

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

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In recent years, it has become apparent that behavioural and brain lateralization at the population level is the rule rather than the exception among vertebrates. The study of these phenomena has so far been the province of neurology and neuropsychology. Here, we show how such research can be integrated with evolutionary biology to understand lateralization more fully. In particular, we address the fact that, within a species, left- and right-type individuals often occur in proportions different from one-half (e.g. hand use in humans). The traditional explanations offered for lateralization of brain function (that it may avoid unnecessary duplication of neural circuitry and reduce interference between functions) cannot account for this fact, because increased individual efficiency is unrelated to the alignment of lateralization at the population level. A further puzzle is that such an alignment may even be disadvantageous, as it makes individual behaviour 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 when individual asymmetrical organisms must coordinate their behaviour with that of other asymmetrical organisms. Brain and behavioural lateralization, as we know it in humans and other vertebrates, may have evolved under basically 'social' selection pressures.

Keywords: cerebral lateralization; brain asymmetry; laterality; hemispheres; theory of games; evolutionarily stable strategy

1. INTRODUCTION

Research in the past 20 years firmly establishes that most vertebrates show lateral biases in behaviour. For instance, toads (Lippolis *et al.* 2002), chickens (Evans *et al.* 1993) and fishes (De Santi *et al.* 2001) react faster to predators approaching from the left. Left-side biases also exist in interactions with conspecifics in fishes (Sovrano *et al.* 1999, 2001), toads (Robins *et al.* 1998), lizards (Deckel 1995), chickens (Vallortigara 1992; Vallortigara *et al.* 2001), sheep (Peirce *et al.* 2000) and primates (Casperd & Dunbar 1996; Vermeire *et al.* 1998; Weiss *et al.* 2002). When handling objects, on the contrary, many animals have right-side biases (chickens (Mench & Andrew 1986); toads (Vallortigara *et al.* 1998); pigeons (Güntürkün & Kesh 1987); crows (Hunt *et al.* 2001); and humans (McManus & Bryden 1992)). The direction of the bias for a given function (e.g. right-hemisphere bias for spatial functions (Vallortigara *et al.* 2004) and left-hemisphere bias for categorizing stimuli and controlling considered responses (Rogers & Andrew 2002)) is often consistent across taxa (fishes, amphibians, reptiles, birds and 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, i.e. what proportion of individuals is biased in each direction. For instance, right-handers greatly outnumber left-handers in humans (McManus 2002). 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 from 10% to 35% of the population. We refer to this as a population-level lateralization (Denenberg 1981). 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 § 2). Despite extensive research on lateralization, the determinants of population-level lateralization remain largely unexplored. In § 2 we argue that lateralization at the population level cannot be explained by studying the neuropsychology of individuals, nor can it 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 individual 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 (Rogers 2000; see also Güntürkün *et al.* 2000). 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 fishes (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

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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 a one-locus model where one allele causes right-handedness and another causes 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 (owing to loss of one allele by genetic drift). However, data from many populations, including Middle Age England, point to a rather stable proportion of ca. 85% right-handers (Steele & Mays 1995).

3. A GAME-THEORETICAL ANALYSIS

According to § 2, 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 conferring a specific disadvantage on majority-type individuals. Then, why are left and right biases not equally abundant, given that this appears to be 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 in § 2). Such a situation would have the advantages of individual-level lateralization (brain efficiency) without the disadvantages of population-level lateralization (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 to be the normal condition.

The possibility we explore here is that population-level lateralization may arise when the fitness of an individual

asymmetrical organism depends on what other individual 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, owing to such selection pressures, an uneven mixture of left- and right-type individuals can be evolutionarily stable then the stability of lateralization across taxa would follow from common ancestry, given that lateralization appears to be phylogenetically very old (Vallortigara & Bisazza 2002). We now formalize a simple game-theoretical 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 § 4).

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 the probability of prey escape 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 when predators are detected (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 $p(x)$, indicating the probability that a prey survives an attack, given that a proportion x of its group-mates have the same lateralization. A simple but fairly general way of writing $p(x)$ is:

$$p(x) = p_0 + cg(x) - l(x), \quad (3.1)$$

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 x of other prey (both $g(x)$ and $l(x)$ are assumed to be positive). This cost is assumed to arise from predators having more success with the more common prey type. The parameter c allows us to regulate the relative importance of $g(x)$ and $l(x)$.

