively at many levels. An important interaction takes place between the visual telencephalic areas and the subtelencephalic regions. Of particular note is the relationship between the telencephalic Wulst and the optic tectum (Bagnoli *et al.* 1982). Each Wulst has a direct ipsilateral connection to the optic tectum (Manns *et al.* 2007) through the tractus septomesencephalicus (TSM, figure 1*b*). Interhemispheric differences in the tectofugal and thalamofugal pathways and the way they interact with each other might be related to the common asymmetrical pattern observed in vertebrates' behaviour.

3. ASYMMETRIES OF ASCENDING, DESCENDING AND COMMISSURAL SYSTEMS

Several studies in pigeons evince anatomical and physiological asymmetries in tectofugal subtelencephalic ascending pathways that could shape information heading for each hemisphere. Neurons in the optic tectum (Güntürkün 1997*a*), the rotundus (Manns & Güntürkün 1999) and the associated nucleus subpretectalis (Freund *et al.* 2008) are larger in the left hemisphere, suggesting lateralized processing of information. Moreover, the number of contralateral tectorotundal projections is asymmetrical, having about twice the number of projections from the right optic tectum to the left rotundus as in the opposite direction (Güntürkün *et al.* 1998; figure 2*a*). Thus, the left hemisphere receives more information (at least by the tectal route) about the right visual field than the right hemisphere receives about the left visual field.

Electrophysiological studies provide some support for these findings by showing that rotundal single units with responses to ipsilateral eye stimulation occur exclusively in the left thalamus (Folta *et al.* 2004). Valencia-Alfonso *et al.* (in preparation) confirmed in a much larger sample of recorded neurons that twice as many neurons in the left rotundus had bilateral visual
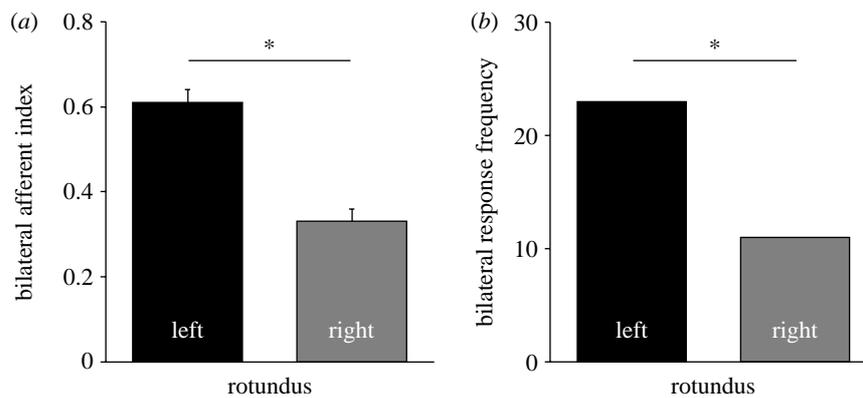
Figure 2. Asymmetry of the bilateral representation in the left rotundus. (*a*) Anatomically, cells in the left rotundus show more bilateral afferents from the tectum compared with the right rotundus (Güntürkün *et al.* 1998). A bilaterality index of 1 describes equal amount of ipsilateral and contralateral afferents, while 0 means only contralateral afferents. (*b*) Accordingly, electrophysiological evidence (Valencia-Alfonso *et al.* in preparation) shows that more neurons respond to both ipsi- and contralateral eye stimulation in the left rotundus. Bars show s.e.; $^*p = 0.01$.
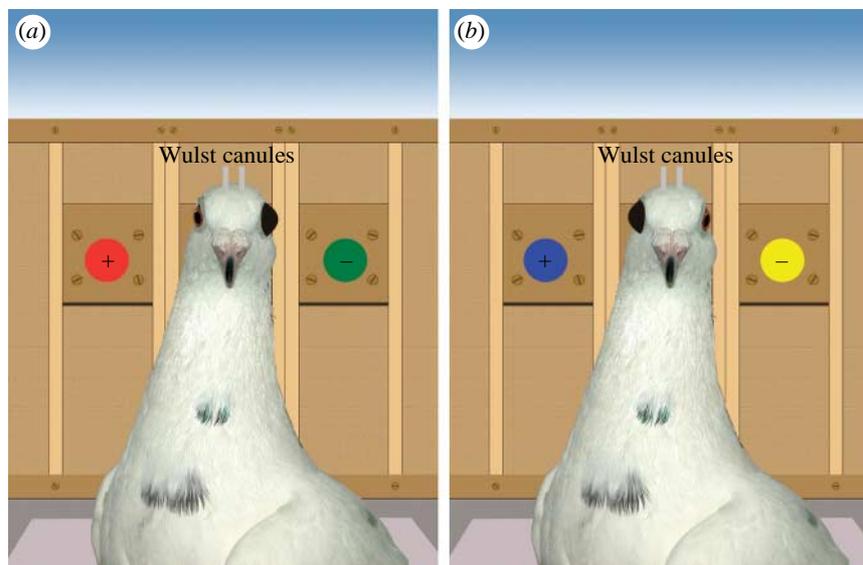

