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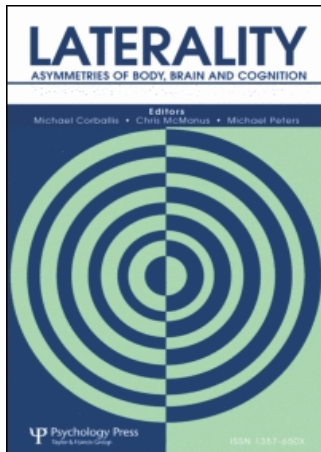
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Asymmetry of visually guided sexual behaviour in adult Japanese quail (*Coturnix japonica*)

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Sexually active adult Japanese quail (*Coturnix coturnix japonica*) were trained to run across either a left- or a right-turning runway to obtain sexual access to a conspecific of the opposite sex. The birds tested with only their right eye in use showed significantly higher latencies to complete the runway task than the birds tested binocularly and those using the left eye. In all of the three experimental conditions, male birds were significantly faster than their female counterparts. Generally, these findings are compatible with previous evidence for lateralisation in sexually motivated behaviour in birds. However, unlike the previous findings that suggested a loss of lateralisation in pattern discrimination in quail during adulthood, the present study shows that asymmetries in visually guided sexual behaviour persist in adult quail. Thus, our study implies that ontogenetic and lateralised changes within the visual system can be differently organised for different output pathways.

In recent years, an increasing amount of evidence has shown that hemispheric lateralisation is not unique to humans or mammals. As a matter of fact, cerebral lateralisations have been shown in a variety of vertebrates, including birds (Rogers & Andrew, 2002). Because avian brains lack a corpus

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callosum and display a virtually complete decussation of optic fibres at the optic chiasm, visual input can easily be restricted to one hemisphere without the need for invasive surgical procedures (Weidner, Reperant, Miceli, Haby, & Rio, 1985). This makes birds an excellent animal model for brain lateralisation (Güntürkün, 1997a, 1997b; Rogers & Andrew, 2002; Vallortigara, 2000; Vauclair, Yamazaki, & Güntürkün, 2006).

In studies using different bird species, several instances of visual lateralisation have been obtained by using procedures in which birds are required to distinguish between different visual patterns—e.g., in zebra finches (Alonso, 1998), chicks (Mench & Andrew, 1986), pigeons (Fersen & Güntürkün, 1990; Güntürkün, 1997a; Güntürkün & Kesch, 1987; Güntürkün & Kischkel, 1992), parids (Clayton & Krebs, 1993), corvids (Clayton & Krebs, 1994), and quails (Valenti, Sovrano, Zucca, & Vallortigara, 2003). Generally, it has been shown that birds exhibit a right eye/left hemisphere (RE/LH) dominancy in tasks requiring the discrimination between visual features. This was also true for tasks where animals are required to remember the correct patterns after periods of several months (Fersen & Güntürkün, 1990). Also, in tasks where the animals locate food by a single salient cue that is used like a beacon or a landmark at a goal location, a RE/LH superiority is visible (Prior & Güntürkün, 2001; Prior, Wiltschko, Stapput, Güntürkün, & Wiltschko, 2004; Ulrich et al., 1999; Wiltschko, Traudt, Güntürkün, Prior, & Wiltschko, 2002). The cognitive nature of this left–right difference is still debated. It is possible that it represents an asymmetry in the ability to categorise stimuli and events (Andrew, 1999) or may arise due to a differential specialisation of left and right hemispheres in the analysis of different stimulus properties (Vauclair et al., 2006).

In some avian species like domestic chicks or quail, this RE/LH superiority of feature discrimination disappears in adulthood (Rogers & Andrew, 2002). For example, Valenti et al. (2003) did not find any behavioural lateralisation of adult male quail in the pattern discrimination task, although they did find an apparent RE/LH superiority when they had tested 2-week-old birds. This loss of asymmetry during ontogeny is interpreted by the authors as being linked to the transient anatomical asymmetry of the thalamofugal visual pathway in chicks and, possibly, quail (Rogers & Deng, 1999). Very recently, however, adult quail were seen to show a LE/RH or RE/LH preference when seeing a familiar or unfamiliar bird, respectively (Zucca & Sovrano, in press). This indicates that some brain asymmetry exists in adult quail when tested within the social domain.

