



# The local enhancement conundrum: In search of the adaptive value of a social learning mechanism



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## ABSTRACT

Social learning mechanisms are widely thought to vary in their degree of complexity as well as in their prevalence in the natural world. While learning the properties of a stimulus that generalize to similar stimuli at other locations (stimulus enhancement) *prima facie* appears more useful to an animal than learning about a specific stimulus at a specific location (local enhancement), empirical evidence suggests that the latter is much more widespread in nature. Simulating populations engaged in a producer–scrounger game, we sought to deploy mathematical models to identify the adaptive benefits of reliance on local enhancement and/or stimulus enhancement, and the alternative conditions favoring their evolution. Surprisingly, we found that while stimulus enhancement readily evolves, local enhancement is advantageous only under highly restricted conditions: when generalization of information was made unreliable or when error in social learning was high. Our results generate a conundrum over how seemingly conflicting empirical and theoretical findings can be reconciled. Perhaps the prevalence of local enhancement in nature is due to stimulus enhancement costs independent of the learning task itself (e.g. predation risk), perhaps natural habitats are often characterized by unreliable yet highly rewarding payoffs, or perhaps local enhancement occurs less frequently, and stimulus enhancement more frequently, than widely believed.

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## 1. Introduction

Social learning and the processes underlying it have long been the center of debates among those studying human and animal behavior and cognition (Zentall and Galef, 1988; Heyes and Galef, 1996; Laland and Galef, 2009; Hoppitt and Laland, 2013). Its great attraction stems from the roles it plays in child development, animal cognition, the evolution of human culture, and from the question of animal culture (Rendell et al., 2011; Hoppitt and Laland, 2013). Key questions associated with these debates include: What are the similarities and differences between human culture and animal social learning and tradition? Do humans deploy more advanced social learning mechanisms compared to other animals? Are these mechanisms the key to understanding the immense success of human culture? And why did some social learning mechanisms evolve in some species, but not in others?

In studying the evolution of social learning, as in studying the evolution of any biological phenomenon, it is useful to identify its levels of complexity. Over the years, the field of social learning has accumulated a long list of underlying processes, ranging from what are thought to be the relatively simple process of local enhancement to what are regarded as more advanced forms of

social learning, such as production imitation (Zentall and Galef, 1988; Whiten and Ham, 1992; Heyes, 1994; Hoppitt and Laland, 2008). While the precise neural underpinnings of social learning processes are not well understood, it would seem highly plausible that some of these mechanisms require greater cognitive capacities than others; indeed, this assumption is widespread in the animal social learning literature. But even among the seemingly simpler mechanisms, empirical studies provide extensive evidence for the existence of some processes, but very little evidence of the existence of others. This is the case for local enhancement and stimulus enhancement, where there are currently far more clear-cut reports of the former than the latter (Hoppitt and Laland, 2008).

Local enhancement occurs “when after, or during, a demonstrator’s presence, or interaction with objects, at a specific location, an observer is more likely to visit or interact with objects in that location” (Hoppitt and Laland, 2008 after Thorpe, 1963). Stimulus enhancement occurs “when observation of a demonstrator (or its products) exposes the observer to a single stimulus at time  $t_1$ , and single stimulus exposure effects a change observed in the observer detected, in any behavior, in time  $t_2$ ” (Heyes, 1994 after Spence, 1937). It has been suggested that local enhancement is a special case of stimulus enhancement (Galef, 1988); however this is highly debatable (Hoppitt and Laland, 2008, 2013) and recent evidence suggest that these are two distinct processes (Webster and Laland, 2012).

Intuitively, stimulus enhancement, or the ability to generalize knowledge of a stimulus at a specific location to similar stimuli

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elsewhere, would appear more beneficial to the learner than acquiring knowledge solely about a specific location alone. However, a recent review of the literature (Hoppitt and Laland, 2008) finds that very few studies incontrovertibly demonstrate stimulus enhancement in animals, whilst in contrast local enhancement appears much more common, and would seem to command far more supportive evidence. Part of the reason for the low occurrence of stimulus enhancement in the literature stems from the difficulty of distinguishing stimulus enhancement from other social learning mechanisms, such as observational conditioning or observational response–reinforcer learning (see Hoppitt and Laland, 2008 for a comprehensive review).

This difficulty in distinguishing between social learning mechanisms, together with the observation that multiple processes may simultaneously be deployed by animals under natural conditions (Hoppitt et al., 2012), raises concerns over the usefulness of current definitions. While, as stated above, it is widely believed that some mechanisms are more cognitively advanced than others, current terms are overlapping, not mutually exclusive, and frequently difficult to distinguish from each other (Hoppitt and Laland, 2008). In light of these difficulties, Hoppitt and Laland (2013) suggest a pragmatic framework for the identification and conceptualization of social learning mechanisms. In this framework, an event of social transmission can be classified by four readily observable criteria: context-specificity, sensitivity to the outcomes of the demonstrator's actions, action-specificity, and novelty of the action or action-sequence. Using these criteria, all current widely discussed social learning processes can be distinguished. The practicality of this method of classification becomes apparent when trying to model the social learning process and break it into its building blocks, as we show here.