Figure 3. Forced choice task. Before each session, one of the eyes was covered with a patch and the pigeon was subjected to a monocular training in which always the same two isoluminant colours were simultaneously presented, each on one pecking key, over 60 trials. One of them was rewarded (S+) with access to food for 3 s. Pecking of non-rewarded colour (S−) would lead to 20 s of darkness. On the next day, the other eye performed the same task with two different colours. The presentation of S+ and S− was balanced in the right and left key to avoid a side bias. As a result, each eye/hemisphere ((*a*) right eye/left hemisphere training and (*b*) left eye/right hemisphere training) was exposed to only two colours (known colours), and never to the pair used with the other eye (unknown colours). Discrimination performance was tested for known and unknown stimuli under normal conditions and under reversible tetrodotoxin anaesthesia in the left Wulst (LW), right Wulst (RW), or both Wulsts (BW). For details see the electronic supplementary material.

input, compared with the right rotundus (figure 2*b*). Additionally, although rotundal cells responding only to contralateral stimulation were strongly modulated by the left Wulst (LW), the aforementioned cells with a bilateral representation were not modulated by descending forebrain projections. Thus, the rotundal neurons that might constitute the asymmetrical representation at the thalamic side were not under top–down control and were only operating in a bottom–up mode. Güntürkün & Hahmann (1999) obtained lesion data that are also in accordance with these anatomical and physiological evidences for an asymmetry of representation. The ascending tectofugal pathway then possibly creates a more bilateral representation at the forebrain level. The first aim of the present study is to test the functional consequences of this ascending asymmetry.

In addition, commissural pathways are possibly lateralized. Keysers *et al.* (2000) discovered that the left tectum is able to inhibit activity in the right tectum to a larger extent than vice versa. This would suggest that when the left hemisphere is active, a strong inhibition towards the right hemisphere is exerted, but not the other way around. Transecting this inhibitory intertectal commissure results in a reversal of behavioural asymmetries, probably because the right hemisphere is no longer inhibited (Güntürkün & Böhringer 1987). These studies imply an imbalance of inhibition between the two tecta. Probably, the left tectum has a higher probability to gain control over tectofugal processing by inhibiting the contralateral right side. This lateralized tecto-tectal inhibition is modulated by the forebrain. Two forebrain pathways, the tractus occipitomesencephalicus (TOM) and the TSM,

descend towards the ipsilateral tectum and are known to modulate tectal response properties (Leresche *et al.* 1983). Güntürkün & Hoferichter (1985) were able to show that a transection of the left but not the right TOM affected visual discrimination performance. Thus, it is possible that the forebrain interacts not with the neurons within the tectum itself, but with inhibitory tecto-tectal pathways, with the left descending system having a much stronger impact than the right. Up to now, this descending asymmetry was tested for the TOM only. The TSM descends from the Wulst towards the tectum. The second aim of the present study is to analyse the functional consequences of the descending asymmetry via the TSM. This was accomplished by temporarily inactivating the Wulst on either side.