A right-hemispheric dominancy appears when the task is mostly of a spatial nature and requires a relational analysis of the shape of the surroundings. For example, Rashid and Andrew (1989) binocularly trained the chicks to find a piece of food buried under sawdust. When the birds were tested under a monocular left condition, they were able to use the cues

leading to food; but their food search performance was considerably impaired under a monocular right condition. In the same vein, Diekamp, Regolin, Güntürkün, and Vallortigara (2005) used the food cancellation task, an adapted form of cancellation tasks that are widely used during neuropsychological testing of human participants, to examine visuospatial bias in domestic chicks (*Gallus gallus*) and pigeons (*Columba livia*). They found a remarkable bias towards the left hemispace in both bird species. These and other studies (Clayton, 1993; Freire & Cheng, 2004; Tommasi, Gagliardo, Andrew, & Vallortigara, 2003; Tommasi & Vallortigara, 2001; Vallortigara, Pagni, & Sovrano, 2004; Vallortigara, Regolin, & Pagni, 1999) provided support for the laterality in spatial or topographic tasks.

Generally, hemispheric specialisations have been examined in feeding systems, with foraging being the related behaviour. Far fewer studies have addressed the question of lateralisation outside the feeding system—e.g., escape responses in marsupials (Lippolis, Westman, McAllan, & Rogers, 2005), avoidance responses in toads (Lippolis, Bisazza, Rogers, & Vallortigara, 2002), and aggression in fish (Bisazza & de Santi, 2003). To our knowledge, only three animal studies have specifically addressed behavioural lateralisation of the sexual behaviour system (Bullock & Rogers, 1986; Rogers, Zappia, & Bullock, 1985; Ventolini et al., 2005). In Rogers et al. (1985) the authors demonstrated that precocious copulation was more under control of the LE/RH in young chicken. Bullock and Rogers (1986) showed a long-lasting elevation of copulatory behaviour after a unilateral injection of monosodium glutamate into the left hemisphere in young cockerels. In Ventolini et al. (2005) the authors reported a preferential left hemifield and thus right hemisphere use during courtship and copulatory behaviour in black-winged stilts. Thus, these three studies point to a larger involvement of right hemispheric mechanisms in sexual behaviour.

Over more than 20 years, Japanese quail (*Coturnix coturnix japonica*) have become one of the primary species in laboratory studies of sexual behaviour (Domjan, Mahometa, & Mills, 2003; Mills, Crawford, Domjan, & Faure, 1997). However, possible visual asymmetries of their sexual behaviour have remained untouched. Male quail are particularly suitable for studies of sexual behaviour, because of their vigorous and distinctive copulatory behaviour (Adkins-Regan & Watson, 1990; Domjan, 1998, 2005; Domjan et al., 2003). Male quail very quickly learn to approach females when being reinforced with access to copulation. Although female quail also show approach response to male conspecifics, their approach is less vigorous (Domjan & Hall, 1986).

As noted above, Valenti et al. (2003) described an age-transitory lateralisation in pattern discrimination in male quail. This is largely typical for domestic chicks (Rogers & Andrew, 2002), although the sub-adult pattern probably does not completely disappear in adult hens (McKenzie,

Andrew, & Jones, 1998). The critical question is whether the transient asymmetries in visually guided behaviour only disappear in adults when tested in the context of feeding, or may be present when tested for sexual behaviour. To answer this question, adult quail have to be tested under monocular conditions when tracking their way to a sexual partner. We have therefore tested visually guided sexual behaviour in adult quail in a runway where the bird was unable to see the partner directly from the start position.

METHOD

Subjects

Subjects were 60-day-old, sexually mature and active quail, 36 female and 36 male, of which 6 female and 6 male birds were used as stimulus birds. Because one male subject did not walk in the runway due to an illness, this bird was excluded from the data analysis.

