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Thinking About Development: The Value of Animal-Based Research for the Study of Human Development

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Abstract

Gottlieb promoted the value of a developmental psychobiological systems approach to the study of human development. This approach recognizes the importance of comparative, animal-based research to advancing our understanding of the complexities and dynamics of the process of development. The major contribution of animal developmental studies is their provision of food for thought (hypotheses, not facts) about human development and general principles of development. Here we briefly describe how, guided by Gottlieb's pioneering vision, we have utilized coordinated studies of non-human animal and human infants to begin to identify patterns of selective attention and perceptual processing that are common across species in early development. Our converging findings highlight the importance of multimodal (intersensory) redundancy in guiding and constraining early perceptual learning in avian and mammalian species.

Keywords

comparative developmental psychology; perceptual development; intersensory redundancy; psychobiology; Gilbert Gottlieb

Gilbert Gottlieb's contributions to developmental science are both wide and deep, covering such topics as imprinting, perceptual development, behavioral plasticity, and the links between developmental and evolutionary theory. He also championed the importance of what he termed "the developmental psychobiological systems view" to the study of human development (e.g., Gottlieb, 1983, 1991, 2001; Gottlieb & Krasnegor, 1985; Gottlieb, Wahlsten, & Lickliter, 2006). The developmental psychobiological systems view he promoted had its origins in the study of animal behavioral development (e.g., Kuo, 1967; Gottlieb, 1971; Lehrman, 1953, 1965; Schneirla, 1957). This psychobiological research tradition was primarily concerned with the development of species-typical behavior of animals in their natural habitats, with a particular interest in the behavioral and psychological adaptations distinctive to each species and how these adaptations were modified in response to changing internal and external conditions. The rich interplay between internal organismic factors (e.g., gene expression, hormone secretion, neuronal growth and pruning) and external environmental factors (e.g., temperature, diet, social interaction) that contribute to animal behavioral development (see Michel & Moore, 1995 for an overview) highlighted to Gottlieb the importance of adopting a "systems" perspective for the study of human development. As he pointed out, it is the bidirectional traffic within and across levels of the organism/environment system that both guides and constrains the course of individual development (Gottlieb, 1991,1997,2003).

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The inherent experimental limitations associated with human-based research makes identifying and examining the bidirectional dynamics of human behavioral development particularly challenging. Experimental modification of genetic, neural, physiological, or social factors are largely prohibited in our experimental designs. Gottlieb appreciated that programmatic developmental experiments with animals could help overcome some of these limitations. From his view, animal experiments could both suggest new methods for human research (Gottlieb, 1985) and point to topics or themes of development that had been overlooked or underappreciated in human-based studies. Gottlieb argued that animal research was most useful for thinking about human development when kept at the level of generalities, not specifics. He recognized that the degree to which animal models faithfully mimicked their presumed human counterparts in the arenas of psychological, social, or behavioral function would always remain open to question (Gottlieb & Lickliter, 2004). Animal-based research can, however, provide new questions, methods, and hypotheses for the study of human behavior and in cases where animal and human-based findings converge, they can reveal potential general principles of development that can contribute to a fuller understanding of human ontogeny (e.g., Harper, 2005; Lickliter, 2000). For example, using findings from birds and rodents, Turkewitz and Kenny (1982) proposed that developmental limitations on sensory input during the perinatal period was an important contributor to the typical patterns of perceptual and cognitive development observed during early infancy. Similarly, Harper (2005), based on his review of animal-based studies, documents the transmission to offspring of parental phenotypic responses to environmental challenges even when the young do not experience the challenges themselves, suggesting fertile areas of investigation for human-based studies.

We have been strongly influenced by Gottlieb's emphasis on the value of a comparative-based approach to the study of human development (Lickliter & Bahrick, 2000, 2001, 2004). In this article we briefly explore how the integration of animal and human-based research is contributing to a deeper understanding of the development of intersensory perception, a topic that Gottlieb also found of considerable interest over the course of his distinguished career (Gottlieb, 1993; Gottlieb, Tomlinson, & Radell, 1989; Radell & Gottlieb, 1992). Our rationale for promoting a more explicit focus on animal-oriented research in developmental psychology is not to provide a "stand-in" for the study of human development. Rather, in keeping with Gottlieb's psychobiological systems perspective, we suggest that comparative work can provide simpler and more experimentally accessible systems that can be probed to identify and define themes or principles of development that can then be tested (albeit in a more limited way) with humans (see Lickliter, 2000 for further discussion).

