# The origin of reaction norms

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### What are reaction norms?

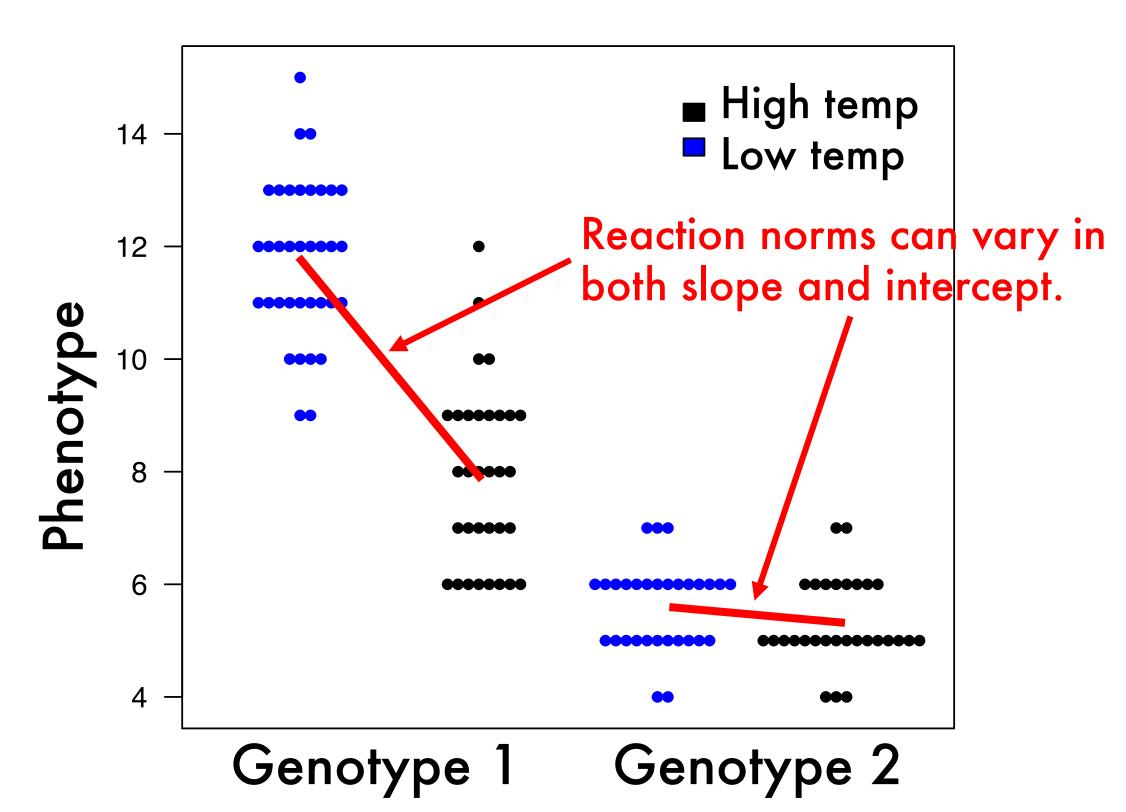


Fig. 1. Phenotypic response of two genotypes to temperature variation. Means are joined by a red line indicating the average reaction norm for each genotype.

Reaction norms describe the potential range of phenotypic variation of a single genotype under different environmental conditions (Fig. 1).<sup>1</sup>

# Why should we care?

The reaction norm is:

- Foundational in genetics.<sup>2</sup>
- Employed widely after popularization by Lewontin<sup>3</sup> and others in 1970s (**Fig. 2**).

