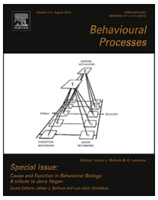
Behavioural Processes 117 (2015) 92–96

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Should neuroecologists separate Tinbergen's four questions?

Louis Lefebvre*

Department of Biology, McGill University, Montréal, Québec, Canada

ARTICLE INFO

Article history:
Available online 5 June 2014

Keywords:
Tinbergen
Modular cognition
Domain-general cognition
Evo devo
Brain evolution

ABSTRACT

Neuroecologists have been criticized for deriving mechanistic explanations about brains and cognition from functional results. Historically, it appears however that the first functional predictions about adaptive hippocampal specialization for spatial memory of stored food were preceded, not followed, by the mechanistic paradigm of massive modularity that was dominant in the 1990s. More attention is paid nowadays to domain general aspects of cognition and to neural connectivity. Attention is also now given to evo devo principles of brain organization, which suggest conserved routes to evolutionary changes in the brain driven by conserved developmental schedules. Knowledge gained in answering each of Tinbergen's four questions is thus useful in making predictions concerning the other ones.

This article is part of a Special Issue entitled: In Honor of Jerry Hogan.

'Neuroecology' is the term that has been given in recent years to the ecological study of brains and cognition (Sherry, 2006). While much of neuroscience is built around model organisms (e.g. rats and mice) that are studied in the lab and chosen mostly for their availability and the accumulated knowledge on them of molecular genetics and neuroanatomy, neuroecologists choose their organisms on the basis of evolutionary adaptations that make a particular behaviour and its presumed neural substrate stand out in a restricted number of taxa. Examples are the song repertoires and nuclei of oscines (Devoogd et al., 1993; Szekely et al., 1996), the spatial memory and hippocampus of food storers (Krebs et al., 1989; Sherry et al., 1989), polygynous rodents (Jacobs et al., 1990), brood parasites (Corfield et al., 2013; Sherry et al., 1993) and territorial hummingbirds (Ward et al., 2012), the sensitive periods and medial mesopallium of imprinted chicks (Horn, 2004), the pain response and sodium-channel pathways of scorpion-eating grasshopper mice (Rowe et al., 2013), the affiliative behaviours and social brain network of group living primates (Dunbar, 1998; Sallet et al., 2011) and the feeding innovations and pallial areas of opportunistic birds (Lefebvre et al., 1997). By definition, neuroecology thus has a closer relationship with functional and evolutionary questions than other branches of neuroscience, which are primarily concerned with mechanisms.

1. Mechanistic vs. functional questions

Historically, neuroecology is the application of behavioural ecology to the study of brains and cognition (Sherry, 2011). Because behavioural ecology is an intellectual descendent of ethology, ideas from the earlier approach are sometimes invoked when controversies flare up in the later one. The debate that opposed critics (Bolhuis, 2005; Bolhuis and Macphail, 2001, 2002; Brodin and Bolhuis, 2008) and proponents (Dwyer and Clayton, 2002; Hampton et al., 2002; MacDougall-Shackleton and Ball, 2002; Shettleworth, 2003) of neuroecology a few years ago is typical of this. One key issue in this debate was the extent to which neuroecologists erred in thinking about memory and brain mechanisms in functional terms. The most outspoken critics, Bolhuis and Macphail (2001) stated that: "functional questions and questions about mechanisms are fundamentally different, and (...) results from one domain cannot be used as explanations in the complementary domain. Thus, for example, a functional interpretation of why an animal performs a certain behaviour does not explain the cognitive and neural mechanisms governing that behaviour." (p. 426).

Jerry Hogan has played an important role in the genesis of this argument (Bolhuis, 2005). In a 1994 paper, Hogan insisted that structure and function are distinct categories that should not be confused. Hogan defended the logical autonomy of Tinbergen's (1963) four questions, the idea that the mechanisms, development, evolution and function of behaviour are parallel questions that are not reducible to each other. The distinction was particularly important in the dialogue between ethologists and psychologists, the latter often focusing on mechanistic questions to the exclusion of functional ones. I remember asking a psychologist studying rat

---

* Correspondence to: Department of Biology, McGill University, 1205, Avenue Docteur Penfield, Montréal, Québec H3A 1B1, Canada. Tel.: +1 514 398 6457.
E-mail address: louis.lefebvre@mcgill.ca

http://dx.doi.org/10.1016/j.beproc.2014.05.006
0376-6357/© 2014 Elsevier B.V. All rights reserved.

copulation *why* males in this species had repeated ejaculations and short intromissions, in contrast to many other mammals, and she answered 'that's the way the spinal generator works' (Truitt and Coolen, 2002), instead of thinking in terms of sperm competition (Dewsbury, 1981).

Behavioural ecology inherited the proximal/ultimate distinction from ethology, providing new functional predictions for questions that had previously been looked at in proximal terms. A mechanistic focus is not very successful at dealing with an animal that is hungry, yet leaves an area where it can still find food and goes to feed elsewhere, but a functional approach based on optimality and diminishing returns is. The question of *how* that animal assesses information and arrives at a behaviour that optimizes net rate of energy intake was not a priority for early behavioural ecologists. They relied instead on the notion of 'gambit' to focus on phenotypic outcomes rather than the genes (Grafen, 1984) or learning rules (Fawcett et al., 2013) leading to them, assuming that neither genetic architecture or psychological mechanisms would constrain which phenotypes can evolve.