A comparative, convergent-operations approach to developmental research

Experiential manipulations of human infants are necessarily severely limited in scope and duration. Animal studies provide the opportunity to employ a variety of research methods, including experiential deprivation and experiential augmentation, not generally possible with human subjects. As Gottlieb demonstrated in his elegant work on species-identification in ducklings, one important advantage of the use of animals to study perceptual, behavioral, or social development is the ability to modify the type, timing, or amount of particular experience available to the embryo or infant. In addition to this advantage of precise experiential control, animals also provide the opportunity to supplement behavioral measures with neurophysiological manipulations and measures (Dmitrieva & Gottlieb, 1992; Markham, Toth, & Lickliter, 2006) also not usually possible with humans.

Studies of human infants are not only limited in design, they are also labor intensive and widely known to be sensitive to influences of task, context, infant state, and small changes in procedures, stimuli, and measures. As a result, findings from experiments with infants typically require more rigorous replication across diverse conditions than do most adult-based studies.

Convergent findings across animal and human infants can provide a stronger argument that research findings from human infants are not task-specific or caused by extraneous variables. For example, our joint animal and human-based investigations of the development of intersensory perception (Bahrick & Lickliter, 2000, 2004; Bahrick, Lickliter, & Flom, 2006; Lickliter, Bahrick & Honeycutt, 2002,2004; Lickliter, Bahrick, & Markham, 2006) utilizes experiments that differ across subject sample (bobwhite quail chicks vs. 2–8 month-old human infants), task (auditory learning vs. visual discrimination), stimuli (maternal assembly call vs. naturalistic objects striking a surface), response system (locomotion vs. visual fixation), procedure (two choice auditory preference test vs. infant control habituation), and developmental stage (embryos and neonates vs. infants). When converging results are obtained across such broad differences, we can be more confident that our findings point to themes or principles of early development that are generalizable across a variety of tasks, stimuli, procedures, response systems, developmental stages, and species. We can also invest less effort in replication and testing across diverse conditions with human infants when animal-based findings reveal comparable processes. Thus, a convergent animal-human approach can be a powerful and efficient means for uncovering basic developmental principles.

Of course, achieving such confidence is more likely when animal and human studies are designed from a collaborative framework that has forged a common language, formulated interrelated questions, and designed overlapping procedures from the outset to generate findings that more readily translate across domains. This type of cooperation and coordination across levels of analysis, methods, and laboratories can provide a broader and deeper understanding of the process of development, using fewer resources than separate research programs would require. It is interesting to note that the importance and benefits of such a convergent-operations approach was recognized some forty years ago by one of Gottlieb’s own mentors, the pioneering developmentist Zing-Yang Kuo (1967,1970). Despite Kuo and Gottlieb’s efforts to emphasize its value to the study of human development, the application of a convergent-operations approach has been slow in coming to mainstream developmental psychology.

The development of intersensory perception

In a review of the study of infant perceptual development Haith, (1993) concluded that the exploration of human infant sensory and perceptual processes is a field unto itself, with little attempt to unite theory, concepts, and methods used for studying infancy with those used for studying older children, adults, or other animal species. This has certainly been the case in our area of research focus, intersensory perception, despite the fact that animal findings have contributed a wealth of useful guidelines for asking questions about the nature of human infant selective attention, perceptual processing, and learning. For example, animal-based research has provided a number of advances in our understanding of the emergence of intersensory capacities, including the importance of the timing of sensory experience relative to the developmental organization of the organism during perinatal development (Kenny & Turkewitz, 1986; Lickliter, 1993; Spear & McKinzie, 1994), and the influence of early social interaction on perceptual organization (Columbus & Lickliter, 1998; Gottlieb, 1993; McBride & Lickliter, 1993). Animal-based research has also demonstrated that the senses are interconnected in complex ways, even prenatally, such that manipulations to one sense modality (for example, augmented visual experience) can alter not only visual functioning, but auditory and intersensory functioning as well (Lickliter & Banker, 1994; Radell & Gottlieb, 1992).

Despite this evidence for strong links between the sensory systems during early development, most researchers focused on human perceptual development have not included conditions of multimodal stimulation in studies of unimodal perceptual functioning, or vice versa, even though both types of stimulation are routinely encountered by the developing infant. Indeed, a historical focus on the specificity of the senses has led to subdivisions within psychology for studying perception, cognition, and memory in separate sense modalities (e.g., visual perception, auditory perception). Intersensory perception has typically been viewed as a separate research area and there is currently a lack of integration between research on unimodal and multimodal functioning (e.g., Kellman & Arterberry, 1998). Consequently, research findings from the two areas are not well integrated and studies of unimodal and multimodal perception are difficult to compare, as they typically employ different methods and measures. Furthermore, few investigators actually compare responsiveness in one sense modality to responsiveness in two or more sensory modalities concurrently. Achieving a more integrated and ecologically valid account of perceptual development will require an investigation of the effects of unimodal and multimodal stimulation on perceptual responsiveness in single research designs (Lickliter & Bahrick 2000, 2001). This approach was utilized by Gottlieb in his investigations of the phenomenon of developmental intersensory interference (Gottlieb, et al., 1989; Radell & Gottlieb, 1992), in part because it permitted assessment of interactions between unimodal and multimodal perception not otherwise possible, including how they might change developmentally.

