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Lateralization of behaviour in zebra finches (*Taeniopygia guttata*)

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ABSTRACT. *Lateralization of behaviour in zebra finches (*Taeniopygia guttata*).* 35 male and female zebra finches were observed in their home aviary with the aim to find out asymmetries of spontaneous behaviour. For allopreneeng and bill-wiping, a significant preference was found for turning to the right side of the body, whereas other behavioural patterns show no lateral tendencies. Relationships between such behavioural laterality and asymmetry of cerebral function are discussed.

KEY WORDS: Neuroethology, Brain Asymmetry, Behavioural Laterilization, Visual System, Zebra Finches.

Introduction

Despite the symmetrical organization of organisms with respect to the cephalocaudal axis, animals sometimes systematically use one of the two sides of the body for tasks that require a unilateral orientation or the use of the limbs to manipulate. Right-handedness in humans is the best-known example of this and although it has not yet been demonstrated whether or not populational trends exist, strong individual preferences for using one or other hand have also been found in non-human primates (Hatta & Koike, 1990; Byrne & Byrne, 1991; Fagot et al, 1991). These and other cases of behavioural laterality, such as the asymmetry in rotation in rats (Glick & Cox, 1978) and several cases of "footedness" in birds (Friedman & Davis, 1938; Rogers & Workman, 1993) and even anurans (Bisazza et al., 1996) lead one to suppose that the asymmetric use of left and right could be a widespread natural phenomenon.

Zebra finches show an asymmetric orientation during one of the phases of courtship in which the male approaches the female on the same perch and displays one of his flanks. Observation of this behavioural pattern revealed a significant tendency to display the right flank and so to fixate the female with the right eye (Workman & Andrew, 1986). It is still a matter of conjecture whether this asymmetric orientation of the male depends on

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laterality in eye use, which would suggest a differential specialization of the cerebral hemispheres or, conversely, whether it has to do with locomotor bias (ten Cate et al., 1990; ten Cate, 1991; Workman and Andrew, 1991).

Existence of laterality in the avian brain has been known since Notebohm (1971) described the asymetrical control of song in passerines. Not only functional but also structural asymmetries in the avian brain are now well known. The main visual pathways (thalamofugal and tectofugal) are asymmetrically organized (see review by Rogers, 1996). It is possible that laterality in cerebral function could manifest itself in birds in the preferential use of one eye or the other. Certain anatomic characteristics of the avian nervous system lead to a large independence in the functioning of both cerebral hemispheres, in contrast to mammals. For one thing, the total decussation of the optic nerve in the chiasma means that the majority of projections from each eye go to the contralateral forebrain. For another thing, the absence of a large interhemispheric connective system such as the corpus callosum means that communication between the hemispheres is limited (Portmann and Stingelin, 1961). In addition, because the eyes are laterally located on the head, the field of vision of each eye is almost completely separate from the other. If the cerebral hemispheres are differentially specialized, the bird could take advantage from such interhemispherical autonomy to choose between the use of one or other eye depending on need (Workman & Andrew, 1986; Vallortigara et al., 1995).

Many behavioural patterns which concern orientational movements towards companions or to oneself, can be carried out on either side with respect to the cephalocaudal axis of the organism. The present work consists of an observational study of the habitual behavioural patterns of this species, with the aim of determining whether the animals present any spontaneous asymmetric preferences.

Materials and Methods

The zebra finch is a highly gregarious species. In the wild the species lives in fairly large groups and social activity is intense. The subjects used for the present study were the 35 members (18 females and 17 males) of a colony housed in an aviary measuring 3m2, where the subjects lived without any social restriction. The size of the aviary allowed them to carry out the majority of their behavioural repertoire, including that of flight. One of the four walls and the roof of the room were of translucent plastic, so providing a source of natural light. The aviary was fitted with several perches situated at different orientations and levels. Food, water and other elements (sand, cuttle-bone, charcoal) were available ad libitum and supplied in bowls placed symmetrically at the right and left of the enclosure. Both the elements within the aviary and the aviary itself were completely symmetrical with respect to the light source in order that the subjects did not receive any spacially-biased influence. During the period of data collection, human presence within the aviary was limited to the provision of food and water and the cleaning of the enclosure, with no manipulation nor disturbance by the observer during or between observation sessions.

