

example [17,18]? What information is being represented in the strengthened functional connectivity patterns that follow learning episodes? Does the enhanced functional connectivity represent off-line 'replaying' of the learning experience as shown in the rat studies [12,13]? Does off-line processing of recently acquired memories represent an early process of consolidation (see also [19])? How do learning related resting state functional connectivity changes relate to activity patterns recorded during subsequent periods of sleep (for example [20])? The authors' approach may prove promising in revealing novel connections between off-line processing of recently acquired memories and subsequent resting state activity.

References

1. Raichle, M.E., and Mintun, M.A. (2006). Brain work and brain imaging. *Annu. Rev. Neurosci.* 29, 449–476.
2. Lampl, I., Reichova, I., and Ferster, D. (1999). Synchronous membrane potential fluctuations in neurons of the cat visual cortex. *Neuron* 22, 361–374.
3. He, B.J., Snyder, A.Z., Zempel, J.M., Smyth, M.D., and Raichle, M.E. (2008). Electrophysiological correlates of the brain's intrinsic large-scale functional architecture. *Proc. Natl. Acad. Sci. USA* 105, 16039–16044.
4. Fox, M.D., and Raichle, M.E. (2007). Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nat. Rev. Neurosci.* 8, 700–711.
5. Buckner, R.L., and Vincent, J.L. (2007). Unrest at rest: default activity and spontaneous network correlations. *NeuroImage* 37, 1091–1096.
6. Miall, R.C., and Robertson, E.M. (2006). Functional imaging: is the resting brain resting? *Curr. Biol.* 16, R998–R1000.
7. Albert, N.B., Robertson, E.M., and Miall, R.C. (2009). The resting human brain and motor learning. *Curr. Biol.* 19, 1023–1027.
8. Martin, T.A., Keating, J.G., Goodkin, H.P., Bastian, A.J., and Thach, W.T. (1996). Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain* 119, 1183–1198.
9. Lee, J.H., and van Donkelaar, P. (2006). The human dorsal premotor cortex generates online error corrections during sensorimotor adaptation. *J. Neurosci.* 26, 3330–3334.
10. Ghilardi, M., Ghez, C., Dhwana, V., Moeller, J., Mentis, M., Nakamura, T., Antonini, A., and Eidelberg, D. (2000). Patterns of regional brain activation associated with different forms of motor learning. *Brain Res.* 871, 127–145.
11. Smith, C. (1996). Sleep states, memory processes and synaptic plasticity. *Behav. Brain Res.* 78, 49–56.
12. Foster, D.J., and Wilson, M.A. (2006). Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature* 440, 680–683.
13. Diba, K., and Buzsáki, G. (2007). Forward and reverse hippocampal place-cell sequences during ripples. *Nat. Neurosci.* 10, 1241–1242.
14. Louie, K., and Wilson, M.A. (2001). Temporally structured replay of awake hippocampal ensemble activity during rapid eye movement sleep. *Neuron* 29, 145–156.
15. Lee, A.K., and Wilson, M.A. (2002). Memory of sequential experience in the hippocampus during slow wave sleep. *Neuron* 36, 1183–1194.
16. Braun, A.R., Balkin, T.J., Wesenten, N.J., Carson, R.E., Varga, M., Baldwin, P., Selbie, S., Belenky, G., and Herscovitch, P. (1997). Regional cerebral blood flow throughout the sleep-wake cycle. An H2(15)O PET study. *Brain* 120, 1173–1197.
17. Peigneux, P., Orban, P., Baeteau, E., Degueldre, C., Luxen, A., Laureys, S., and Maquet, P. (2006). Offline persistence of memory-related cerebral activity during active wakefulness. *PLoS Biol.* 4, e100.
18. Fox, M.D., Snyder, A.Z., Zacks, J.M., and Raichle, M.E. (2006). Coherent spontaneous activity accounts for trial-to-trial variability in human evoked brain responses. *Nat. Neurosci.* 9, 23–25.
19. Korman, M., Doyon, J., Doljansky, J., Carrier, J., Dagan, Y., and Karni, A. (2007). Daytime sleep condenses the time course of motor memory consolidation. *Nat. Neurosci.* 10, 1206–1213.
20. Huber, R., Ghilardi, M.F., Massimini, M., and Tononi, G. (2004). Local sleep and learning. *Nature* 430, 78–81.

