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The Concept of Homology as a Basis for Evaluating Developmental Mechanisms: Exploring Selective Attention Across the Life-Span

ABSTRACT: *Research with human infants as well as non-human animal embryos and infants has consistently demonstrated the benefits of intersensory redundancy for perceptual learning and memory for redundantly specified information during early development. Studies of infant affect discrimination, face discrimination, numerical discrimination, sequence detection, abstract rule learning, and word comprehension and segmentation have all shown that intersensory redundancy promotes earlier detection of these properties when compared to unimodal exposure to the same properties. Here we explore the idea that such intersensory facilitation is evident across the life-span and that this continuity is an example of a developmental behavioral homology. We present evidence that intersensory facilitation is most apparent during early phases of learning for a variety of tasks, regardless of developmental level, including domains that are novel or tasks that require discrimination of fine detail or speeded responses. Under these conditions, infants, children, and adults all show intersensory facilitation, suggesting a developmental homology. We discuss the challenge and propose strategies for establishing appropriate guidelines for identifying developmental behavioral homologies. We conclude that evaluating the extent to which continuities observed across development are homologous can contribute to a better understanding of the processes of development.* © *2012 Wiley Periodicals, Inc.* Dev Psychobiol 55: 76–83, 2013.

Manuscript Received: 7 November 2011
Manuscript Accepted: 28 March 2012
Correspondence to: Robert Lickliter
Contract grant sponsor: NICHD
Contract grant numbers: RO1 HD048423
Contract grant sponsor: NSF
Contract grant numbers: BCS 1057898
Contract grant sponsor: NICHD
Contract grant numbers: RO1 HD053776
Contract grant sponsor: NICHD
Contract grant numbers: KO2 HD0649433
This material is based upon work supported by the National Science Foundation under Grant No. BCS-1023899.
Article first published online in Wiley Online Library (wileyonlinelibrary.com): 18 June 2012
DOI 10.1002/dev.21037 • © 2012 Wiley Periodicals, Inc.

INTRODUCTION

The process of development is historical. What occurs earlier guides and constrains what can occur later. As such, the study of development resembles the study of evolution in that both are concerned with continuity and modification of phenotypic traits over spans of time. Evolutionary biology has long used the concept of homology to make sense of the continuity of structure across species (Brigandt, 2003; de Beer, 1971; Donoghue, 1992; Hall, 1994, 2003; Reidl, 1978; van Valen, 1982). Can the concept of homology also be useful to help developmentalists identify continuity of behavior and cognition across individual development? Are behavioral patterns observed at two different points in development in fact the same? Do they arise from the same underlying mechanisms of development? As it turns out, these are not easy or straightforward questions to answer, as the diversity of opinions and points of view represented in this special issue make abundantly clear.

The historical roots of the homology concept come from comparative biology, in particular comparative anatomy (Barry, 1837; Owen, 1848). For the last 60 years, biologists have typically used some form of Remane's (1952) criteria for identifying morphological homologies. These criteria include (1) physical position, (2) special quality (the distinctiveness of a character or trait), and (3) connection to evolutionary intermediates. These criteria do not, however, easily translate into the identification of behavioral homologies (Scholz, 2005; but see Atz, 1970; Ereshefsky, 2007; Matthen, 2007). What are the appropriate criteria for identifying developmental behavioral homologies? How do we determine if a trait or characteristic present in adults is homologous (*the same*) or simply analogous (*similar*) to a trait or characteristic present earlier in development? In this article we explore these challenging issues by using our own research focus, intersensory perception, to ask whether and how the concept of homology might aid in furthering our understanding of perceptual development across the life-span. In particular, we ask whether observed continuities in the deployment of selective attention from infancy to adulthood are best understood in terms of homology, and whether the concept of homology can help foster the discovery of common developmental processes and mechanisms at play across the life-span. It is important to note that we restrict our focus to behavioral evidence, but homology can exist at different levels of analysis, including genetic, neural, and physiological.

