

The evolution of brain lateralization: a game theoretical analysis of population structure*

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Abstract

In recent years, it has become apparent that behavioural and brain lateralization is the rule rather than the exception among vertebrates. The study of lateralization has been so far the province of neurology and neuropsychology. We show how such research can be integrated with evolutionary biology to more fully understand lateralization. In particular, we address the fact that, within a species, left- and right-type individuals are often in a definite proportion different from 1/2 (e.g., hand use in humans). We argue that traditional explanations of brain lateralization (that it may avoid costly duplication of neural circuitry and reduce interference between functions) cannot account for this fact, because increased individual efficiency is unrelated to the frequency of left- and right-type individuals in a population. A further puzzle is that, if a majority of individuals are of the same type, individual behaviour becomes more predictable to other organisms. Here we show that alignment of the direction of behavioural asymmetries in a population can arise as an evolutionarily stable strategy (ESS), when individually asymmetrical organisms must coordinate their behaviour with that of other asymmetrical organisms. Thus, brain and behavioural lateralization, as we know it in humans and other vertebrates, may have evolved under basically “social” selection pressures.

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1 Introduction

Research in the last twenty years firmly establishes that most vertebrates show lateral biases in behaviour. For instance, toads (Lippolis et al. 2002), chickens (Evans et al. 1993) and fish (De Santi et al. 2001) react faster to predators approaching from the left. Left-side biases also exist in interactions with conspecifics, in fish (Sovrano et al. 1999, 2001), toads (Robins et al. 1997), lizards (Deckel 1995), chickens (Vallortigara 1992; Vallortigara et al. 2001), sheep (Peirce et al. 2000) and primates (Casperd & Dunbar 1996; Weiss et al. 2002; Vermeire et al. 1998). When handling objects, however, many animals use preferentially their right limbs (chickens: Mench & Andrew 1986; toads: Vallortigara et al. 1998; pigeons: Güntürkün & Kesh 1987; crows: Hunt et al 2001; humans: McManus & Bryden 1992). The direction of the bias for a given function (e.g., right hemisphere bias for spatial functions, Vallortigara et al., in press) is often consistent across taxa (birds, reptiles, mammals), suggesting an ancient (very likely homologous) origin in early vertebrates (Vallortigara et al. 1999).

The main topic of this paper is the population structure of lateralization, that is what proportion of individuals is biased in one or the other direction. For instance, right-handers greatly outnumber left-handers in humans. Indeed, in most species where a lateral bias is present for a behaviour, left- and right-biased individuals are not equally common, with the minority type making up 10% to 35% of the population. We refer to this as a population-level lateralization. It appears to be the most common situation (e.g., all examples above), although left- and right-type individuals are equally abundant in some cases (see below). Despite extensive research on lateralization, the determinants of population-level lateralization remain largely unexplored. Below we argue that lateralization at the population level cannot be explained by studying the neuropsychology of individuals, nor it can be a mere by-product of genetic expression. We then apply concepts from evolutionary biology to show that uneven mixtures of left- and right-biased individuals can arise, and be evolutionarily stable (Maynard-Smith 1982), when individually asymmetrical organisms must coordinate with other asymmetrical organisms.

2 Individual efficiency and the genetics of lateralization

The traditional explanation of brain lateralization is that it avoids costly duplication of neural circuitry with the same function (Levy 1977), as well as decreasing the interference between different functions. For instance, dominance by one side of the brain may prevent the simultaneous initiation of incompatible responses in organisms with laterally placed eyes, such as fish (Andrew 1991; Vallortigara 2000). However, it seems that a quest for individual efficiency cannot explain the

population structure of lateral biases. To see why, let us indicate with (A,B) a brain in which the left side dominates for function A, and the right side for function B. According to the efficiency hypothesis, an (A,B) brain would be superior to an (AB,AB) brain, i.e. a non-lateralized brain with both functions on both sides. However, the two opposite lateralizations (A,B) and (B,A) would be equally efficient, and there would be no reason for one of them to be more common. The findings of McGrew & Marchant (1999) illustrate this point clearly. The authors studied foraging in chimpanzees (so-called “termite fishing”) and found that individuals with a stronger hand preference forage more efficiently, but this does not depend on which hand is preferred. Indeed, right- and left-handed foragers appear to be equally common among chimpanzees.

Studies of the genetics of lateralization further strengthen the opinion that individual-level lateralization does not automatically produce population-level lateralization. For instance, mice can be artificially selected for the strength of paw preference, but not for the direction of this preference (Collins 1985). The same holds for asymmetrical eye morphology in *Drosophila subobscura* (Maynard-Smith & Sondhi 1960). In humans, the inheritance of handedness fits well one-locus models where one allele causes right-handedness and another left- or right-handedness at random (McManus & Bryden 1992; Annett 1995; Corballis 1997). This genetic mechanism could lead to any proportion of right-handers between 50% and 100%, and if handedness were selectively neutral we would expect to observe one of these extremes (due to loss of one allele by genetic drift). Yet, data from many populations, including Middle Age England, point to a rather stable proportion of about 85% right-handers (Steele & Mays 1995).