Failing to account for reaction norms:

- confounds association analyses,
- biases heritability estimates.<sup>4</sup>

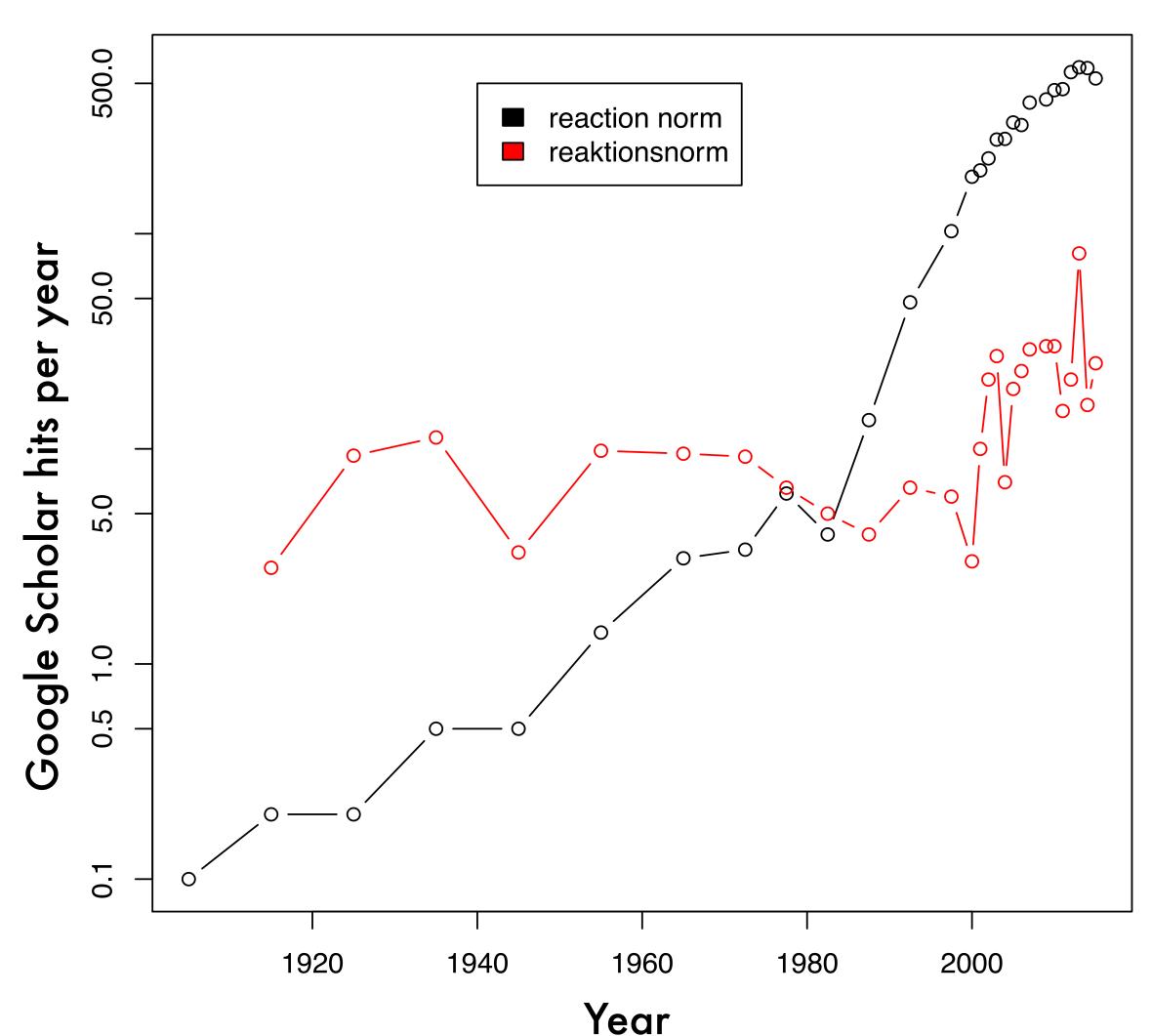


Fig. 2. Hits for two searches over time. By decade 1905-1965, by 5 years 1965-2000, and annually after 2000.