4. TESTING THE PROCESSING OF UNIHEMISPHERIC INFORMATION

The aim of the present study was twofold. First, we intended to test the functional consequences of an asymmetrical representation during the acquisition of a colour discrimination task. Second, we wanted to analyse the functional architecture of the asymmetrical top–down forebrain regulation at a behavioural level.

To this end, we trained pigeons on a monocular forced choice task in which the animals had to discriminate between rewarded (S+) and non-rewarded (S−) colours on two pecking keys. These were presented simultaneously to one eye, while the other one was temporarily covered with an eye cap. Each eye learned to discriminate a different pair of colours with display isoluminance. The colours used were balanced across subjects and presentation side in the Skinner box (figure 3). Daily training sessions (60 trials) were performed with alternating eyes until each eye reached 90 per cent of correct responses in three successive sessions. Owing to the almost total crossing in the visual pathway of the pigeon, occlusion of an eye restricts visual input mostly to the hemisphere contralateral to the seeing eye. Thus, at the end of the training sessions, each hemisphere had only experience with one pair of colours, but was never directly exposed to the other pair. As a consequence, there was a pair of 'known' and 'unknown' colours for each eye/hemisphere (figure 3).

After discriminations were monocularly learned, the pigeons were chronically implanted with steel canules in the hyperpallium accessorium of the left and right Wulst (RW; anterior 12.0, lateral ±1.5 and depth 2.0, according to Karten & Hodos pigeons' brain atlas, 1967; for details see methods in the electronic supplementary material). After one week of recovery, the animals were tested with normal training sessions to evaluate any post-surgery effects on performance. All pigeons showed discrimination performance above 90 per cent with each eye, evincing no impairments owing to the surgery. Then, each eye was separately tested with a mixture of trained (known) and untrained (unknown) colours. Trials presenting unknown colours constituting 10 per cent of the session, were presented randomly and were not rewarded (catch trials) in order to prevent any direct learning. These test sessions were performed under normal conditions (None), and
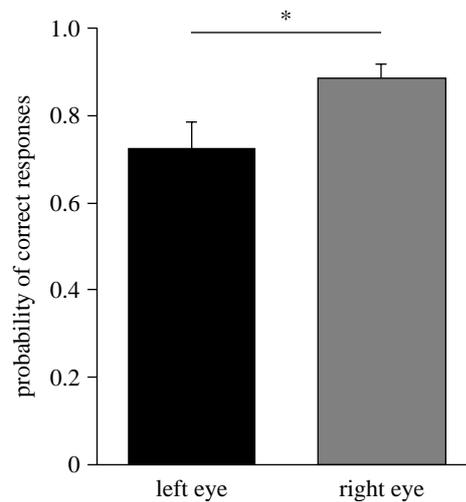
Figure 4. Superior performance of the right eye/left hemisphere for the discrimination of the unknown colour pair, which was learned with the other eye. In order to evaluate the interhemispheric transfer of information after the training phase, we tested each eye with the colours learned by the other eye. Both hemispheres performed above chance but correct responses with the right eye were significantly higher ($t = 2.13$; $p = 0.001$) compared with the left. Bars show s.e.; $^*p = 0.001$.

under temporarily inactivation of the LW, RW or both Wulsts (BW). Transitory inactivation of the Wulst was accomplished with injections of tetrodotoxin, which temporarily blocks neuronal sodium channels, through the implanted canules. The sessions were performed on different days to allow recovery from the injections. The order of Wulst inactivation conditions as well as the eye tested were balanced across the subjects.