3 A game-theoretical analysis

According to the previous section, individual efficiency and genetic mechanisms appear compatible with populations in which individuals with opposite lateralization are equally common. Nevertheless, most vertebrates are lateralized at the population level for many functions. Indeed, population-level lateralization poses a further puzzle. If most individuals show a bias in the same direction, their behaviour becomes more predictable to other organisms (Hori 1993), potentially conveying a specific disadvantage to majority-type individuals. Then, why aren't left and right biases equally abundant, given that this appears compatible with both individual efficiency and the genetics of lateralization? In other words, it seems that evolution could have led (at least in principle) to individually asymmetrical organisms in the absence of population-level asymmetry (cf. the artificial selection studies cited above). Such a situation would bring the advantages of individual-level lateralization without the disadvantages of population-level later-

alization (predictability by other organisms). In fact, in the absence of specific selective pressures favouring population-level asymmetry, and with the alleged advantages of individual lateralization, we would expect populations where individuals with opposite lateralization are equally common.

The possibility we explore here is that population-level lateralization may arise when the fitness of individually asymmetrical organisms depends on what other individually asymmetrical organisms do. Examples of relevant selection pressures may be the need for coordination between individuals of a social species, and antagonistic interactions between lateralized individuals. If, due to such selection pressures, an uneven mixture of left- and right-type individuals can be evolutionarily stable, then stability of lateralization across taxa would follow from common ancestry, given that lateralization appears phylogenetically very old (Vallortigara & Bisazza 2002). We now formalize a simple game theory model showing that population-level lateralization can indeed be evolutionarily stable, although not in all conditions. The model is framed in the context of prey-predator interactions, but can be extended to other scenarios (see below).

We consider predators and group-living prey meeting in contests where prey have two lateralization strategies available: “left” and “right”. We assume that, when a predator attacks, lateralization affects prey escape probability in two ways. First, prey lateralized in the same direction have a greater chance of keeping together as a group. This assumption is motivated by empirical research showing that lateralization can affect both the time of detection of predators (Lippolis et al. 2002) and the direction in which prey tend to escape (Cantalupo et al. 1995). Our second assumption is that predators are better at capturing the prey type they meet more often. For instance, predators may learn to anticipate prey escape movements, or to approach prey from a given direction. Let us write $p(x)$ the probability that a prey survives an attack, given that a proportion x of its group-mates have its same lateralization. A simple yet fairly general way of writing $p(x)$ is:

$$p(x) = p_0 + cg(x) - l(x) \quad (1)$$

where p_0 is a baseline escape probability, $g(x)$ represents the benefit gained, under attack, by keeping together with a proportion x of fellow prey, and $l(x)$ represents the cost of having the same directional bias as a proportion of other prey (both and are assumed positive). This cost is assumed to arise from predators having more success with the more common prey type. The parameter c allows to regulate the relative importance of $g(x)$ and $l(x)$.

If we indicate with a and $1 - a$, respectively, the proportion of left- and right-type prey in the population, we can use equation (1) to write the respective escape

probabilities as:

$$p(a) = p_0 + cg(a) - l(a) \quad (2)$$

$$p(1-a) = p_0 + cg(1-a) - l(1-a)$$

The condition for a given proportion a^* to be an evolutionary equilibrium is that the escape probabilities of left- and right-type prey be equal, that is

$$p(a^*) = p(1-a^*) \quad (3)$$

Furthermore, the equilibrium is stable if natural selection works to restore the proportion whenever slight deviations occur. This means that a small increase in the proportion of left-type prey, say by an amount ε , should increase the escape probability of right-type prey, and vice-versa. In formulae:

$$p(a^* + \varepsilon) < p(1 - a^* - \varepsilon) \quad (4)$$

$$p(a^* - \varepsilon) > p(1 - a^* + \varepsilon)$$

(Technically, it must be possible to find a value of ε such that the above equations hold for all smaller values). These equations provide us with a simple, general framework to study the evolutionary stability of populations composed of left- and right-type prey. The existence and nature of equilibria depends, of course, on what $g(x)$ and $l(x)$ are. Current knowledge, unfortunately, does not yield a detailed answer. To illustrate the possible outcomes of our model, we show below two specific forms of the functions $g(x)$ and $l(x)$, inspired from biological reality. We leave open to future research to establish the most appropriate functions in any concrete situation.

We have linked $l(x)$ to the ability of predators at capturing a given prey type, as a function of this type's abundance. That is, this function should measure the performance of predators as a function of the amount of practice with a given prey type. Empirically, performance curves of this kind are often well approximated by a negatively-accelerated function (Mackintosh 1974), which in the present context can be written

$$l(x) = 1 - \exp(-kNx) \quad (5)$$

where N is group size, and larger values of the positive parameter k lead to faster increase of performance with increasing prey abundance.

