Sensitive periods in cognitive development: a mutualistic perspective
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The theory of mutualism posits that general cognitive ability emerges, at least in part, due to positive reciprocal interaction between distinct cognitive abilities during development. In other words, cognitive abilities at a given developmental time point govern the rate of growth in other cognitive abilities. Moreover, this emerging field of work finds that the strength as well as the nature of these interactions differs during developmental time: in other words, there are sensitive periods when small individual differences may have especially pronounced, long-lasting consequences for cognitive development. Here, I review the literature on mutualistic effects, and show how it can shed new light on sensitive periods. I do so by considering sensitive periods as periods where interactions between (cognitive) domains differ in strength and/or in kind.

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Introduction
Cognitive ability in adulthood predicts many lifespan outcomes, including job performance, educational achievement, income, morbidity and mortality (e.g. Ref. [1]). Although a large body of literature (e.g. [40]), has examined individual differences in cognitive ability, comparatively little is known about the developmental processes that lead to these differences. Although developmental theories exist, they are often poorly formalized and may even be indistinguishable in cross-sectional data. Here I will discuss a particular developmental hypothesis, that of mutualism. This theory is fully formalized [2,3] - In other words, it can be expressed as a series of mathematical equations that capture explanatory principles, and allow for the reproduction of key observed phenomena. Mutualism posits positive interactions between distinct cognitive abilities as playing a crucial role in development. Below I outline the mutualism model, discuss the emerging evidence, and show how formalizing such a developmental theory as a mathematical model allows us to conceptualize sensitive periods in two distinct and novel ways: Quantitative sensitive periods (the magnitude of effects differs across developmental periods), and qualitative sensitive periods (the nature of the effects differ across developmental periods). I will discuss preliminary evidence for each type of sensitive period, and how to move these ideas forward.

The mutualism model: background and evidence
The theory of mutualism [3,4] shows how the simple assumption that there are distinct cognitive abilities which have (predominantly) positive, reciprocal effects during development provides an alternative explanation for the positive manifold: The observation ability tests are universally positively correlated, yielding a dominant first factor, often described as ‘general intelligence’. A representation of the mutualism model as a network of interactions is shown in Figure 1 (e.g. Ref. [5]). Here, each individual has several distinct cognitive abilities (e.g. vocabulary, memory, reasoning). The core hypothesis is that these separate abilities facilitate each other’s growth through, likely, a myriad of distinct mechanisms. For example, better short-term memory may facilitate the acquisition of vocabulary, which in turn allows one to decompose abstract problems into manageable mental chunks, leading to a virtuous cycle of development.

Empirical evidence in favour of the mutualism model has been emerging in the literature. For instance, in 784 adolescents (age 14–24) Kievit et al. [6] found positive, reciprocal coupling between vocabulary and reasoning over time – In other words, children with greater vocabulary skills showed more rapid gains in fluid reasoning and vice versa. These mutualistic effects were replicated and extended in a younger sample (N = 227, age 6–8, [7]). Notably, in both these papers a quantitative representation of a developmental general intelligence factor more poorly fit the data.

In line with these findings, Sewasew and Schroeders [8] found that standardized tests of verbal and mathematical ability showed strong, positively reciprocal effects between the two domains across 3 waves (grade 1, 3 and 5). A recent meta-analysis [9] observed strong,
The mutualism model as a network model (adapted from Ref. [3]). The abilities are a selection of those observed in the relevant literature, including vocabulary (voc), reasoning (reas), working memory (WM), viso–motor integration (VMI) and processing speed (PS).

reciprocal effect between language and mathematics, showing robust (partial \( r = .20/.22 \)) effects such that higher language at baseline was associated with more rapid mathematics gains, and vice versa. Bailey, Oh, Farkas, Morgan, and Hillemeier [10**] observed similar but smaller effects. Moreover, they demonstrated in some detail how important model specification is in estimating and interpreting coupling effects. Willoughby, Wylie & Little [11] used an advanced analytic approach to separate within from between subject effects, and observed that greater early reading achievement was associated with more rapid growth in executive functions.

Mutualistic effects have also been observed for more specific cognitive skills, especially so in the field of language acquisition and reading. For instance, Quinn et al. [12] observed that higher vocabulary scores were associated with more rapid gains in reading ability – But not vice versa. Lervåg et al. [13] used a correlated latent growth curve model to show strong positive associations between baseline reading comprehension and growth in vocabulary, and vice versa, and a positive effect between baseline fluid reasoning and rate of vocabulary increase (but not reading ability). In a sample including students from distinct linguistic backgrounds, Zhang et al. [14**] observed that verbal working memory predicted later reading ability above and beyond the self-propagating effect - although this effect was relatively weak for the aggregate sample and only emerged later on (grade 2) in development. Van Bergen et al. [15] observed mutually beneficial, reciprocal effects between children’s print exposure and reading skills. Regarding general mathematical aptitude, Hutchison et al. [16] observed positive, reciprocal coupling between symbolic (digits) and non-symbolic (i.e. number of dots) numerosity in young children. Zooming in more granularly within mathematical skills, Elliot et al. [17] investigated the potential bidirectional associations between approximate number sense and mathematical ability. In line with mutualism, early approximate number sense was associated with greater growth in mathematical ability, as well as vice versa. Findings in line with mutualism have also been observed beyond traditional laboratory settings – Two recent studies used complementary analytic approaches in an educational game setting to tease apart coupling effects among distinct mathematical skills. On et al. [18] used a continuous time random effects model to demonstrate that counting and addition provide mutually beneficial interactions over time, and Hofman et al. [19] observed similar findings using a distinct (latent change score) framework.