We use the term homology in this context as a relationship of "sameness" due to a common developmental precursor. More specifically, we view developmental homology as those behaviors observed at two different periods of development that are shown to be a product of or depend on the same developmental mechanism. An alternative would be behavioral patterns observed across different points in development that despite their apparent "sameness," actually arise from different underlying mechanisms or processes. For example, questions have been raised regarding whether neonatal behaviors (such as imitation) arise from the same underlying processes or mechanisms as similar behavior observed in later development (Suddendorf, Oostenbroek, Nielsen, & Slaughter, 2012).

THE CASE OF INTERSENSORY PERCEPTION

Adults are remarkably skilled at selectively attending to specific features or aspects of objects and events, picking out information that is relevant to their needs, goals, and interests, and ignoring irrelevant stimulation. For example, we easily pick out a friend in a crowd, follow the flow of action in a ball game, and attend to the voice of the speaker at a cocktail party in the context of competing conversations. We long ago learned to pick out human speech from non-speech sounds and parse continuous speech into meaningful words by ignoring variations across speakers, accents, and intonation. Similarly, we have learned to parse the visual array into coherent objects and surfaces despite variation due to lighting and shadow and interruption of surfaces due to occlusion. The foundations of these remarkable skills, easily taken for granted by experienced perceivers, develop across infancy as a result of ongoing experience with objects and events. This rapid perceptual development depends on improving attentional allocation and economy of information pick up for regularities in aspects of the environment (Bahrick & Lickliter, 2002; Gibson & Pick, 2000).

In this light, the newborn infant faces a significant developmental challenge following birth—how to become increasingly economical and efficient at attending to multimodal stimulation that is unitary (coherent across the senses and originating from a single event) and relevant to their needs and actions, while ignoring stimulation across the senses that is incoherent or less relevant. For example, how do infants learn that the sights and sounds of a person speaking or a ball bouncing constitute a unitary audiovisual event as opposed to separate streams of sight and sound? This is a challenging task, as the environment provides far more stimulation from objects and events than can be attended at any given time and the infant has very little experience to draw on for effectively allocating selective attention. Infants must quickly learn to attend to variations in incoming stimulation that have meaning, relevance, and coherence (e.g., coordinated changes in the face and voice of a single speaker amidst unrelated changes in other objects and people) and ignore other variations that are relatively meaningless (differences in lighting and shadow across cohesive objects, variations in speaker voice, or intonation across the same phoneme). What factors determine which information is selected and integrated by infants and which information is typically ignored during early development?

A large body of research has indicated that the detection of amodal information such as temporal synchrony, rhythm, tempo, and intensity is a cornerstone of early perceptual development (Bahrick & Lickliter, 2002; Lewkowicz, 2000; Lewkowicz & Lickliter, 1994). *Amodal information* is information that is not specific to a particular sense modality. Rather, it is information that can be conveyed redundantly across multiple senses, including fundamental dimensions of stimulation such as time, space, and intensity. By attending to amodal information, there is no need to learn to integrate stimulation across the senses in order to perceive unified objects and events, as proposed by constructivist accounts of early perceptual and cognitive development (e.g., Piaget, 1952, 1954). Perceiving amodal relations, combined with an increasing sensitivity to the statistical regularities of the environment, effectively ensures that young inexperienced perceivers will preferentially attend to unified multimodal events, such as people speaking, dogs barking, or keys jingling.

Temporal synchrony is the most fundamental type of amodal information, in part because it can only be detected across two or more sensory systems. Temporal synchrony refers to the simultaneous co-occurrence of stimulation across the senses (e.g., audiovisual) with respect to onset, offset, and duration of sensory patterning. Temporal synchrony facilitates the detection of nested amodal properties such as rhythm, tempo, and duration across the senses (Bahrick, 2001; Lewkowicz, 2000). Indeed, temporal synchrony has been proposed as the ‘‘glue’’ that binds stimulation across the senses (Bahrick & Lickliter, 2002; Bahrick & Pickens, 1994; Lewkowicz, 2000). For example, by attending to audiovisual synchrony, the sounds and sights of a single person speaking will be perceived together as a unified event, providing a basis for meaningful processing of the event as an integrated whole.