In order to test our first hypothesis concerning the functional consequences of an asymmetric bilateral representation in ascending pathways, the difference in performance between the left and right eye under normal conditions (None) was tested using a Student's *t*-test. Because ascending systems promote a more bilateral representation within the left hemisphere, we expected that under normal conditions, the right eye (left hemisphere) would have better performance discriminating unknown colours that were learned with the left eye (right hemisphere). Our results corroborate this hypothesis confirming an asymmetrical subtelencephalic basis for a more bilateral representation within the left side of the brain. Since pigeons learned the task equally fast with both hemispheres during the training phase (*t*-test, $p > 0.05$), both hemispheres were performing equally well on the visual discrimination task. Coherently, no asymmetry in discrimination performance for the known stimuli was found. When tested for their performance on the unknown stimuli, the pigeons performed above chance level with both the left and the right hemispheres. However, there was a higher interhemispheric transfer of information towards the left side of the brain. The right eye/left hemisphere system showed a significantly higher performance ($t = 2.31$; $p = 0.001$) for the stimuli learned with the ipsilateral eye (figure 4). Since discrimination performance was equal for the known colour for the left and the right eye, the asymmetry
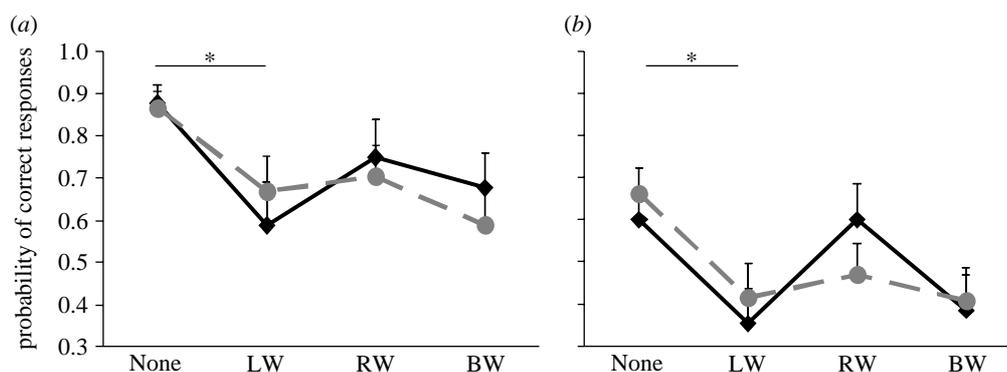
Figure 5. Asymmetric modulation of the left Wulst (LW) on the colour discrimination task. LW inactivation impaired performance of the left eye (black diamonds, LE) and the right eye (grey circles, RE) for (*a*) known and (*b*) unknown stimuli compared with the None condition, while right Wulst (RW) or both Wulst (BW) inactivation showed no significant changes compared with None. (*a*) During Wulst inactivation, the discrimination performance of known stimuli was significantly affected ($F_{3,36} = 3.94$; $p = 0.016$). The main influence was determined by anaesthesia in the LW ($p = 0.012$), while there was no such significant difference after the anaesthesia of RW ($p = 0.408$) or BW ($p = 0.085$). (*b*) In a similar way, analysis of performance to unknown stimuli showed that there was a significant impact of Wulst anaesthesia ($F_{3,36} = 4.22$; $p = 0.012$). *Post hoc* analyses showed that the main influence in this effect was the decrease in performance under the LW condition ($p = 0.002$), while performance was not significantly affected after RW ($p = 0.095$) or BW anaesthesia ($p = 0.131$). Bars show s.e.; $^{*}p = 0.05$.

found when discriminating the unknown colours is likely to occur due to a higher amount of transfer towards the left hemisphere and not due to a generally higher discrimination performance using this hemisphere. Thus, these results confirm the superior capacity of the left hemisphere to handle a more bilateral representation of the visual stimulus in the brain compared with the right hemisphere.