Stimulus properties, selective attention, and perceptual learning

Multimodal stimulation provides two distinct types of information to the sensory systems, *redundant* and *nonredundant* information. Redundantly specified properties of objects and events are termed *amodal* properties. Amodal stimulus properties are not tied to a particular sensory modality but are redundant across two or more senses. For example, the sights and sounds of a ball bouncing share temporal synchrony, rhythm, and tempo (rate of occurrence). When the same temporal information is detected in two modalities simultaneously, it can specify the unitary nature of the audible and visible stimulation and separate it from other events that do not share its structure. We consider detection of amodal relations to be fundamental for organizing early perceptual development because it provides a powerful means by which relatively naive infants can determine which patterns of sensory stimulation belong together and which are unrelated (Bahrick, 2004, Gibson & Pick, 2001). For example, detection of amodal temporal synchrony, rhythm and tempo may focus an infant's attention on the sights and sounds of a person speaking or on the visual and acoustic impacts of a bouncing ball. Consequently, the multimodally presented person or ball would be perceived as a unitary entity. Sensitivity to amodal relations can also act as a buffer against forming inappropriate associations across the senses, as infants would not readily relate the sounds of speech with other objects that do not share the temporal structure of the speech sounds.

A prolific body of research conducted over the past 25 years, inspired in large part by James and Eleanor Gibson's ecological approach to perception, has demonstrated that even young infants are adept perceivers of amodal stimulation (see Bahrick, 2004; Lewkowicz, 2000; Lickliter & Bahrick, 2000; Walker-Andrews, 1997 for reviews). For example, infants can detect amodal relations uniting visual and acoustic stimulation, including temporal synchrony, rhythm, and tempo during the first months following birth (e.g., Bahrick, 1983, 1987; Lewkowicz, 1992, 1996). Converging evidence from both animal and human studies (e.g., Hultsch, Schleuss, & Todt, 1999; Hollich, Newman, & Jusczyk, 2005) suggests that denning the conditions that facilitate and attenuate selective attention and perceptual processing of amodal (redundant) stimulus properties is critical to understanding how perception works in the natural multimodal environment and for developing applications to natural learning contexts.

To provide an organizing conceptual framework for making sense of how infant attention and perception of the properties of objects and events develop in a multimodal environment, we

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have proposed an *intersensory redundancy hypothesis* (IRH, Bahrick & Lickliter, 2000, 2002; Bahrick, et al., 2004). The IRH synthesizes knowledge gained from behavioral research on animal and human infants with findings from the neural and physiological levels of analysis. "Redundancy" refers to the synchronous temporal alignment between two sources of collocated, patterned stimulation. We have proposed that intersensory redundancy recruits infant attention, causing amodal stimulus properties (e.g., rhythm, tempo) to become "foreground" and others properties to become "background" in bimodal stimulation. This leads to an initial advantage in processing and learning properties that are specified in more than one modality.

In contrast, unimodal sensory stimulation fosters attention to nonredundantly specified properties, including modality-specific properties that provide information specific to a single sense such as color, pattern, pitch, timbre, to a greater extent than does bimodal stimulation. This unimodal facilitation of modality-specific properties occurs in part because there is no competition for attention from redundancy. Because most events are multimodal, we argue that there is a general processing advantage for amodal over modality-specific properties in early infancy. Moreover, available evidence suggests that this processing advantage can have a cascading effect on cognition, language, and social development (which emerge from multimodal learning contexts) by establishing initial conditions which favor processing of amodal information (Bahrick & Lickliter, 2002; Gogate & Bahrick, 1998).

All events (for example, a person speaking) provide both redundantly specified (e.g., rhythm and tempo of speech) and nonredundantly specified (e.g., timbre of voice, facial features) properties for exploration. The IRH makes several basic predictions regarding the dynamics of the perception of stimulus properties during early development. Each of these predictions was derived from and has received empirical support from our coordinated studies of quail embryos and chicks and human infants (see Bahrick & Lickliter, 2002; Bahrick et al., 2004 for overviews). A key prediction of the IRH is that during early development, intersensory redundancy available in multimodal stimulation is highly salient and this salience promotes selective attention and learning of redundant (amodal) properties of events by infants more effectively than does unimodal stimulation. Since most events are multimodal, this selective attention gives initial advantage to the perceptual processing, learning, and memory of redundant stimulus properties over non-redundant stimulus properties during early development. For example, we found greater sensitivity to amodal properties when intersensory redundancy was available than when it was not. Three-month-old human infants discriminated a change in the tempo of a toy hammer tapping during redundant bimodal (audiovisual) but not during unimodal (auditory or visual) stimulation (Bahrick, et al., 2002). Similarly, 5-month-old infants discriminated a change in a complex rhythm in bimodal audiovisual but not unimodal or asynchronous audiovisual presentations (Bahrick & Lickliter, 2000). Further, consistent with the developmental prediction of the IRH, perception becomes more flexible with additional experience and older infants discriminate the amodal properties of rhythm and tempo in both bimodal and unimodal stimulation (Bahrick & Lickliter, 2004).