THE INTERSENSORY REDUNDANCY HYPOTHESIS

It is clear that infants quickly establish efficient patterns for selectively attending to meaningful and relevant stimulation and coherent multimodal objects and events. Attention becomes increasingly efficient and flexible with experience, eventually evolving into the expert patterns of adult selective attention. A central issue for developmental science is to uncover what principles govern this process. We have proposed and provided empirical support from animal and human infants for the intersensory redundancy hypothesis (IRH), a framework based on four general principles that we think guide this developmental process (Bahrick & Lickliter, 2000, 2002, 2012; Lickliter & Bahrick, 2004). Intersensory redundancy is provided by an event when the same amodal information (e.g., rhythm, tempo, intensity changes) is simultaneously available and temporally synchronized across two or more sense modalities. For example, in synchronized audiovisual speech, the same rhythm and tempo of speech can be perceived by looking and by listening; thus, the rhythm and tempo are redundantly specified. Predictions 1 and 2 of the IRH address the nature of selective attention to different properties of objects and events and predictions 3 and 4 are developmental predictions that address implications of the IRH across the life span:

(1) Redundantly specified, amodal properties are highly salient and detected more easily in bimodal synchronous stimulation than are the same amodal properties in unimodal stimulation (*intersensory facilitation*).
(2) Non-redundantly specified, modality specific properties are more salient and detected more easily in unimodal stimulation than are the same properties in bimodal, synchronous stimulation, where redundantly specified amodal properties compete for attention (*unimodal facilitation*).
(3) Across development, infants' increasing perceptual differentiation, efficiency of processing, and flexibility of attention lead to detection of both redundantly and non-redundantly specified properties in unimodal, non-redundant and bimodal, redundant stimulation.
(4) Intersensory and unimodal facilitation are most pronounced for tasks of relatively high difficulty in relation to the expertise of the perceiver, and thus should be apparent across the life-span.

Here we focus on principle 1 (intersensory facilitation) and principle 4 (role of task difficulty). Infant-based research consistently indicates that redundancy across the senses promotes attention to redundantly specified properties of objects and events, at the expense of other non-redundantly specified stimulus properties, particularly in early development when attentional resources are most limited (Bahrick & Lickliter, 2002, 2012; Bahrick, Lickliter, Castellanos, & Vaillant-Molina, 2010). Animal-based research has likewise demonstrated intersensory facilitation for redundant amodal stimulus properties during both prenatal and early postnatal development (Lickliter & Bahrick, 2004; Lickliter, Bahrick, & Honeycutt, 2002). Studies of human infant affect discrimination, prosody discrimination, numerical discrimination, sequence detection, and abstract rule learning have also shown that intersensory redundancy facilitates earlier detection of the information of interest when compared to non-redundant unimodal exposure to the same information (e.g., Flom & Bahrick, 2007; Farzin, Charles, & Rivara, 2009; Frank, Slemmer, Marcus, & Johnson, 2009; Jordan, Suanda, & Brannon, 2008; Lewkowicz, 2004; see Bahrick & Lickliter, 2012 for a review). Of course, factors such as complexity, familiarity, length of exposure, and the level of expertise of the perceiver also affect the deployment of early selective attention.

DEVELOPMENTAL CONSIDERATIONS

Early development is a period during which task demands are typically high and attentional resources are limited. Infants are relatively naïve perceivers of objects and events, and therefore perceptual processing of most objects and events is likely rather difficult and effortful. Consequently, intersensory facilitation (better discrimination of an amodal property in redundant bimodal stimulation than unimodal stimulation) should be most pronounced in early development. Intersensory facilitation occurs because the most salient properties of stimulation are detected earlier in processing time than less salient properties. In early development, in a typical bout of exploration there are insufficient attentional resources for processing less salient properties. When attentional skills improve, attention can progress more rapidly down the salience hierarchy (see Bahrick & Lickliter, 2012). Thus, as infants gain more experience and perceptual expertise, they come to discriminate amodal properties in both multimodal (redundant) and unimodal (non-redundant) stimulation.