Our second goal was to analyse the functional implications of a possible asymmetric top–down modulation through the TSM. We therefore compared each eye performance in the discrimination task under different conditions of Wulst inactivation. The analysis was conducted with a repeated-measure ANOVA using the trained eye (left–right) and Wulst inactivation (None, LW, RW and BW) as within factors for both known and unknown stimuli. Bonferroni *post hoc* tests were used to test for specific differences. This gave us the opportunity to test whether this descending system has an asymmetrical effect similar to what was obtained by Güntürkün & Hoferichter (1985) for the TOM. We expected that inactivation of the Wulst would reduce activity within the descending telencephalotectal pathway via the TSM.

The multivariate analysis with Wulst inactivation and eye as within factors showed no significant differences for the trained eye factor in the discrimination performance. Using the right or the left eye, the pigeons showed similar discrimination levels in all experimental conditions, suggesting that both hemispheres were equally capable of performing the task, and were similarly affected by the different forebrain inactivation. Therefore, they were analysed as a single population of data. However, inactivation of the Wulst had an important impact ($F_{3,36} = 3.95$; $p = 0.016$). Inactivation of the LW accounts for most of the variance, because, during inactivation of this Wulst, the discrimination performance of both eyes for the trained colours (known colours) was significantly lower compared with the None condition ($p = 0.012$), while inactivation of the RW or even BW was not significantly

different from the None condition (figure 5*a*). The same situation occurred for 'unknown colours'. There was a significant impact of the forebrain inactivation on the pigeon's performance for both eyes while discriminating colours to which they were previously never exposed ($F_{3,36} = 4.22$; $p = 0.012$). The *post hoc* analysis showed again that this was mainly caused by an impaired discrimination performance after the LW was inactivated compared with the None condition ($p = 0.002$), while there was no significant decrement when the RW or even BW were inactivated (figure 5*b*). In summary, we observed that inactivation of the LW led to significant impairments in discrimination not only in the right eye/left hemisphere, but also in the left eye/right hemisphere, for both known and unknown stimuli (figure 5). Inactivation of the RW, and more remarkably, of BW, produced no significant changes. This suggests that there is an asymmetric left forebrain influence on tectofugal ascending activity, supporting the idea of a top–down modulation that contributes to the generation of lateralized representation. Taken together, our main results support, at the behavioural level, both the more bilateral representation and the asymmetric forebrain influence associated with the left hemisphere. In the following sections, these two main issues are discussed in the context of ascending and descending mechanisms for brain asymmetries.

(a) Asymmetric transfer of interhemispheric information and ascending systems

Given the almost total crossing of the visual system in birds, behavioural experiments involving monocular training allow us to investigate the 'knowledge' that one hemisphere possesses. The better performance of the left hemisphere in discriminating colours learned exclusively with the right hemisphere is in accordance with the evidence reviewed above that the left-sided rotundal projections transmit a high proportion of bilateral visual information. Thus, already at the level of ascending systems, the left hemisphere knows more

about the input to the right than vice versa. This finding could also explain the results of Diekamp *et al.* (1999), who found a more efficient transfer from left-eye knowledge towards the right than vice versa. This means that the left rotundus receives more information about the colours learned by the right hemisphere. It is therefore able to integrate information from both eyes to a higher extent than the right rotundus. As a consequence of these anatomical and functional properties of the interhemispheric commissures, the more bilateral information might then be transposed to the forebrain, giving the left hemisphere a more bilateral representation of the monocular discrimination task.