If we indicate with a and $1 - a$, respectively, the proportions of left- and right-type prey in the population, we can use equation (3.1) to write the respective escape probabilities as:

$$\begin{aligned} p(a) &= p_0 + cg(a) - l(a), \\ p(1 - a) &= p_0 + cg(1 - a) - l(1 - a). \end{aligned} \quad (3.2)$$

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

$$p(a^*) = p(1 - a^*). \quad (3.3)$$

Furthermore, the equilibrium is stable if natural selection works to restore the proportion a^* 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:

$$\begin{aligned} p(a^* + \varepsilon) &< p(1 - a^* - \varepsilon), \\ p(a^* - \varepsilon) &> p(1 - a^* + \varepsilon). \end{aligned} \quad (3.4)$$

(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 depend, of course, on the form of $g(x)$ and $l(x)$. Current knowledge, unfortunately, does not yield a detailed answer. To illustrate the possible outcomes of our model, we examine below specific forms for the functions $g(x)$ and $l(x)$, motivated by biological reality. We leave it to future research to establish the most appropriate functions in any given situation.

We have linked $l(x)$ to the ability of predators to capture 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

$$l(x) = 1 - \exp(-kNx), \quad (3.5)$$

where N is group size, and larger values of the positive parameter k lead to faster improvements in 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 $1/(1 + Nx)$ if a prey individual remains with a fraction x of individuals from a larger group of N . The probability of *not* being chosen as a target is therefore

$$g(x) = 1 - \frac{1}{1 + Nx}. \quad (3.6)$$

This expression can be used in equation (3.1) as the benefit of group living to an individual prey, when a proportion x of prey use the same strategy (because 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 constantly to target one prey in the midst of many (Pilcher 1986)—are insufficiently known and will not be considered here.

Employing equations (3.5) and (3.6), together with the equilibrium and stability conditions (3.3) and (3.4), we have analysed 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 (3.1) for $N = 50$ and $k = 0.25$. The figure shows that for small c the only stable population consists of left- and right-type prey in equal numbers. This corresponds to situations in which lateralization-mediated effects of group living on escape probability are small (see equation (3.1)), for instance in the case of solitary prey or of lateral biases that do not influence group cohesion. This equilibrium becomes unstable for larger c (larger group effects), giving

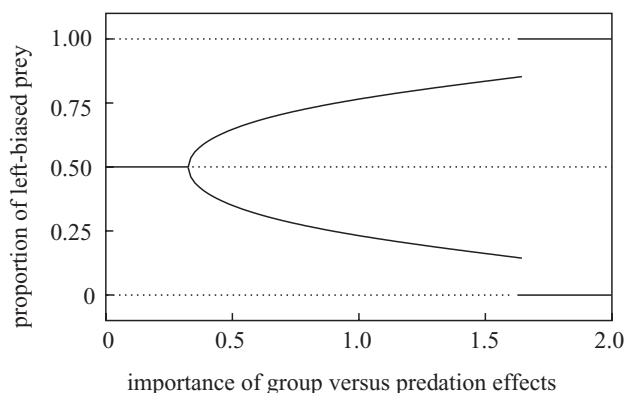


Figure 1. Equilibrium proportion of left-type prey in a group-living species as a function of the parameter c in equation (3.1) (see § 3 for details). Solid lines, stable equilibria; dotted lines, unstable equilibria. Parameters used are $N = 50$ and $k = 0.25$, see equations (3.5) and (3.6).

way to stable populations consisting of left- and right-type prey in unequal numbers. Because the model does not assume any intrinsic benefit of left or right lateralization, there are always two equivalent solutions, one with a majority of left-type prey and one with a majority of right-type prey. In this situation the majority of prey gain protection by keeping together, but pay a cost because predators are better at handling them. A minority of prey enjoy the same escape probability by trading off protection from the group against 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 large enough 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 turning preferences when viewing a simulated predator in 20 fish species, they found that six out of 10 solitary species (no group effects, or $c = 0$ 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 appear to be many possibly contrasting selective pressures on lateralization (Raymond *et al.* 1996), and this might result in the kind of frequency dependence discussed in § 3. 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 do not know whether this is exploited by conspecifics.

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

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