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Cognitive Ecology: Environmental Dependence of the Fitness Costs of Learning

A recent study has found that butterflies maintain behavioural plasticity useful to them in rare environments by reducing associated costs in common environments. Butterflies use innate sensory biases to locate common green hosts, but learn to modify these preferences to find rare, red host-plants.

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Learning allows animals to modify their behaviour in response to changes in their environment. If the environment remains relatively constant, however, it could be adaptive to rely on inflexible innate behavioural patterns to reduce (or eliminate) costs associated with learning [1]. Yet species living in relatively consistent environments can often adjust their phenotype successfully in alternative environments, suggesting that the costs of maintaining phenotypic

plasticity could be low [2,3]. In a recent study Snell-Rood and Papaj [4] experimentally tested these theoretical predictions for the maintenance of phenotypic plasticity under consistent environmental conditions.

In theory, phenotypic plasticity should be adaptive if an organism regularly encounters at least two different environmental conditions with similar frequencies. As the chances of an organism encountering an alternative environment decrease, so too do the benefits of retaining plasticity. But plasticity could be

maintained if the operating costs in the common environment are reduced, such that costs are only paid when the organism encounters alternative (rare) conditions. Operating costs in the common environment could be reduced by using a fixed, innate, behavioural pattern adapted to these specific conditions. If the organism encounters the rare environment, the default, innate, behavioural phenotype can be modified by learning. Hence, the organism only pays the operating costs of plasticity when (or if) it encounters the rare environment (Figure 1).

Snell-Rood and Papaj [4] addressed these predictions empirically using the flexibility in host-plant choice of cabbage white butterflies (*Pieris rapae*) as their behavioural phenotype. They assessed the costs of maintaining phenotypic plasticity in this behavioural trait by controlled manipulation of the environment in

which the butterflies could operate [5]. Female butterflies were allowed to search for oviposition sites in environments containing either green (common) or red (rare) cabbage (*Brassica oleracea*) host-plants (Figure 2). Host-plants were presented in arrays containing plants on which this species does not lay eggs (non-hosts). The butterflies showed very different patterns of behaviour in green or red host environments. Females were considerably more efficient at finding green rather than red host-plants at the start of the experiment. Although host-finding efficiency improved in both environments with increasing experience, consistent learning of red-hosts led to very similar levels of host-finding efficiency in red- and green-host environments by the end of the experiment. This differential effect of learning in the two environments was also highlighted by the colour of non-hosts chosen. In the green-host environment, almost all non-hosts chosen were green. In contrast, butterflies learning to locate red-hosts showed a marked drop in the number of green non-hosts chosen as they became more experienced.

These results agree with previous studies indicating this species has a strong innate preference for green host-plants, but that it can learn alternative colours in an oviposition context [6]. In this study, individual butterflies in the red-host environment whose initial colour choice was less green-biased were more successful in terms of overall host-finding efficiency. However, no such association was found for individual butterflies tested in the green-host environment. Family level differences in both host-finding efficiency and innate colour choice suggest this variation is at least partly determined by genetic variation. Interestingly, there were no family-level correlations in behaviour across the two host-environments. Therefore, butterflies from the family with the greatest host-finding efficiency in the green-host environment were not the best at finding hosts in the red-host environment, indicating there is no ‘supergenotype’ [3] which performs best in both

environments. Family differences were more pronounced in the red-host environment, and variation in both host-finding efficiency and colour choice became increasingly variable among families as individuals tested gained more experience in this environment.

So behavioural plasticity varies among families, especially in the red-host environment, but does this affect fitness? The plasticity of a family, measured as the absolute difference in total colour choice between host environments, was strongly positively correlated to the number of hosts found in the red-host, but not green-host, environment. Assuming the number of host-plants located in a given environment is a good proxy measure of fitness, this suggests greater plasticity enhances fitness in a context dependent way (in only one host environment). The absence of a correlation in a full-sibling family’s host-finding efficiency in either environment indicates that this potential fitness benefit in the rare (red-host) environment doesn’t compromise fitness in the common (green-host) environment.

Snell-Rood and Papaj’s [4] empirical results are consistent with theoretical predictions regarding the maintenance of plasticity by reducing (or eliminating) operating costs paid in the most commonly encountered environmental conditions. Here innate green preferences appear to confer an advantage in terms of host-finding efficiency in the common (compared to the rare) environment. Families able to vary colour choice across host environments, relative to less plastic families, appear to suffer no costs in the green-host environment but have enhanced fitness in the red-host environment.