As demonstrated in several bird species (Catania 1965; Ogawa 1966; Mello 1968; Meier 1971; Green 1978; Francesconi *et al.* 1982; Remy & Watanabe 1993), interhemispheric transfer of information can only be accomplished through one of the subtelencephalic commissures, and it seems to be sensitive to lesions in the tecto- but not in the thalamofugal system (Watanabe *et al.* 1986). More specifically, interocular transfer of pattern, brightness and colour discrimination was impaired by section of supra-optic decussation (Francesconi *et al.* 1982) but not by the tectal commissure (Catania 1965; Cuénod & Zeier 1967; Meier 1971; Cuénod 1974; Burkhalter & Cuenod 1978). In addition, only birds with lesions of the ventral supra-optic decussation (where tectorotundal information passes) showed impaired transfer (Watanabe 1985). Taken together, these experiments show that interhemispheric transfer of information is likely to occur through the tecto-rotundal commissure. Since these fibres are asymmetrically organized (Güntürkün *et al.* 1998), this can explain the bias of bilateral information towards the left hemisphere.

Although bottom–up ascending systems explain asymmetric bilateral representations and lateralized interhemispheric transfer, they are not sufficient to elucidate why inactivation of the left but not of both forebrains reduces task performance. Therefore, the possibility of an asymmetric descending forebrain modulation of inhibitory commissural interactions is discussed in §4*b*.

(b) Descending asymmetric modulation

Following inactivation of the LW, monocular discrimination performance was impaired for both eyes for known and unknown stimuli. Neither inactivation of the RW nor, astonishingly, simultaneous inactivation of both forebrain structures resulted in significant deficits (figure 5). Consequently, there is an asymmetric telencephalic modulation, but this effect cannot be attributed to a unihemispheric left forebrain influence, but to a descending impact on the balance of subtelencephalic interactions that is more affected by the left hemisphere. Such a deficit pattern cannot be explained by only referring to asymmetries of ascending visual pathways.

A possible explanatory mechanism was already proposed in the 1960s. Sprague (1966) investigated the influence of telencephalic and mesencephalic lesions on visually guided behaviour in cats. Their results showed that unilateral posterior cortical lesions resulted in contralateral hemianopia, which was

abolished by damaging the contralateral superior colliculus. This suggests that the two superior colliculi constitute an inhibitory balance across the midbrain commissures. Descending projections from the cortex excite the ipsilateral colliculus. Shifts of visual attention from one visual hemifield to the other are then funnelled as descending activations towards one colliculus, leading to an inhibition of the other side. Lesions of one cortex result in an imbalance of the colliculo-collicular inhibition and therefore produce a complete inhibition of the lesioned side. Given that the interhemispheric commissure between the colliculi has inhibitory properties, this balance could be restored when the contralateral colliculus is lesioned. This hypothesis was confirmed by transecting the commissure, resulting in a restoration of the behavioural effects of the cortical lesion. Additional research in mammals supports this hypothesis at the behavioural (Wood 1973; Sherman 1974) and electrophysiological (Goodale 1973; Saraiva *et al.* 1976; Silakov 1977) level.

Studies in birds corroborate the asymmetric nature of forebrain modulation on the subtelencephalic balance. Unilateral lesions of the left TOM, connecting the telencephalic arcopallium with the optic tectum in pigeons, lead to severe deficits in the total number of pecking responses emitted under both monocular and binocular conditions, while lesions of the right and of the bilateral TOM lead to no deficits at all (Güntürkün & Hoferichter 1985). Furthermore, Nau & Delius (1981) found deficits after unilateral, but not after bilateral lesions of the Wulst in pigeons. In our study, only unilateral inactivation of the LW impaired discrimination performance, while inactivation of BW had a less pronounced effect. This behavioural evidence is supported by electrophysiological findings showing that the Wulst is capable of influencing the neural responses within the optic tectum (Bagnoli *et al.* 1979). Since functional lateralization depends strongly on a dynamic asymmetrical balance between left and right subtelencephalic processes, descending projections acting on one or the other side could differently affect the equilibrium. Anatomically, the descending pathways from the Wulst onto the tectum have the same amount of ipsilateral fibres within each hemisphere (Manns *et al.* 2007). Thus, it is likely that not the descending system is lateralized, but the telencephalothalamic transmission at the tectal level. Indeed, inhibitory intertectal regulation is stronger from the left to the right optic tectum (Keysers *et al.* 2000). Inactivation of the LW could therefore alter the dynamics of the intertectal inhibition more profoundly than RW anaesthesia. This telencephalic participation might provide the left hemisphere with a dominant executive control as outlined below.