The subjects had been incubated at 38°C in continuous light, and hatched in the laboratory. The birds were descendants of a stock obtained from the Poultry Science Department of the Mediterranean University of Turkey. The birds were maintained in groups for the first 2 weeks after hatching and then reared individually in metal cages (25 × 23 × 20 cm) without any restriction of food and water. The brooder and colony rooms were maintained on a 16L:8D schedule, with lights on at 6:00 a.m.

Before the start of the experiment, the birds were equalised for their sexual experience. To do so, each bird was provided with 5-minute copulatory opportunity with one of its conspecific of opposite sex in their colony cages, once a day and for 5 consecutive days.

Apparatus

Two identical runways were used, one of which turned left, the other turned right, with a start and a goal chamber at each end (see Figure 1). The runways were constructed in such a way that the goal chamber was not visible from the start chamber, and vice versa. The end chambers were separated from the runway by sliding doors. The walls of the runway were made of 18-mm plywood and were painted white. The sliding door at the start chamber was wooden, but the door at the goal chamber was wire mesh. The floor and the ceiling of the apparatus were made of wire mesh. A video camera installed above the runway was used to record experimental sessions. The video recordings were used to measure the time that subjects took to get to the goal chamber from the start chamber.

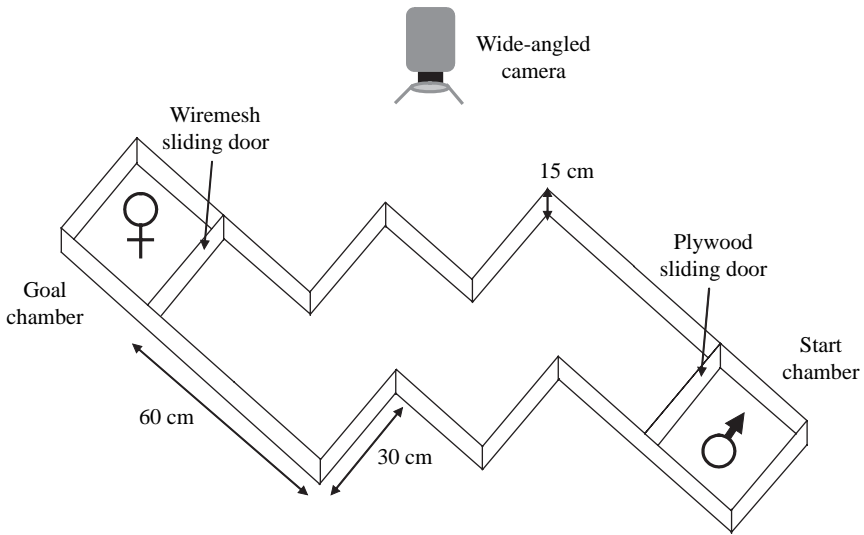


Figure 1. A schematic drawing of the left-turning runway.

Procedure

Equal numbers of female and male subjects ($n = 10$ females and 10 males in each group) were randomly assigned to right-eye/left-hemisphere (RE/LH, thus the right eye is in use), left-eye/right-hemisphere (LE/RH), and binocular (BIN) groups. Velcro rings were glued around the left eyes of the birds in RE/LH group, and the right eyes of the birds in LE/RH group. The animals were left undisturbed in their colony cages for a week to get accustomed to the Velcro ring on their eyes.

The subjects were given five habituation trials in the different compartments of the runway, in a randomised fashion. Each trial took 5 minutes a day, and lasted for 5 consecutive days. During the habituation, the sliding doors were open and the end chambers were empty.

At the end of the habituation period, equal numbers of female and male subjects in each group were randomly assigned to either left-turning or right-turning runway conditions. Then, by attaching a cone of opaque material to the Velcro ring, the left/right eye was patched as described in Prior et al. (2004). The experiment consisted of one test trial each day for 6 days. Each test day consisted of morning and afternoon sessions. The sessions were counterbalanced for each bird across the trials.