In this paper, we set out to explore the ecological conditions that favor stimulus and local enhancement through the use of evolutionary models. To do this, we simulate social learning in the context of a simple social foraging scenario: the producer–scrounger game (Barnard and Sibly, 1981; Giraldeau and Caraco, 2000; Giraldeau and Dubois, 2008). In this game, individuals at any particular point in time can be either producers, who search for resources independently, or scroungers, who follow others in the group and parasitize on their findings. Scrounging may require less time and effort compared to producing, but its success critically depends on the presence of producers in the group; therefore, the two strategies are negatively frequency dependent, resulting in a mixed evolutionarily stable strategy (Barnard and Sibly, 1981).

This game is a useful framework for studying both individual and social learning: when producing, an individual may acquire information about its environment independently while when scrounging, it may acquire information through others (Giraldeau and Caraco, 2000; Arbilly et al., 2011). We assume that an individual's fitness is a positive function of the payoff it has accumulated throughout its lifetime—while producing or scrounging or both. When producing, an individual uses previously learned information to decide which patch to visit, and therefore its producing success relies heavily on its learning strategy: whether it learns individually when producing, whether it learns socially when scrounging, and which learning mechanism (local learning or stimulus learning) is used in either case.

In accordance with Hoppitt and Laland's (2013) framework for identifying mechanisms of social learning, we distinguish between local and stimulus enhancement by the specificity of the context: is the forager learning about the specific location of a patch, or is it learning about a stimulus, such that it can generalize the knowledge it acquires to similar stimuli at other locations? Strictly, this criterion alone is insufficient to exclude other social learning mechanisms. Nonetheless we believe that this distinction is a practical first step in exploring the evolution of these social learning

mechanisms. Hence what we characterize as conditions that favor stimulus enhancement may more accurately be described as conditions that favor stimulus enhancement or other social learning mechanisms that are stimulus-specific (e.g. observational conditioning). We address this issue further in the discussion.

## 2. The model

### 2.1. The population

We simulated a population of  $n = 100$  social foragers. For mathematical convenience we assume haploid genetics. We specify that the behavior and learning abilities of each individual are influenced by three genes: (1)  $F$ , a social foraging gene, which determines its carrier's probability of using the producer, and (complementarily) the scrounger strategy (hence  $1 - F$  is the probability of using the scrounger strategy). We assume 11 possible alleles in this gene ( $F_0, F_1, \dots, F_{10}$ ), ranging from pure scrounging ( $F_0$ ), through mixed strategies of producing and scrounging ( $F_1 - F_9$  where  $F_1$  codes for 10% probability of producing and 90% probability of scrounging,  $F_2$  for 20% producing and 80% scrounging, etc.), to pure producing ( $F_{10}$ ). (2)  $I$ , an individual learning gene, which determines the learning mechanism used when a forager plays the producer strategy. This gene has three possible alleles: non-learning ( $I_0$ ), individual local learning ( $I_1$ ), or individual stimulus learning ( $I_2$ ). (3)  $S$ , a social learning gene, which determines the learning mechanism deployed when a forager plays the scrounger strategy. This gene also has three possible alleles: non-learning ( $S_0$ ), learning by local enhancement ( $S_1$ ) or learning by stimulus enhancement ( $S_2$ ).

In all simulations, in the first generation the population carried each  $F$  gene allele with equal probability, but the  $I_0$  allele and the  $S_0$  allele were fixed (i.e. agents were complete non-learners). Learning alleles  $I_1, I_2, S_1$  and  $S_2$  were introduced in subsequent generations via random mutation.

A generation was composed of  $T$  time steps; at each step agents were allotted a social foraging strategy (probabilistically, according to their  $F$  genotype). After  $T$  steps, foragers were ranked according to the payoff they had accumulated throughout their lives, and the top 50% gave rise to the next generation (truncation selection). We assumed that each surviving agent produced two genetically identical offspring. These offspring were subjected to random mutation occurring in all three genes at a rate  $\mu = 1/n$  (i.e. 0.01) per generation. Once the new generation was produced, the parental generation died, maintaining the population at a constant size.

### 2.2. The environment

The environment was composed of  $H = 100$  food patches, each belonging to one of three types:  $E_1, E_2$  and  $E_3$ , occurring at equal probability (0.33). The locations of patches belonging to each type were shuffled for each new generation, but remained constant across a generation's lifetime. Patch types differed in the value of the food items they provided, the probability of obtaining these items, and their overall expected payoff. To simulate a non-trivial, yet natural, learning task, we assumed a negative relationship between the value of the food item and the probability to obtain it. That is, the most valuable food items were assumed to be the least likely to be found, but on average the patches that contained valuable food items were the most profitable. Recurring failures to find food in these most profitable patches serve a number of purposes: they necessitate repeated sampling for proper evaluation of the patches, and they provide an inherent disadvantage to the pure producing strategy (see Arbilly et al., 2010 for analysis); this, consequently, gives social learning an advantage over individual learning

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