For example, 3-month-old infants show intersensory facilitation, discriminating a change in the tempo of a toy hammer tapping (from fast to slow, or vice versa, defined by number of beats per minute) in redundant (synchronous) audiovisual stimulation, but not in non-redundant stimulation (unimodal visual or asynchronous audiovisual; Bahrick, Flom, & Lickliter, 2002). However, by 5 months of age infants no longer show intersensory facilitation for this relatively easy tempo contrast. Rather, they are able to detect the easy tempo changes regardless of whether they receive redundant or non-redundant exposure (Bahrick & Lickliter, 2004). We also presented 5-month-old infants with more difficult, fine-grained tempo contrasts (of moderate and high difficulty) in redundant (synchronous, audiovisual) and non-redundant (unimodal visual) conditions (Bahrick et al., 2010). Stimulus events from the earlier Bahrick and Lickliter (2004) study served as the condition of low difficulty. We hypothesized that when older (5-month-old) infants are presented with difficult tempo contrasts, they should revert to the intersensory facilitation patterns that younger (3-month-old) infants show for the easy tempo contrasts. To test this prediction, we assessed discrimination of moderate and difficult changes in tempo (contrasts in beats per minute) in 5-month-old infants. Consistent with our predictions, 5-month-olds showed significant discrimination of a change in tempo in the context of both unimodal, non-redundant and bimodal, redundant stimulation (i.e., no intersensory facilitation) when the task was of low or moderate difficulty. In contrast, when tempo contrasts were of high difficulty, 5-month-olds showed discrimination only in bimodal redundant stimulation, and not in unimodal non-redundant stimulation, paralleling the pattern of facilitation shown by 3-month-olds in our earlier study (Bahrick et al., 2002). Thus, under conditions of high-task difficulty, older (5-month-old) infants show the patterns of *intersensory facilitation* shown by younger (3-month-old) infants, where tempo discrimination was evident only in the presence of intersensory redundancy.

Facilitating effects of intersensory redundancy should also be apparent during early phases of learning for a variety of tasks across the life-span. In other words, intersensory facilitation would be expected for learning in domains that are novel, for tasks that require discrimination of fine detail, for speeded responses, and for problems of relatively high-cognitive load. Children and adults continue to develop expertise across the life-span, acquiring new information and learning to perceive finer distinctions such as learning a new language or playing a new musical instrument. In early stages of learning, expertise is low in relation to task difficulty, and consequently task demands are high. The IRH predicts that when task demands are high, and attention is more challenged, children and even adults should experience intersensory facilitation. In other words, when learning new material that challenges skill level or requires greater effort or executive function, intersensory redundancy should promote selective attention, perceptual processing, and learning in older perceivers. Like infants, for children and adults under challenging conditions, attention should progress more slowly along the attentional salience hierarchy, leading to intersensory facilitation. We have recently demonstrated intersensory facilitation under conditions of high-task difficulty but not low-task difficulty for preschool-age children in a tempo discrimination task similar to that used in our infant study (Bahrick, Krogh-Jespersen, Naclerio, & Lau, 2011).

Studies with older infants and children across other skill domains, including motor and cognitive development, also indicate that under conditions of higher task difficulty and cognitive load, performance often reverts to that of earlier stages of development (Adolph & Berger, 2005; Berger, 2004). For example, infants and toddlers show regressions to more immature, but more practiced forms of behavior in difficult contexts and under conditions of increased cognitive load (Berger, 2004; Corbetta & Bojczyk, 2002). Research findings from studies of adult perception (e.g., Kaplan &

Berman, 2010; LaVie, 1995, 2005; McDowd & Craik, 1988) are also consistent with this view. For example, research with adults has demonstrated that bimodal cues capture spatial attention more effectively than unimodal cues under conditions of perceptual load (Santangelo, Ho, & Spence, 2008; Santangelo & Spence, 2007), and that older adults are slower to respond to unimodal stimuli than are younger adults (Laurienti, Burdette, Maldjian, & Wallace, 2006). These results suggest that intersensory information likely plays a key role in directing attention in demanding events or situations across the life-span.