A systematic record was made prior to the observation sessions of the spontaneous distribution of the subjects within the aviary. This distribution was shown to be spatially homogeneous, in that the animals did not show a preference for sitting on either the left or the right of the aviary. As a general rule, the birds perched facing the centre of the enclosure and not facing into the corners. Therefore, a more frequent positioning on perches of either the left or the right could imprint a directionality in movements, for example in the direction of the principal light source. Such an asymmetry could introduce a bias in the observational data, specially in behaviour involving orientation movements towards other birds in the aviary.

The behavioural patterns selected for observation were chosen from the repertoire of habitual behaviour of the species. Some of these actions are individual and others involve other members of the colony. The selected criterion was based on two premisses: a) that the movements were necessarily unilateral with respect to the cephalocaudal axis; and b) that the animal could choose to which of the two sides to direct such movements. They were as follows:

1) Allopreening: a light pecking over the plumage of another bird. This behaviour occurs frequently to clean those parts of the body where the bird itself could not reach with its bill (Martin, 1984), generally the head.

2) Bill-wiping: a rapid stroking of each side of the bill alternately on the perch. This motor pattern is also quite frequent and, according to Goodwin (1982), it is commonplace in this species as a displacement activity.

3) Resting posture: at any time during the day, the birds may adopt their sleeping position, which they maintain for periods of several minutes. This they do by turning the head backwards, either to the left or to the right, and resting it amongst the feathers of the nape.

All these behavioural patterns were recorded while the birds were perching, never when they were on the ground or on the edges of the feeding bowls. For allopreening, whether the bird turned its neck towards the right or the left to reach the companion was recorded. With respect to bill-wiping, subjects sitting on the perches (with their claws perpendicular to it) have to turn their neck to the right or left and lower their head to reach the perch. For the resting posture, the side of the body towards which the head had been turned to rest on the nape was recorded.

For data collection, a scan sampling method was used (Lehner, 1979) consisting of rapid censuses of the entire group of animals at regular intervals. In each sweep the side to which any animal was displaying one of the above patterns was registered. The interval between each sweep was two minutes, this being sufficient to allow the animals to change their activity. Data for males and females were recorded separately in order to detect any sex differences. The observation sessions occurred on successive days, between 11.00 and 17.00 and totalled 14 hours of observation split into seven sessions each of two hours duration.

Results

For statistical analysis, a chi-squared test was applied for each of the observed behavioural patterns, analysing the data for males and females separately. Table I shows the percentages of movements occurring to the left or to the right hand side. For allopreening and bill-wiping, a statistically significant asymmetric tendency was found and, in both cases, the right hand side was preferred. Birds prefer to preen by turning the head to the right and to bend their body towards the right side to reach the perch with the bill. The same trend was found for

Table I. Percentages of the observed behavioural patterns ocurring to the left or to the right of the cephalocaudal axis, with results of chi-squared test and statistical significance.
[Porcentajes de ocurrencia de las conductas observadas hacia la derecha o hacia la izquierda del eje cefalocaudal, con los resultados del análisis chi-cuadrado y su significación estadística.]

	Preferred turn side			
Behavioural patterns	Left	Right	c^2*	P**
Allopreening				
males	35.06	64.94	15.54	<0.001
females	42.72	57.28	4.36	<0.05
Bill-wipping				
males	33.33	66.67	22.33	<0.001
females	40.22	59.78	7.04	<0.01
Resting posture				
males	45.07	54.93	2.83	NS
females	48.52	51.48	0.12	NS

*df = 1.
** NS indicates P > 0.05.

males and females. However, the males showed more notable differences than the females (see table I for statistical results). In the resting posture, no significant differences were observed.

Discussion

A clear and significant asymmetry exists in certain motor patterns, namely allopreening and bill-wiping, and importantly, the preferred tendency in both cases is towards the right of the body. No asymmetric tendency was found in resting posture.