Each subject was tested with both the left and the right runway in balanced order. In each trial, a stimulus bird was placed in the goal chamber, and a subject of opposite sex was placed in the start chamber of either the left-turning or the right-turning runways. The subject was given 30 seconds

in the start chamber for settling, and then the sliding door was raised to let the bird walk in the runway. When the goal chamber was visible to the subject, the door was raised. The couples were given a 3-minute copulatory opportunity. After the copulatory period, they were housed individually in the colony cages to ensure the birds' sexual motivation elevated until the next test session. Test trials were videotaped for later quantification. The visually guided runway performance was measured as the time that a subject took to reach the goal chamber. A chronometer was started when the door of the start box was raised, and it was stopped as the door of the goal box was opened. The analyses of runway performances were based on the sixth trial of the experiment.

RESULTS

Findings of the preliminary data exploration for normality and homogeneity suggested a logarithmic transformation of the data. After this transformation, Levene's Test of Equality of Error Variances indicated a non-significant effect, $F(5, 53) = 1.64$, $p = .165$. Therefore data analyses were carried out with the transformed data by an ANOVA, with Eye in use (RE/LH, LE/RH, and BIN conditions) as between-subject factors and Sex as within-subject factor. The ANOVA revealed significant main effects of Eye in use, $F(2, 53) = 73.31$, $p < .01$, $\eta^2 = .74$, and Sex of the subjects, $F(1, 53) = 11.96$, $p < .01$, $\eta^2 = .18$. However, Eye in use \times Sex interaction was not found to be significant, $F(2, 53) = 1.58$, $p = .22$, $\eta^2 = .06$ (see Figures 2 and 3).

The multiple comparisons carried out by employing the Scheffe test demonstrated that the animals in the BI condition significantly differed in runway performance from the animals in the LE/RH condition, $MD = -0.38$, $CI_{95\%} = (-0.51, -0.25)$, $p < .01$, and the animals in the RE/LH condition, $MD = -0.64$, $CI_{95\%} = (-0.78, -0.51)$, $p < .01$. Also, the RE/LH group's performance was significantly lower than the LE/RH group's runway performance, $MD = 0.26$, $CI_{95\%} = (0.13, 0.40)$, $p < .01$.

DISCUSSION

The present study revealed a prominent left eye/right hemisphere (LE/RH) advantage when adult quail approached their sexual partner. This finding implies that asymmetries of the visual system in quail are only transient when tested for visual discrimination, but not in the context of sexual behaviour. Thus, ontogenetic changes of lateralised visual pathways may be differently organised for different output systems.

The quail of the present study were faster in approaching their sexual partners when seeing with the LE/RH. This is in accordance with studies in

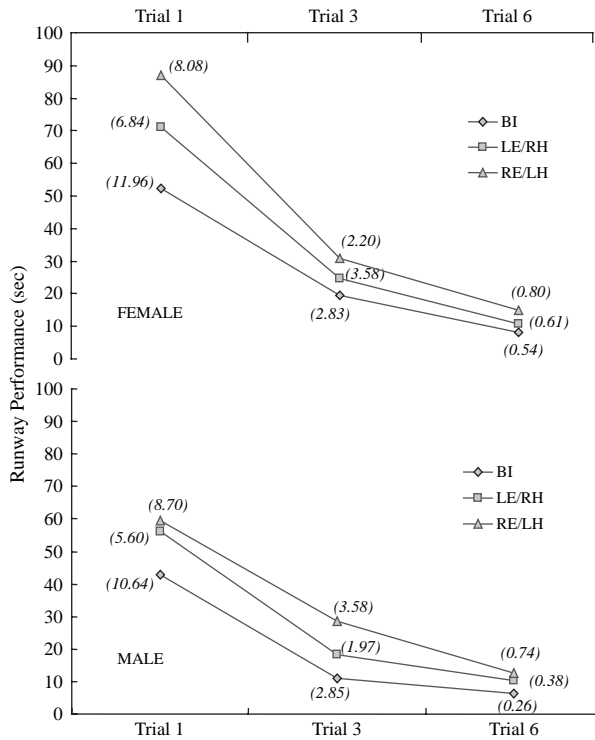


Figure 2. Mean runway performances (seconds) of the female and male subjects on the first, third, and sixth test trials (\pm SEM shown in parentheses).