DO ADULTS BENEFIT FROM INTERSENSORY REDUNDANCY?

We recently assessed the relationship between task difficulty and intersensory facilitation in adults in a task assessing detection of tempo (Bahrick et al., 2009). In this preliminary study, we manipulated task difficulty by familiarizing adults with a single trial depicting a toy hammer tapping a four-beat rhythm at a particular tempo under conditions of either unimodal visual (non-redundant) or bimodal audiovisual (redundant) stimulation. Following the presentation of this standard tempo, adults received 16 test trials in which there was no change in tempo, a tempo change of 25% (low difficulty), 17% (moderate difficulty), and 9% (high difficulty), with four trials of each difficulty level presented in one of two random orders. The number of trials in which participants correctly discriminated the tempo change (same or different) was recorded. Our results indicated that in addition to demonstrating the effects of task difficulty, adults show enhanced discrimination of the amodal property of tempo in the context of redundant audiovisual stimulation as compared with unimodal visual stimulation.

If these preliminary findings of intersensory facilitation in adults are supported across additional studies, we can ask whether evidence for the salience of intersensory redundancy in our task during adulthood is homologous or simply analogous with the salience of intersensory redundancy we have observed in infancy. In particular, our behavioral findings raise the question of whether and to what extent the observed continuity in the deployment of selective attention from infancy to adulthood could be an example of a developmental behavioral homology. In addition to behavioral evidence, neurophysiological evidence (e.g., Hyde, Jones, Flom, & Porter, 2011; Reynolds, Bahrick, Lickliter, & Riggs, 2010) can provide additional insights about the nature and scope of changes versus continuities in perceptual processing over the course of development.

ASSESSING BEHAVIORAL HOMOLOGIES

The field of developmental psychology has not directly addressed the various issues and challenges that surround the notion of homology and its application, in part due to the field's enduring concern with the debate between stage theories and the continuity of development. As a result, there are few if any guidelines for how to distinguish between the same versus similar traits observed across different periods of development. If we are to incorporate the concept of homology into developmental science, we will need a framework for evaluating whether behavioral or cognitive phenomena observed across development of an individual are the "same" or simply "similar". Identifying and defining what constitutes "the same" will require mapping out how perceptual and cognitive skills are organized and employed across ontogeny, how they become better coordinated with experience, and how they support real-time behavior. In addition, determining which are the most relevant features of perceptual and cognitive skills for establishing sameness versus similarity across development is a critical step in any attempt to explore whether a given behavior is conserved or transformed across development. No such guidelines or criteria are currently in place (but see Atz, 1970 for useful discussion).

For example, using our current example of intersensory facilitation, evidence accumulated over several decades of infant based perception research indicates that selective attention is initially more stimulus-driven during early development and with experience becomes increasingly endogenous and modulated by top down processes, including the individual's goals, plans, and expectations (e.g., Colombo, 2001; Johnson, Posner, & Rothbart, 1991; Ruff & Rothbart, 1996). Thus, for experienced perceivers prior knowledge, categories, goals, plans, and expectations typically guide selective attention and information pick-up (e.g., Chase & Simon, 1973; Neisser, 1976; Schank & Ableson, 1977). Given the significant differences at play in the deployment of attention between infants and adults, determining whether the use of intersensory redundancy to guide perceptual discrimination in adults is homologous (*the same*) or simply analogous (*similar*) to earlier patterns of selective attention seen during infancy is a major methodological challenge. Are there useful guidelines or strategies that can be employed for addressing this challenge?