Our studies of quail embryos and chicks converge with those of human infants. For example, quail embryos learned an individual maternal call four times faster and remembered the call four times longer into postnatal development when intersensory redundancy was provided by synchronizing a light with the rate and rhythm of the notes of the maternal call (Lickliter, et al, 2002, 2004). Further, we found that intersensory redundancy can direct attention to amodal properties in bimodal stimulation and this redundancy can educate attention to the same amodal properties in subsequent unimodal stimulation where no intersensory redundancy is available. When quail embryos received brief redundant bimodal (auditory and visual) exposure to the temporal features of an individual maternal call followed by unimodal (auditory) exposure to the same call, they showed a significant preference for the familiarized call following hatching.

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In contrast, embryos receiving an equivalent amount of auditory exposure or the reverse order of stimulation (unimodal → bimodal) showed no evidence of learning the maternal call in postnatal testing (Lickliter, et al, 2006).

The IRH also predicts that in unimodal stimulation, infant selective attention to nonredundantly specified properties is facilitated as compared with the same nonredundantly specified properties in bimodal stimulation. This is the case because in unimodal stimulation the lack of redundancy allows other nonredundant or modality-specific properties (such as color, pitch, or timbre) to be selectively attended. Not all interactions with objects and events make multimodal stimulation available and in these cases, nonredundant and modality-specific stimulus properties should stand out because there is no competition from highly salient redundant properties. We again tested 5-month-old infants to assess their detection of orientation (a property available visually but not acoustically) under conditions of bimodal (audiovisual) and unimodal (visual) stimulation. After habituation to films of a hammer tapping in one of two orientations (upward vs. downward), infants detected a change in orientation following unimodal visual habituation, but not following bimodal audiovisual habituation (Bahrick, Lickliter, & Flom, 2006). Optimal differentiation of visible (modality-specific) qualities of an event occurs when there is no concurrent auditory stimulation, which creates intersensory redundancy and competes for infants’ attention. In contrast, we found greater sensitivity to amodal properties when intersensory redundancy was available than when it was not (Bahrick & Lickliter, 2000; Bahrick et al, 2002). Given that selective attention provides the foundation for what is perceived and learned, a fuller understanding of what guides this process and how it changes developmentally seems essential for effective theories of learning and memory. The IRH provides one testable framework for how attentional allocation can guide and constrain perceptual processing, learning, and memory during early development.

Concluding thoughts

We have provided converging evidence across species, developmental periods, and properties of events that support the predictions of our intersensory redundancy hypothesis. Our animal and human-based findings demonstrate the salience of intersensory redundancy for guiding attentional and perceptual processes during early development and indicate how, in a predominately multimodal environment, selective attention and perceptual learning can initially be guided and constrained by detection of amodal relations. Our findings also reveal the conditions under which attention to amodal properties is not facilitated and attention to modality-specific properties and nonredundant aspects of stimulation are favored. As predicted, we found that modality-specific properties of stimulation are best differentiated by infants when competition from intersensory redundancy is not present. Selective attention and perceptual processing in young infants thus appears to be guided and constrained by a dynamic interaction between the nature of the stimulus properties explored (amodal vs. modality-specific) and the types of stimulation available (multimodal vs. unimodal).

We have reached a point in the study of infancy where “what”questions are being replaced by “how” questions (Sullivan, et al, 2006; Thelen & Smith, 1994). We argue that this shift in emphasis from descriptive to explanatory research is best served by coordinated efforts across levels of analysis, methods, and species. Inspired by the pioneering empirical and conceptual work of Gilbert Gottlieb, we are applying a convergent-operations approach utilizing coordinated studies of animal and human infants to begin to identify invariant patterns of perceptual responsiveness that exist across species during early development. This effort involves a back-and-forth exchange that allows animal-based research to inform studies of human infant development and human-based research to likewise inform studies of animal infant development. In our view, Gottlieb’s emphasis on integration (nature and nurture; genes and environment; field and laboratory-based experiments; animal and human-based research) provides a valuable heuristic for achieving a deeper understanding of the intricacies of development. The dynamic webs of resources, relationships, and influence involved in development require us to go beyond single levels of analysis, single-variable designs, or single experimental probes and toward multiple assessments across different domains, conditions, and tasks. As the collected articles of this special issue make clear, this integrative perspective promoted by Gilbert Gottlieb will continue to positively influence the course of developmental science for many years to come.

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