Taken together, these experiments lead to the general concept that lateralization at the midbrain level is modulated in a top–down manner by the forebrain. Since the intertectal connection is asymmetrically organized, inactivation of the left can cause a greater imbalance in the intertectal interaction, resulting in the observed asymmetric performance in a discrimination task. Therefore, asymmetric ascending pathways and descending modulatory inputs cooperate

in the processing and analysis of visual representation in order to give one hemisphere an advantage during visual discrimination.

5. COMPARATIVE PERSPECTIVES IN AN ASYMMETRIC REPRESENTATION

The experimental evidence reviewed and presented in this paper leads to the general idea that asymmetries of visual function in pigeons result at least in part from a dynamic interaction between ascending and descending systems. On the one hand, there is a bottom–up asymmetric subtelencephalic system, which sends more bilateral information via the thalamic rotundus to the left telencephalon. This explains the higher capacity of this hemisphere to process bilateral information and its access to information that is processed by the other hemisphere. On the other hand, the forebrain exerts a modulation on the asymmetric intertectal balance, adding telencephalic influence to an asymmetrically organized brainstem system that results in left hemisphere dominance for executive control.

Asymmetrical representations are common among many species, including humans. For both hand movements and visual attention tasks, there is evidence that one hemisphere has a better bilateral representation than the other one. For hand motor control, the left hemisphere seems to have a more bilateral representation. Movements of both the right and left fingers activate responses within the left hemisphere. By contrast, the right hemisphere was only activated by movements of the left fingers (Kim *et al.* 1993; Durwen & Herzog 2008; Herzog & Durwen 2008). For visuospatial attention, by contrast, it is the right hemisphere that has a more bilateral representation. This is visible in visuospatial attention tasks in which the right parietal lobe is active during attentional shifts towards both visual fields, while the left parietal lobe is only active after shifts towards the contralateral hemisphere (Corbetta *et al.* 1993; Vandenberghe *et al.* 1997). As a result of this bilateral representation on the right side, patients with right parietal lesions neglect the left visual hemifield, while left lesions usually produce no neglect (Weintraub & Mesulam 1988). There is also evidence that in humans such bilateral representations could be linked to an asymmetric velocity of transfer towards the specialized hemisphere (Nowicka *et al.* 1996). Marzi *et al.* (1991) found that visuomotor information was transferred faster from the right to left hemisphere and then vice versa (Nalcaci *et al.* 1999). Asymmetries for a certain brain function could therefore go along with asymmetries of the respective representation. This arrangement might result from the need of the dominant system to integrate all information across hemifields to properly guide behaviour. Since an integration of sensory information via forebrain commissures goes along with long delays owing to the commissural conduction time (Ringo *et al.* 1994), a bilaterality of ascending projections towards the functionally dominant representation could be the evolutionary solution.

Our second major result is that the left hemisphere has a higher impact on the inhibitory tecto-tectal system. By this mechanism, the left forebrain is essentially able to temporarily gain control over the behavioural output of the animal. Theories on the evolutionary advantage of cerebral asymmetries have always revolved around the concept of a singular executive control to decide between two behavioural alternatives that result from processes within the two hemispheres (Vallortigara & Bisazza 2002). These theories usually assume partly overlapping and thus hemisphere-specific modes of information processing. Information is subsequently transferred for executive control to the functionally dominant side (Aboitiz 1992; Ringo *et al.* 1994). Most probably, the virtually complete unilateral control of language or other processes in split-brain patients results from such a process (Heilmann 1995; Gazzaniga 2000). In birds, this exclusive single-hemisphere control could be enabled via descending forebrain pathways onto an asymmetrically organized inhibitory tecto-tectal system.

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