Despite the theoretical focus on how phenotypic plasticity is maintained in a variety of environmental conditions [2,7], experimental studies of sensory and cognitive traits within a phenotypic plasticity framework remain surprisingly rare. Further empirical work in this area should be encouraged, as we still know comparatively little about how, and

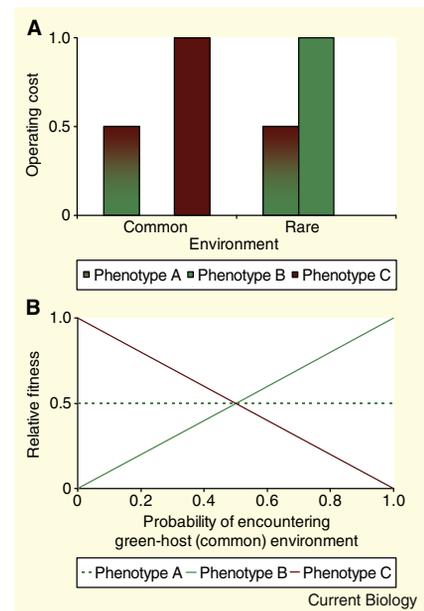


Figure 1. Three theoretical mechanisms for maintaining phenotypic plasticity in common versus rare environments.

(A) Phenotype A specifies a default intermediate phenotype which pays equal operating costs to develop a phenotype appropriate to either environment. Phenotype B specifies a default phenotype that is ideally suited to the common (green-host) environment and bears an operating cost of developing the phenotype only in the rare environment. Phenotype C specifies a default phenotype that is ideally suited to the rare environment and bears an operating cost of developing the phenotype in the common environment. (B) The relative fitness of each of the three theoretical phenotypes varies with the probability of encountering the green-host environment. Where this probability is greater than 0.5 — where the green-host is the common environment — phenotype B has the highest relative fitness of the three phenotypes.

indeed if, behavioural plasticity is adapted to real ecological conditions [8,9]. Learning is likely to be one of the fastest ways to change phenotype in response to shifting environmental conditions. Whilst learning clearly plays a critical role in allowing butterflies to change their host-plant choice for oviposition, it could also be an important agent of phenotypic plasticity in other behavioural contexts. Foraging animals often face a choice between multiple food sources that vary in their relative profitability — this is certainly true of nectar feeders like butterflies. Variation in both innate colour preference [10] and learning performance [9] can have strong adaptive consequences for



Figure 2. Female cabbage white butterfly (*Pieris rapae*) laying eggs on a green cabbage (*Brassica oleracea*) leaf.

Females of this species show an innate preference for green-host plants and have to modify this behaviour in environments where only red cabbage host plants are available. Photograph reproduced with permission from Emilie Snell-Rood.

nectar-foraging bumblebees in particular environmental conditions. Bumblebees seem to use innate colour preferences to find rewarding flowers in the environment they most commonly encounter [10], but can quickly learn to modify their choices as the most profitable flower colours change [9]. The striking similarity between these findings, and those for *P. rapae* [4] in the context of oviposition, suggest future studies could fruitfully investigate the adaptive value of phenotypic plasticity in multiple behavioural contexts [11] — especially tasks for which the rate at which the environment changes could be very different. For example, butterflies may only have to learn a new host-plant once during their lifetime, whereas the flower species providing the best nectar rewards might change many times per day [12].

The types of costs paid are critical to how, and under what circumstances, phenotypic plasticity is maintained [7]. Over the last few years empirical studies have begun to uncover the potential fitness costs associated with modifying behavioural phenotypes [13,14]. Artificial selection for enhanced learning performance in *Drosophila* appears to impose

both global costs in terms of larval competitive ability (irrespective of whether learning ability is used) [13], and also operating costs (reduced fecundity) if flies are repeatedly required to use their learning ability [14]. Butterflies also appear to incur both global ('upfront') and induced ('pay-as-you-go') costs when learning. They pay an operating (information acquisition [7]) cost in the red-host environment in terms of time spent modifying their innate preference for green-hosts [4]. Investment in metabolically expensive neural tissue [15] also appears to represent a global and induced cost of learning. Newly emerged adult butterflies with large mushroom body calyces, compared to their whole brain size, are more likely to improve their ability to find red-hosts through learning [16]. This correlation is consistent with particular individuals paying higher (global) costs to increase the relative size of specific brain regions before it is clear whether the environmental requirements demand enhanced learning ability.