As mentioned in the introduction, asymmetry in motor patterns such as those involved in allopreening can be a manifestation of a locomotor preference to turn to the left or to the right. Nevertheless, some evidence exists which does not support this idea: zebra finches do not show any spontaneous tendency to turn to the left or to the right in a Y-form labyrinth, and they do not learn more easily to find food in the same labyrinth on the basis of its position in the left or the right arm (Alonso, 1994). Asymmetry in birds' behaviour which involves spatial orientation can be understood as a preference to use one of the two eyes, which suggests functional hemispheric specialization. Since allopreening is highly dependent on the visual system (not only to approach the bird but also for the preening action itself), it is reasonable to suppose that this laterality has some relationship with functional asymmetries in vision. Conclusive evidence exists, derived from experiments carried out under monocular conditions, that the left and right hemispheres of birds process visual information in different ways and that one hemisphere can be dominant to the other for certain types of task, at least in pigeons (Güntürkün & Kesch, 1987), and domestic chicks (Andrew, 1983; Rogers, 1986; Vallortigara et al., 1995). The asymmetry in preening behaviour could be a reflection of a preference to use the right eye/left hemisphere (together with the other nervous structures which join these two) for a task which requires visual precision, or else, to use the right field of vision to keep a fellow bird in view.

The right hand side is also preferred for bill-wiping. Such asymmetry could be understood in relation to the cerebral specialization for pecking to feed. Lateralization of feeding as visually guided behaviour is well-known in other avian species. Both domestic chicks and pigeons show a better performance in discriminating food from pebbles when using the right eye (Güntürkün, 1985; Güntürkün & Kesch, 1987; Mench & Andrew, 1986) and the same pattern has been observed in zebra finches (Alonso, 1994). Some authors explain such asymmetry as task-sharing between the two hemispheres for the different skills included in the complex behavioural pattern of searching for food. The left hemisphere (right eye) could be specialized in processing information for visual discrimination or categotization of food targets, whereas the right hemisphere would process the spatial and topographical cues needed to approach food (Rogers, 1996). The act of touching the perch with the bill could have similar functional claims to those involved in pecking food, for which the left hemisphere shows a greater ability, and that could lead to a preference for the right side to make this movement.

Asymmetry in bill-wiping display could also reflect a functional lateralization for behavioural patterns associated with emotions. Lateralization of emotional behaviour has been observed in the domestic chick (Andrew, 1983; Andrew & Brennan, 1983). In humans it is generally accepted that the right hemisphere has a greater emotional implication than the left (Springer & Deutsch, 1981). If we consider, as according to Goodwin (1982), that bill-wiping frequently occurs as a displacement activity, the observed asymmetry would therefore be related to situations of social conflict (Eibl-Eibesfelt, 1979). As was mentioned above, the birds normally face into the aviary and not into the corners, so the fact that they turn to the right implies that it is the left eye/right hemisphere which, in the meantime, wat-

ches what is happening in the aviary. This suggests a better specialization of the right hemisphere for confronting situations with a particular emotional significance. Implications of left and right hemispheres in fear and defensive behaviour would be a worthy subject of further study.

Resumen

Una colonia de 35 pinzones cebra machos y hembras (Taeniopygia guttata) fue observada con el objeto de identificar patrones de comportamiento asimétricos de entre el repertorio conductual habitual del animal. Las sesiones de observación se llevaron a cabo en el propio aviario que los sujetos habitaban, consistente en un recinto cuadrado de 3 m2 cuyo diseño y elementos estaban dispuestos de forma simétrica para evitar un sesgo direccional en el comportamiento. Se eligieron tres conductas: acicalamiento, limpieza de pico sobre la percha y postura de descanso. Un análisis de chi-cuadrado reveló que los sujetos muestran una tendencia significativa a ejecutar las conductas de acicalamiento y limpieza de pico girando el cuerpo hacia derecha. Puesto que la conducta de acicalamiento es altamente dependiente del sistema visual, se considera la posibilidad de que la lateralidad observada guarde relación con una asimetría funcional de los hemisferios cerebrales para las tareas visoperceptivas. En cuanto a la conducta de limpieza de pico sobre la percha, la asimetría puede ser debida a una preferencia mantener al resto de la colonia bajo el campo visual de ojo izquierdo, tal vez por una mayor implicación del hemisferio derecho en comportamiento emocional.