It was the serendipitous discovery of hippocampal enlargement in food storing chickadees (see Sherry, 2011 for an historical account) that presented the strongest challenge to the gambit strategy that behavioural ecologists had used up to then. If selection operating on efficient spatial memory for stored food in overwintering birds (Krebs et al., 1989; Sherry et al., 1989) was accompanied by enlargement of the neural substrate for that cognitive ability, then mechanisms could not be ignored any more. Sherry and Vaccarino (1989) had relied on the neuropsychological literature (e.g. O'Keefe and Nadel, 1978) to plan the lesion study of the chickadee hippocampus that led to their discovery of its large size. That literature was based on lesion studies and single cell recordings and was focused on proximal, not ultimate questions on behaviour.

Following Sherry's discovery, behavioural ecologists proposed that the enlarged hippocampal complex of food-storing species might be an adaptive specialization associated with the use of a specialized memory (Krebs et al., 1989). As neuroecology was gaining in importance, the dominant view in psychology was that brains and cognition were modular. This view was useful with cognitive abilities like spatial memory and learned song. Early on, Harvey and Krebs (1990) had suggested that correlations between ecological variables and whole brain size (which had been studied with mixed success by Harvey and co-authors, e.g. Bennett and Harvey, 1985; Clutton-Brock and Harvey, 1980; Mace et al., 1981) might be difficult to interpret because the brain has many parts that serve different functions. They proposed instead that it might be more fruitful to focus on well-defined brain regions with known functions. This view is still defended by some contemporary behavioural ecologists, e.g. Healy and Rowe (2007). Contrary to what Bolhuis and Macphail (2001) have implied, the history of neuroecology does not suggest that researchers erred in explaining mechanisms based on functional ideas, but the *reverse*: neuroecologists used the mechanistic modular views of the time to derive their functional predictions.

Modularity and domain-specificity are not as dominant in neuroscience today as they were in neuroecology's infancy. For example, social and environmental intelligence were often seen as distinct domains (Seyfarth and Cheney, 2002), but evidence is mounting that they covary. In models, ecological drivers of behaviour (e.g. abundance and predictability of resources in space and time) push social and non-social aspects of intelligence in the same direction (Overington et al., 2008). In primates, social (social learning, tactical deception) and non-social (tool use, extractive foraging) measures of cognition show positive correlations across species (Reader and Laland, 2002) and load on the same general intelligence factor (Reader et al., 2011), while different cognitive tests conducted in captivity also show the positive intercorrelations one would expect from domain-general intelligence (Deaner et al., 2006). van Schaik et al. (2012) have recently proposed that the social brain hypothesis be dropped in favour of a more domain-general view that would include behavioural flexibility and cultural learning.

Tool use also seems to lack many of the characteristics of a domain-specific specialization. Teschke et al. (2011) showed that the woodpecker finch *Cactospiza pallida*, a species that uses tools in the wild and is pre-programmed to do so without prior social or individual learning (Tebbich et al., 2001) is no better than the non-tool using sister species *Camarhynchus parvulus* (small tree finch) at foraging tasks that involve physical cognition. Bird and Emery (2009) have also shown that rooks (*Corvus frugilegus*), which do not use tools in the wild, are capable of spontaneously using and modifying several types of tools in captivity. Innovation, pallial structure size and tool and proto-tool use also covary across clades in birds (Lefebvre et al., 2002) and primates (Reader et al., 2011; Reader and Laland, 2002).

The recent move away from domain-specificity has been encouraged by techniques that allow the mapping of brain connections, as opposed to techniques (e.g. lesions, fMRI) that identify discrete, localized brain areas involved in particular behaviours. The new emphasis on brain networks rather than brain modules is illustrated by the NGRAM citation frequency function presented in Fig. 1. NGRAM is a word-frequency count programme that can reveal cultural trends in the relative use of terms over time (http://www.culturomics.org). The terms '*modular intelligence*' and '*brain modularity*' (Fig. 1A and B) have been declining in frequency since the early 2000s ('*modular brain*', not illustrated, shows the same trend), while the term '*brain connectivity*' has been increasing steadily since the 1990s (Fig. 1C).

What these numbers suggest is not that neuroecologists are right or wrong in linking proximal and ultimate questions, whether they use functional principles to think about mechanisms or data on mechanisms to make functional predictions. It is that scientific paradigms change over time and research questions should be based on heuristic value, not logical a priori. The new field of 'connectomics' (too recent to yield an NGRAM plot) now emphasizes networks and hubs (Bullmore and Sporns, 2012) as well as modules, but we cannot predict what new techniques will change our way of thinking about the brain in the future. Empirically, whole brain size and measures of domain-general cognition *do* vary between clades, whatever the relative roles of distributed neuronal hubs, networks, dedicated brain areas, general intelligence or specialized cognitive modules. If whole brain size (Sol et al., 2005, 2007, 2008) and domain-general problem-solving (Cauchard et al., 2013; Cole et al., 2012) are associated with differences in survival and reproductive success, then selection might be operating on them, just as it operates on whole body size despite the fact that the different parts of the body do different things. If '*evolution of body size*' is a legitimate research area (10,878 articles on a *Web of Science* topic search), it is difficult to see why '*evolution of brain size*' should not be, whatever the dosage of distributed networks, hubs and localized centres a particular period in neuroscience favours.

2. 'Evo' and 'devo' questions

Another interesting trend revealed by NGRAM analysis is the increasing popularity of the term '*evo devo*' (Fig. 1D). In itself, the term seems to be a violation of the autonomy of Tinbergen's questions, as evolution and development are distinct categories in his scheme. As he did for the structural vs. functional dichotomy, Jerry Hogan has argued that developmental questions cannot be reduced to mechanistic ones. Hogan and Bolhuis (2005) state that 'even a complete understanding of molecular mechanisms will not be sufficient for a complete understanding of behavioural development'