Given current knowledge of group effects on predation risk, any choice for $g(x)$ is somewhat speculative. One relatively well-studied effect is so-called "dilution", whereby in a group of n each individual is assumed to have a probability of $1/n$ of being targeted by a predator (Treisman 1975; Foster & Treherne 1981; Burger & Gochfeld 2001). This probability can be approximated by $1/(1 + Nx)$

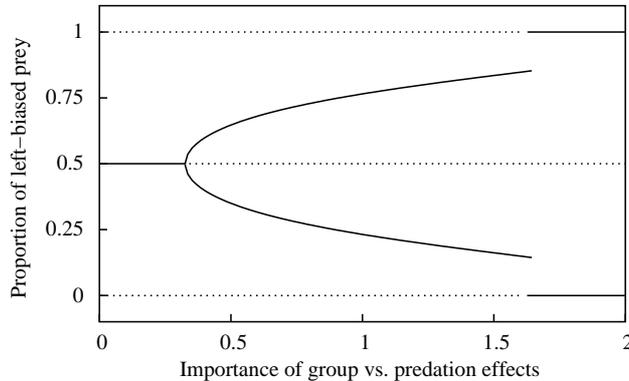


Figure 1: Equilibrium proportion of left-type prey in a group living species as a function of the parameter c in equation (1) (see text for details). Solid lines: stable equilibria; dashed lines: unstable equilibria. Parameters used are $N = 50$ and $k = 5$, see equations (5) and (6) in the text. The equilibrium proportion was obtained by standard methods for solving non-linear equations, as implemented by the `fsolve` function of the GNU/Octave software. Stability was checked using equation (4).

if a prey keeps together with a fraction x of individuals from a larger group of N . The probability of *not* being chosen as target is therefore

$$g(x) = 1 - \frac{1}{1 + Nx} \quad (6)$$

This expression can be used in equation (1) as the benefit of group living to an individual prey, when a proportion x of prey is using its same strategy (since prey with the same strategy are assumed to be more likely to keep together). Other potential effects of group living such as the so-called “confusion” effect — the fact that it might be difficult for a predator to constantly target one prey in the midst of many (Pilcher 1986) — are insufficiently known and will be not considered here.

Employing equations (5) and (6), together with the equilibrium and stability conditions (3) and (4), we have analyzed numerically the existence and stability of equilibria. In figure 1 we plot the equilibrium proportion of left-type prey as a function of the parameter c in equation (1) and for $N = 50$, $k = 5$. The figure shows that for small c the only stable population consists of left- and right-type prey in equal numbers. This correspond to situations in which lateralization-mediated effects of group living on escape probability are small (see equation (1)), for instance in the case of solitary prey or for lateral biases that do not influence group cohesion. This equilibrium becomes unstable for larger c (larger group effects), giving way to stable populations consisting of left- and right-type prey in unequal numbers. Since the model does not assume any intrinsic benefit of left or right lateralization, there are always two specular solutions, one with a

majority of left-type prey and one with a majority of right-type prey. The intuitive content of such a situation is that the majority of prey get protection by keeping together, but pay a cost because predators are better at handling them. A minority of prey manages to enjoy the same escape probability by trading-off protection from the group with an advantage in the face of predators. Figure 1 also shows that the proportion of the majority prey type increases as c gets larger, until only populations composed entirely of one type of prey are stable. This corresponds to situations where the protection offered by the group is so large as to overcome any effect of differential ability in predators. For smaller values of c , populations composed of only one prey type are always unstable.

4 Conclusion

In summary, our model shows that populations consisting of left- and right-type individuals in unequal numbers — the most common situation among vertebrates — can be evolutionarily stable if being lateralized in one or the other direction has frequency-dependent costs and benefits (Raymond et al. 1996). We have argued that, in prey-predator interactions, this can happen because of the interplay between individual lateralization, group living in prey and learning in predators. Vallortigara & Bisazza (2002) provide evidence that fits the model. Testing escape behaviour in 20 fish species, they found that 6 out of 10 solitary species (no group effects, or in the model) showed only individual-level lateralization, whereas all 10 shoaling species studied showed lateralization at the population level ($P < 0.01$, Fisher's exact probability test). Cases other than prey-predator interactions might be studied with the same logic. In social species, for instance, there appears to be ample opportunities for contrasting selective pressures on lateralization (Raymond et al. 1996), and this might result in the kind of frequency-dependence discussed above. In fact, individuals in social species often engage in both cooperation (favouring predictability of behaviour, hence majority-type individuals) and agonistic interactions (favouring unpredictability, hence minority-type individuals). For instance, we know that agonistic interactions in gelada baboons are less likely to be elicited when a conspecific is on the baboon's right side (Casperd & Dunbar 1996), although we ignore whether this is exploited by conspecifics.

In conclusion, our approach to the study of brain and behavioural lateralization offers simultaneously the solution of a riddle (the emergence and maintenance of unequal proportions of individuals with opposite lateralization) and the possibility of a bridge between neuropsychology and evolutionary biology. Whereas increased brain efficiency may have determined the appearance of lateral biases in individuals, social factors (see also Rogers 2000) have likely been crucial in shaping the population structure of such biases.

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