References

Alonso, Y. 1994. *Asimetrías en el comportamiento y en la función cerebral de pinzón cebra* (Taeniopygia guttata). Tesis Doctoral, Universidad de Oviedo.

Andrew, R.J. 1983. Lateralization of emotional and cognitive function in higher vertebrates, with special reference to the domestic chick. In: *Advances in vertebrate neuroethology* (J. P. Ewert, R. R. Capranica & D. J. Ingle, Eds.). New York: Plenum Press.

Andrew, R.J. & Brennan, A. 1983. The lateralization of fear behaviour in the male domestic chick: a developmental study. *Anim. Behav.*, 31:1166-1176.

Bisazza, A., Cantalupo, C., Robins, A. Rogers, L.J. & Vallortigara, G. 1996. Right pawedness in toads. *Nature*, 379:408.

Byrne, R.W. & Byrne, J.M. 1991. Hand preference in the skilled gathering tasks of mountain gorillas (*Gorilla g. berengei*). *Cortex*, 27:521-546.

Eibl-Eibesfeldt, I. 1967. Grundriss der vergleichenden Verhaltensforschung. Munich: Piper.

Fagot, J., Drea, C.M. & Wallen, K. 1991. Asymmetrical hand use in rhesus monkeys (*Macaca mulatta*) in tactually and visually regulated tasks. *J. Comp. Psychol.*, 105, 260-268.

Friedman, H. & Davis, M. 1938. "Left-handedness" in parrots. *Auk*, 55:478-480.

Glick, S.D. & Cox, D.C. 1978. Nocturnal rotation in normal rats: correlation with amphetamine-induced rotation and effects of nogrostriatal lesions. *Brain Res.*, 150:149-161.

Goodwin, D. 1982. *Estrildid finches of the world.* Oxford: Oxford University Press.

Güntürkün, O. 1985. Lateralization of visually controlled behavior in pigeons. *Physiol. Behav.*, 34: 575-577.

Güntürkün, O. & Kesch, S. 1987. Visual lateralization during feeding in pigeons. *Behav. Neurosci.*, 3:433-435.

Hatta, T. & Koike, M. 1991. Left-hand preference in frightened mother monkeys in taking up their babies. *Neuropsychologia*, 29:207-209.

Martin, H.-J. 1984. *Zebrafinken.* München: Grafe & Unzer.

Mench, J.A. & Andrew, R.J., 1986. Lateralization of food search task in the domestic chick. *Behav. Neural Biol.*, 46:107-114.

Lehner, P.N. 1979. *Handbook of Ethological Methods*. New York: Garland.

Notebohm, F. 1971. Neural lateralization of vocal control in a paserine bird I: Song. *J. Exp. Zool.* 177: 229-262.

Portmann, A. & Stingelin, W. 1961. The central nervous system. In: *Biology and comparative physiology of birds*, Vol. II (A. J. Marshall, Ed.), London: Academic Press.

Rogers, L.J. 1986. Lateralization of learning in chicks. *Adv. Study Behav.*, 16: 147-189.

Rogers, L.J. 1996. Behavioral, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. *Neurosci. Biobehav. Rev.*, 20(3): 487-503.

Rogers, L.J. & Workman, L. 1993. Footedness in birds. *Anim. Behav.*, 45: 409-411.

Springer, S.P. & Deutsch, G. 1981. *Left brain, right brain.* New York: Freeman.

ten Cate, C. 1991. Population lateralization in zebra finch courtship: a re-assessment. *Anim. Behav.*, 41:900-901

ten Cate, C., Baauw, A., Ballintijn, M. & van der Horst, I. 1990. Lateralization of orientation in sexually active zebra finches: Eye use asymmetry or locomotor bias? *Anim. Behav.*, 39: 992-994.

Vallortigara, G. Regolin, L. Bortolomiol, G & Tommasi, L. 1995. Lateral asymmetries dur to preferences in eye use during visual discrimination learning in chicks. *Behav. Brain Res.*, 74:135-143.

Workman, L. & Andrew, R.J. 1986. Asymmetries of eye use in birds. *Anim. Behav.*, 34:1582-1584.

Workman, L. & Andrew, R.J. 1991. Population lateralization in zebra finch courtship: an unresolved issue. *Anim. Behav.*, 41:545-546.