Finally, preliminary evidence suggests that mutualistic effects also occur beyond traditional cognitive tests batteries. For instance, Prat et al. [20**] demonstrated that the rate of learning of coding skills in an intervention was positively associated with a battery of traditional cognitive tasks, especially so for language and fluid reasoning skills. Most strikingly, in a simultaneous regression model, language aptitude, fluid intelligence and working memory updating made unique, and similarly strong, positive contributions to learning rate, suggesting multiple distinct cognitive drivers of the rate of coding acquisition. Similarly, Vaci et al. [21] examined a unique life-span dataset of chess ability, and found that individuals with higher general intelligence benefited more from similar amounts of practice. Although neither study looked at reciprocal effects (i.e. it did not model the effects of baseline coding ability or chess ability on gains in other cognitive domains), it demonstrates the importance for understanding of mutualistic effects in supporting gains in ‘real life’ skills (see also Ref. [22]).

The mutualism model and sensitive periods

Taken together, there is a considerable longitudinal evidence for the core hypothesis of the mutualism model: Cognitive abilities often show mutually beneficial, positive effects such that higher baseline abilities in one score are associated with greater rates of changes in others. This conceptualization allows us to think about sensitive periods through a new, quantitative lens. In the below section, I will focus on the implications of mutualistic processes in understanding sensitive periods. Specifically, we can think of sensitive periods in the mutualism model in at least two ways: quantitative and qualitative windows.
Quantitative sensitive periods

First, we may hypothesize that the strength of mutualistic coupling differs across developmental periods. We here follow the conceptualization of Knudsen [23], who defined sensitive periods as periods when ‘the effects of experience are particularly strong on a limited period in development’. This closely mirrors the conceptualization of Gabard-Durnam and McLaughlin [24] who argue, in the context of adverse experiences, that the strength and longevity of the impact of adverse experiences will depend crucially on the developmental time window within which they occur. For instance, we may hypothesize that the beneficial effects of one skill on the development of another are greater in younger children when skills are emerging (Figure 2). The mechanistic reasons for this are as follows: At lower skill levels, it may be that certain key ‘building blocks’ are still rate limiting in (young) children, but when these building blocks are fully achieved in (almost all) adults, they no longer drive individual differences in a meaningful way. For instance, to recall the meaning of a word as a young child likely requires some non-trivial amount of attention and executive function, whereas for adults this action is cognitively effortless. An empirical illustration of quantitative sensitive periods can be found in the coupling effects between vocabulary and reasoning in the Kievit et al. [7**] replication of [6**]. In the original paper, focusing on 14–24 year olds, the authors observed moderately strong (0.14 and 0.21) positive coupling between vocabulary and reasoning, and posited that ‘the coupling effects we observed are likely to be stronger earlier in life and the self-feedback parameters weaker, as developmental change in higher cognitive abilities is most rapid during pre- and early adolescence’. Kievit et al. then tested this hypothesis using exactly the same two tasks in 6–8 year olds, and indeed observed that the reciprocal coupling effects were twice as strong in the younger sample. Similarly, in Brock et al. [25**] eight out of twelve possible mutualistic effects were nominally significant in the youngest wave, whereas in the later wave (between first and second grade), ‘only’ 3 of those positive coupling effects were present. Elliot et al. [17], found that the effect of approximate number sense on mathematical ability was stronger for the younger (T1-T2) than the older (T2-T3) developmental period. In contrast, Lerkkanen et al. [41] observed positive effects from mathematical performance on gains in mathematics, but they showed a less consistent pattern, with weaker effects early on (e.g. r = .13, .16) but stronger effects later on (e.g. r = .31). The developmental implications of understanding quantitative sensitive periods are multiple: understanding when certain coupling effects are at their strongest is crucial for our understanding of the emergence of the associated cognitive faculties, as well as maximizing the potential of developing appropriately timed, maximally efficacious interventions.