young domestic chickens (Bullock & Rogers, 1986; Rogers et al., 1985). These right-hemisphere-based responses, which might be labelled “emotive” and that also cover aggressive and fear-related behaviours, have been described in a large number of species (horses: Larose, Richard-Yris, Hausberger, & Rogers, 2006; marsupials: Lippolis et al., 2005; birds: Hoffmann, Robakiewicz, Tuttle, & Rogers, 2006; toads: Lippolis, Bisazza, Rogers, & Vallortigara, 2002; fish: Bisazza & de Santi, 2003), including humans (Lanteaume et al., 2006). The ANOVA of the present study revealed a main effect for sex and eye but no interaction between sex and viewing condition. This was due to the males being more vigorous in approaching their sexual partners than females (Crawford, Holloway, & Domjan, 1993), without the two sexes being different in terms of asymmetry.

In principle, the LE/RH advantage of our quail could also result from some demand for spatial orientation within our runway. Although we are unable to exclude this possibility, for three reasons it is unlikely to have contributed importantly to the present data pattern. First, a LE/RH

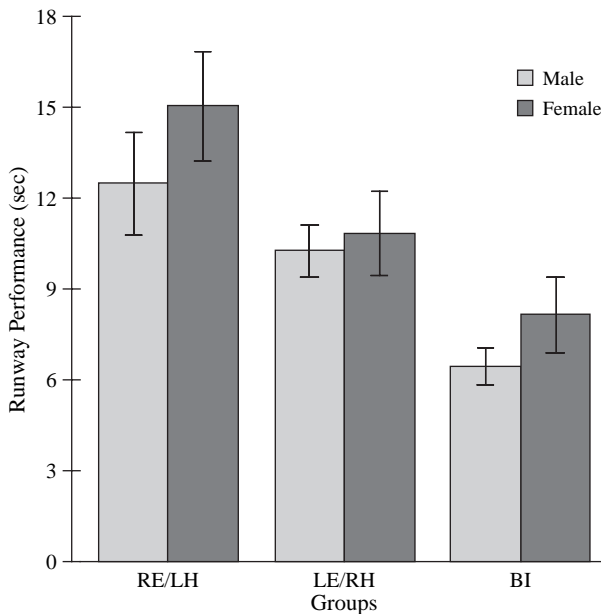


Figure 3. Mean (with 95% Confidence Intervals) runway performances (seconds) of the female and male subjects in the RE/LH, LE/RH and BI conditions.

advantage in spatial orientation usually occurs in tasks where the relations between two items, like walls or chambers, have to be integrated to find the reward (Kahn & Bingman, 2004; Prior, Lingenauber, Nitschke, & Güntürkün, 2002; Tommasi & Vallortigara, 2001; Vallortigara et al., 2004). No such relational cognition was required in our task, where the quails just had to learn that running down the floor was sufficient to approach the sexual partner which was invisible from the starting point. Second, if there had been some demand for spatial cognition, we would have expected some animals to make spatial errors like running back towards the starting point when losing their way in the middle portion of the runway. However, although conducting hundreds of trials, we observed such a behaviour only about half a dozen times. Third, spatial asymmetry seems to be more prevalent in females of domestic chicks (Tommasi & Vallortigara, 2004), while we observed no sex difference. Taken together, we are inclined to believe that the LE/RH advantage in our quail primarily resulted from the activation of a lateralised system mediating visually guided sexual behaviour, and not from asymmetries of spatial orientation.

Valenti et al. (2003) described asymmetries of visual ingestive behaviour that were transient in quail. Since quail belong to the galliform species, like the domestic chick, this passing visual asymmetry was thought to be related

to the transient connectional asymmetries of the thalamofugal visual system observed in domestic chicken (Deng & Rogers, 2002). As in the study of Zucca and Sovrano (in press), our results show that asymmetries of visually guided behaviour can also be seen in adult galliform birds (see also McKenzie et al., 1998). This result implies that ontogenetic and lateralised changes within the visual system are differently organised for different output pathways. Neural components mediating visual feature discriminations seem to display only a short-lived cerebral asymmetry after hatch. However, neural entities that control visually guided sexual behaviour seem to be asymmetrically organised for the complete lifespan of the animal.

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