"... the author has followed the custom of German philosophers and has expressed his views in a complex syntax with many dependent clauses the unravelling of which in many cases is like making out a puzzle." 5

#### Abstract

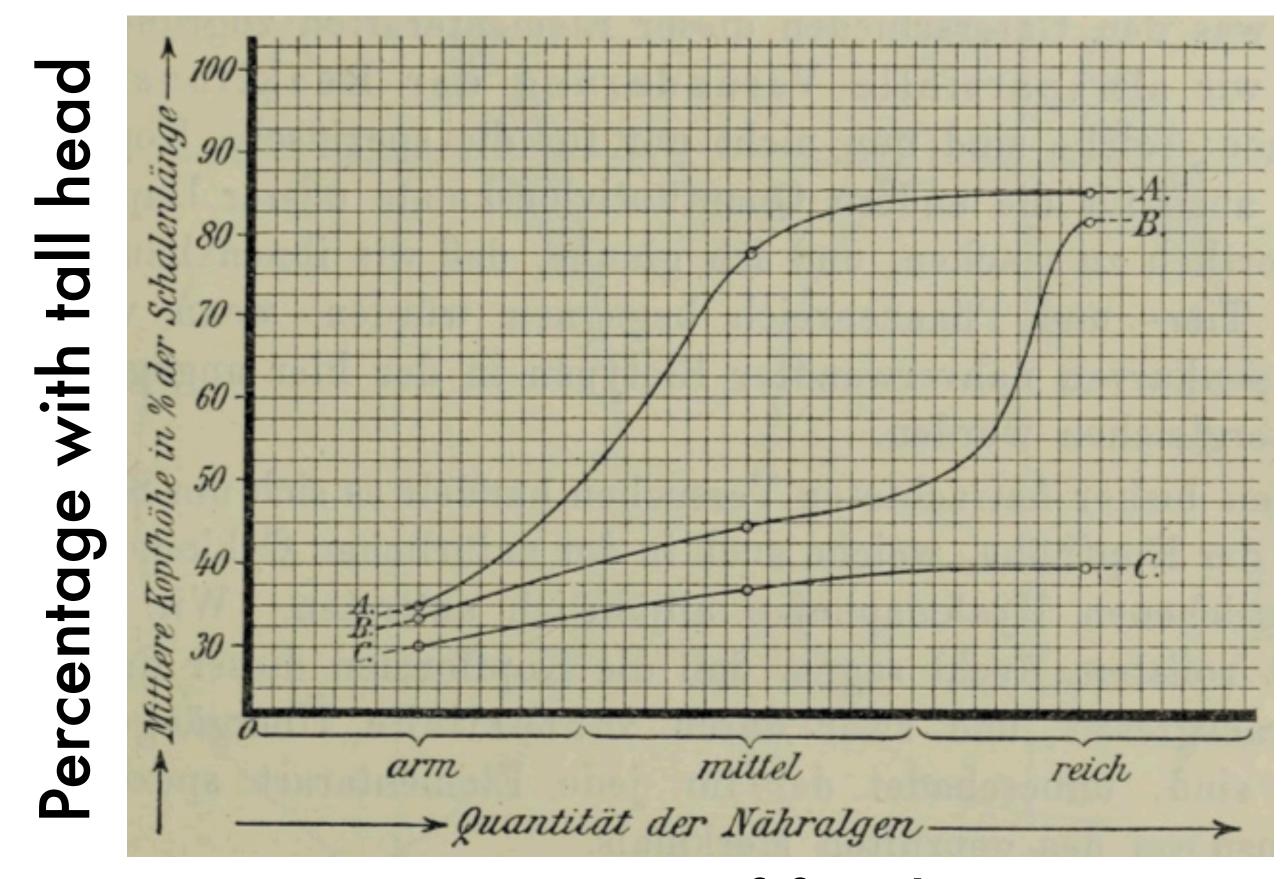
Reaction norms are a foundational concept in genetics. Reaktionsnormen (the original term) were first described by Richard Woltereck in a 1909 paper; until recently the German text of this paper was not digitally available.

I provide a draft translation of this paper into English (<a href="https://github.com/maximilianpress/reaktionsnorm">https://github.com/maximilianpress/reaktionsnorm</a>). I briefly review the chief findings, and note the anticipation of some ideas such as genetic assimilation in the paper.

Secondary literature published in English citing Woltereck's primary text includes some incorrect statements about Woltereck's ideas, possibly due to the lack of an available English text.

# Insights from Woltereck<sup>2</sup>

#### 1. Reaction norms and GxE



#### Amount of food

Fig 3. A, B, C are three *Daphnia* reaction norms demonstrating the environmental dependence of a trait.