It seems to us that a key step in determining whether traits or skills observed across development are homologous will be understanding how a behavioral or cognitive phenomenon (e.g., intersensory facilitation) initially comes about from the coordination of existing skills and processes *and* how things change versus how they stay the same over the course of the life-span. Given that developmental analysis is essential to account for the variation or similarity among phenotypic characters or traits (Lickliter & Harshaw, 2010), establishing the criteria for whether a given phenomena is ‘‘the same’’ across developmental periods will have to be based on a developmental approach. For example, returning to our concern with intersensory perception, by manipulating context (e.g., providing unimodal vs. redundant bimodal stimulation) or task (e.g., easy vs. difficult tempo contrast), one should be able to predict the presence or absence of the phenomenon of interest (intersensory facilitation) across development. In other words, we can assess if similar contexts and similar tasks elicit and maintain the phenomenon of interest at different developmental periods.

This focus on process and mechanism seems to us the most productive route to establishing the necessary and the sufficient conditions for any developmental behavioral homology. Given that developmental psychology is concerned with uncovering underlying mechanisms of behavioral and cognitive development, asking whether behaviors observed at two different periods of development are a product of or depend on the same mechanism (a developmental homology by our working definition) seems to us to be a critical question to pursue. Attempts to identify whether the same mechanisms are at play across developmental periods will likely benefit from a number of approaches, including:

(1) assessing whether similar contexts or tasks elicit and maintain the phenomenon of interest (as highlighted above).
(2) establishing developmental continuity in the behavior of interest across a variety of age groups.
(3) exploring microanalysis of within-individual longitudinal change (see Thelen & Smith, 1994 for multiple examples of this approach).
(4) identifying the boundary conditions for eliciting or maintaining the behavior of interest. For example, young infants successfully match the sights and sounds of a toy train approaching and receding (Bahrick & Pickens, 1994), demonstrating perception of audio–visual distance relations. An investigation of boundary conditions revealed that although infants matched on the basis of changing size, they did not match on the basis of changing luminance or rising/falling motion.
(5) determining whether the expression of the behavior or trait generalizes in a predictable manner to appropriate conditions but not to inappropriate conditions. For example, Smith and colleagues have shown that Piaget’s well known A-not-B error does not generalize from sitting to standing in 10-month-infants, calling into question the mechanisms assumed to be at play by much of cognitive science (Smith, Thelen, Titzer, & McLin, 1999).
(6) determining whether and to what extent the same neural underpinnings are contributing to the behavior or trait of interest across different periods of development (Stiles, 2008).
(7) experimentally controlling for or eliminating the information considered critical to the expression of the behavior to determine if the phenomenon disappears appropriately. For example, we have shown intersensory facilitation is no longer evident in both human and non-human animal infants when auditory and visual stimulation from a single event are presented asynchronously (thereby eliminating redundancy but holding constant the type and amount of stimulation, Bahrick & Lickliter, 2000; Lickliter et al., 2002).

As suggested by several of the other articles in this special issue, a range of other steps, strategies, and levels of analysis will also be of use in applying the construct of homology within developmental science.

CONCLUSIONS

Explaining how morphological structures or behaviors emerge in ontogeny and how they are conserved or transformed over development remains a daunting task for both biologists and psychologists. Given that all homologies are the result of developmental processes, identifying the ways in which behavioral homologies arise and how they are maintained across individuals and across generations will contribute to a better understanding of the phenomenon of development. However, the criteria for determining whether a behavior is ‘‘the same’’ at different points in development are not yet well articulated, and the methods for identifying possible behavioral homologies have yet to be formalized. In our view, applying a developmental point of view to mapping the trajectories of perceptual and cognitive skills across the life-span is a key first step in addressing these difficult challenges.

NOTES

The research reported here was supported by NICHD RO1 HD048423 and NSF BCS 1057898 awarded to RL and NICHD RO1 HD053776 and NICHD KO2 HD0649433 awarded to LB.

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