Butterfly brains also grow larger with experience and age, with enlargement of the mushroom body calyx being correlated with particular host experience [16]. This could indicate butterflies are paying an induced cost — investing in additional neural tissue as they learn about their environment. The fact that honeybee mushroom bodies also grow larger in response to increasing foraging experience, irrespective of age [17,18], and birds can show selective enlargement of the hippocampus following a food storing task [19] support such ideas of experience-dependent neural investment as an induced cost of learning. If neural tissue is so expensive, however, a question for the future is why such large changes in brain size seem to occur in response to accumulation of experience. From a theoretical standpoint the fundamental requirements to record experience through learning are simple — a sense organ and a simple neural circuit with a switch (which can be reinforced). In light of this, we should consider why such large-scale changes in neural architecture are observed over comparatively short periods of time.

References

1. Johnston, T.D. (1982). Selective costs and benefits in the evolution of learning. *Adv. Stud. Behav.* 12, 65–106.
2. Pigliucci, M. (2005). Evolution of phenotypic plasticity: where are we going now? *Trends Ecol. Evol.* 20, 481–486.
3. Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J., and Pigliucci, M. (2006). Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecol. Lett.* 9, 981–993.
4. Snell-Rood, E.C., and Papaj, D.R. (2009). Patterns of phenotypic plasticity in common and rare environments: a study of host use and color learning in the cabbage white butterfly *Pieris rapae*. *Am. Nat.* 173, 615–631.
5. Raine, N.E., Ings, T.C., Dornhaus, A., Saleh, N., and Chittka, L. (2006). Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behavior. *Adv. Stud. Behav.* 36, 305–354.
6. Hern, A., Edwards-Jones, G., and McKinlay, R.G. (1996). A review of the pre-oviposition behaviour of the small cabbage white butterfly *Pieris rapae* (Lepidoptera: Pieridae). *Ann. Appl. Biol.* 128, 349–371.
7. DeWitt, T.J., Sih, A., and Wilson, D.S. (1998). Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* 13, 77–81.
8. Dukas, R. (2004). Evolutionary ecology of animal cognition. *Annu. Rev. Ecol. Syst.* 35, 347–374.
9. Raine, N.E., and Chittka, L. (2008). The correlation of learning speed and natural foraging success in bumble-bees. *Proc. Roy. Soc. B.* 275, 803–808.
10. Raine, N.E., and Chittka, L. (2007). The adaptive significance of sensory bias in a foraging context: floral colour preferences in the bumblebee *Bombus terrestris*. *PLoS ONE* 2, e556. DOI: 10.1371/journal.pone.0000556.
11. Weiss, M.R., and Papaj, D.R. (2003). Colour learning in two behavioural contexts: how much can a butterfly keep in mind? *Anim. Behav.* 65, 425–434.
12. Willmer, P.G., and Stone, G.N. (2004). Behavioral, ecological, and physiological determinants of the activity patterns of bees. *Adv. Stud. Behav.* 34, 347–466.
13. Mery, F., and Kawecki, T.J. (2003). A fitness cost of learning ability in *Drosophila melanogaster*. *Proc. Roy. Soc. B.* 270, 2465–2469.
14. Mery, F., and Kawecki, T.J. (2004). An operating cost of learning in *Drosophila melanogaster*. *Anim. Behav.* 68, 589–598.
15. Laughlin, S.B., van Steveninck, R.R.D., and Anderson, J.C. (1998). The metabolic cost of neural information. *Nat. Neurosci.* 1, 36–41.
16. Snell-Rood, E.C., Papaj, D.R., and Gronenberg, W. (2009). Brain size: a global or induced cost of learning? *Brain Behav. Evol.* 73, 111–128.
17. Withers, G.S., Fahrback, S.E., and Robinson, G.E. (1993). Selective neuroanatomical plasticity and division of labour in the honeybee. *Nature* 364, 238–240.
18. Sigg, D., Thompson, C.M., and Mercer, A.R. (1997). Activity-dependent changes to the brain and behavior of the honey bee, *Apis mellifera* (L.). *J. Neurosci.* 17, 7148–7156.
19. Clayton, N.S., and Krebs, J.R. (1994). Hippocampal growth and attrition in birds affected by experience. *Proc. Natl. Acad. Sci. USA* 91, 7410–7414.

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