#### 2. Inheritance of acquired characters

Independently discovered genetic assimilation? (44 years before Waddington! Fig. 4)

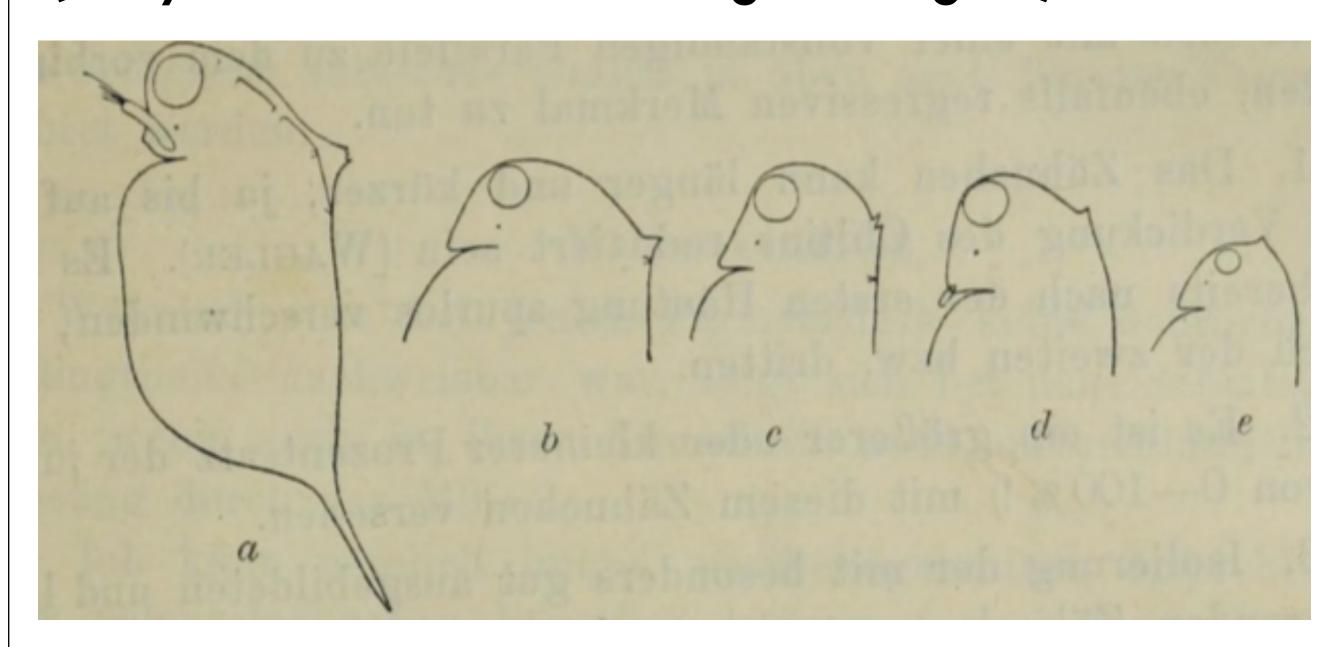


Fig 4. The Daphnia crown toothlet, a variable character stabilized by sustained selection.

## Why a translation?

Because nobody reads the primary literature! Especially if it's not in English!!

Table 1. Accuracy of statements about Woltereck in a well-regarded secondary source<sup>2</sup> published in 2001.

Truth value	Count
Correct	4/10
Opinion-based, misleading	3/10
Incorrect	3/10

English secondary sources are read, not German primary sources (Fig. 5).

- English now dominates scientific literature.
- Woltereck's paper is best case scenario
  (a well-known white guy, related languages).
- How many papers have been lost?