Qualitative sensitive periods

A second way to conceptualize sensitive periods in the mutualism model is that the dynamic process differs in kind across different developmental periods. As Zeanah et al. [26] point out, different developmental timecourses of specific neural circuits, as well as different cognitive
Some preliminary evidence suggests that such qualitatively different sensitive periods do occur. For instance, evidence suggests that temporal associations between reading and mathematics follow a distinct temporal pattern. Early on, mathematical ability predicts later reading (Lerkkanen, Rasku-Puttonen, Aunola, & Nurmi, 2005), perhaps because emergent readers and mathematicians direct a great deal of effort toward decoding symbols (letters and numbers). However, once reading becomes less effortful, it becomes a driving force of knowledge acquisition in its own right, including of more abstract skills. For instance, Brock, Kim and Grismer [25**] examined longitudinal associations between executive functions, reading and mathematics across 3 years. In addition to global mutualistic effects (i.e. a preponderance of positive, cross-temporal path estimates as mentioned above) they also observed more developmentally specific patterns. Most interestingly, they observed that visuomotor integration (copying increasingly complex patterns) positively coupled with all other outcomes (Executive functions, letter word identification and problem solving), but only at kindergarten — not later occasions. This suggests that certain foundational skills are crucial for driving development — but only so at certain sensitive periods. Zhang et al. [14**] observed distinct patterns of coupling effects between verbal working memory and reading, among monolingual, bilingual (fluent) and bilingual (secondary) speakers, suggesting distinct cognitive building blocks supporting higher cognitive outcomes such as reading ability. The wider impact of reading ability also varies across development — van Bergen et al. [15] found that early in childhood, when children are (effortfully) learning to read, the strongest mutualistic effects are from reading fluency to comprehension and print exposure, with the reciprocal effects only emerging later on. In other words, only after reaching a developmental period where most individuals will reach a given skill level (e.g. reading with negligible effort) do other mutualistic effects have the opportunity to play out.

Above I framed qualitative periods as the driving mechanisms varying across time. It can also be informative to consider the possibility of distinct mechanisms operating between populations instead. In this case, the differing constellation of driving patterns should be thought of as differing across groups instead of across time. For instance, Ferret et al. [27] used a rich longitudinal dataset to examine and compare typical children with those with ‘persistently poor reading’ (often described as dyslexia), and observed an absence of the positive, reciprocal coupling between cognitive and reading ability in children with persistently poor reading. Similarly, Lervåg et al. [13] observed patterns between reading comprehension and
vocabulary gains that were remarkably different between bilingual and monolingual children, suggesting differential developmental processes underlying the acquisition of core skills. Finally, Peter et al., [28] found that processing speed longitudinally drives syntactic development—But only for young children with small vocabularies, arguing that the balance of skills that matter for syntactic development shifts over time. Cross-sectional papers reach converging conclusions, with these effects being most pronounced in preterm infants, late talkers and children with low overall abilities (p.16).

Summary
Thinking of cognitive development in the context of mutualism allows us to recast sensitive periods as windows of time where dynamic effects between cognitive abilities differ in kind and/or in strength during different developmental periods (and between distinct populations). Doing so helps us expand the horizon of the (presumed) sensitive period to the time when the coupling effects emerge, rather than the window where the consequences become apparent. Firmly establishing this developmental cascade may offer us the opportunity to develop early warning systems (i.e. disrupted coupling as a leading indicator), and possibly even novel avenues for early intervention.

Above we have focused on cognitive abilities interacting with each other—However, such abilities do not exist in a vacuum. Other domains, probably most notably brain structure and function, as well as mental health, exert considerable influences on the rate of cognitive development which, in turn, may affect neural and mental health development. Although longitudinal data is scarce [29], preliminary evidence suggests specificity of cortical-cognitive mapping compatible with separable cognitive abilities [26,30], and may allow us to tease apart competing hypotheses even when behavioura data alone is ambiguous. Finally, the environment likely plays a crucial role in understanding these processes. For instance, one might imagine that a ‘good school’ (or teacher) is one that manages to achieve a greater degree of positive influence between domains. Similarly, a variety of external challenges such as poverty or abuse may affect the interplay between domains, leading to long term detrimental effects [24,31]. At present, almost no data bearing on this question is available, although large, rich datasets such as ABCD [32] may be able to do so.

Future directions
Although the body of evidence described above is suggestive, it is not yet conclusive. Large scale replications would put these effects on firmer ground. Moreover, the field should move towards increased formalization of theories and models into testable, quantitative hypotheses [24,33]. The theoretical and empirical gains of these studies could be even more rapid and insightful if, rather than (just) testing a given model, multiple plausible quantitative models are directly compared in the same datasets using a model selection framework [34], to see how they fare when balancing complexity, explanatory coherence and predictive accuracy [2]. To achieve these goals, we echo the recommendations by [36] (this issue) to increase massive online data collection, and propose that such studies incorporate longitudinal arms, ideally at multiple levels of temporal resolution. Only then will we truly leverage the confluence of methodological and conceptual advances with novel samples to maximizes the insights gained into sensitive windows in development.

Conflict of interest statement
The author reports no conflict of interest other than citing work which he helped conduct when relevant to the manuscript.

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