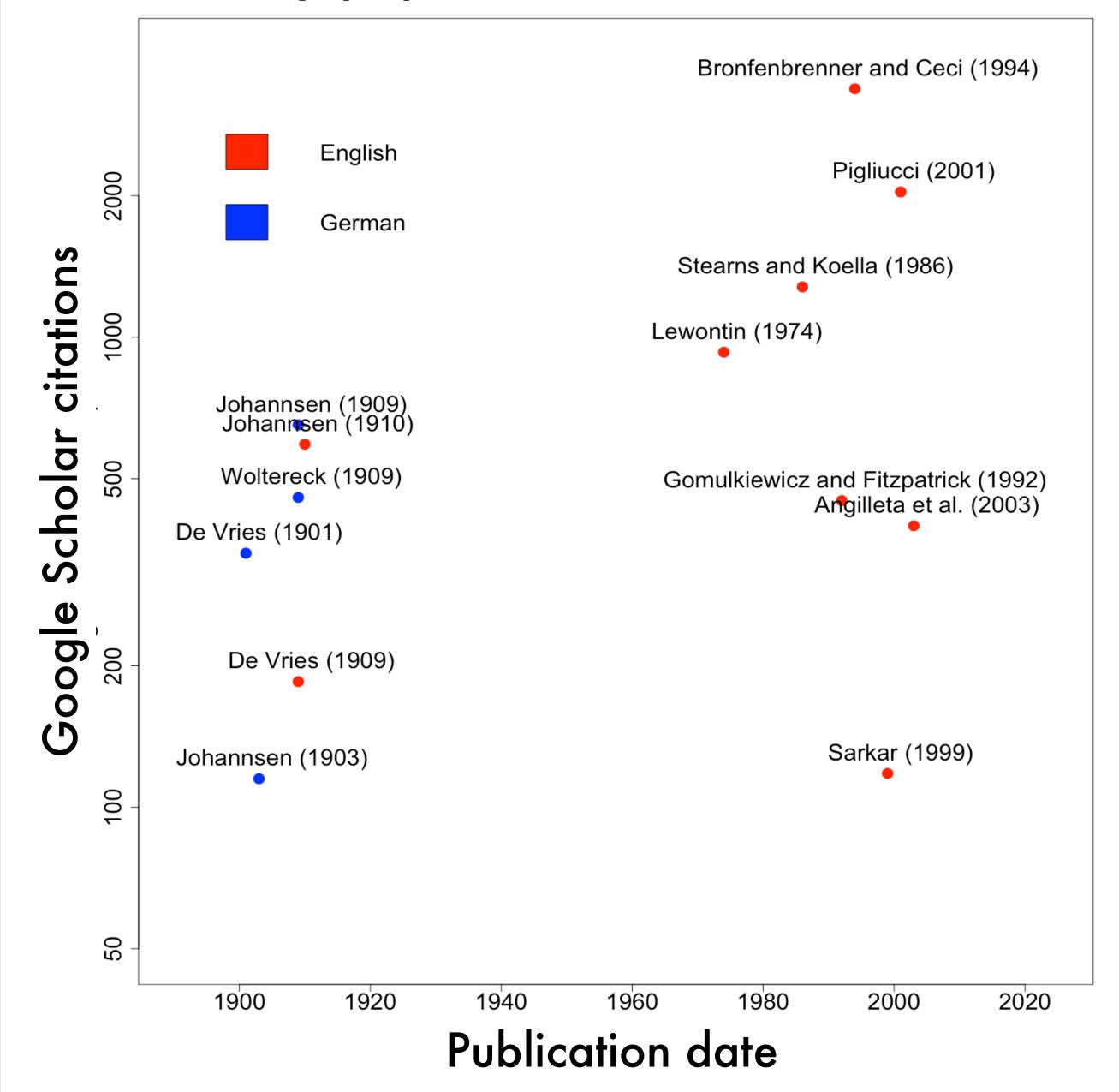


Figure 5. Google scholar citations for a selection of important German and English research documents.

## Literature cited

- 1: Woltereck R. (1909) Verh. d. Deutsch. Zool. Ges. pp. 110-172
- 2: Pigliucci M. (2001) Phenotypic plasticity. JHU Press, Baltimore.
- 3: Lewontin RC. (1974) AJHG 26:400-411
- 4: Dahl et al. (2020) AJHG 106(1):71-91
- 5: MacBride EW. (1932) Nature 130:907-909

# Acknowledgments

I thank the Harvard Biodiversity Heritage Library for the digital version of the German text.