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On a Multistable Dynamic Model of Behavioral and Perceptual Infant Development

ABSTRACT: *In this theoretical work, we treat behavioral and perceptual issues on an equal footing and examine the emergence of mutually exclusive behavioral patterns and perceptual variables during infant development from the perspective of multistable competitive dynamic systems. Accordingly, behavioral modes and modes of perception compete with each other for activation. One and only one mode survives the mode–mode competition, which accounts for the incompatibility of modes being considered. However, the winning behavioral or perceptual state is not predefined. Rather, we argue that during particular stages of maturation multiple modes coexist for the same set of developmental, body-scaled, and environmental parameters or constraints. The winning behavioral or perceptual state depends on these parameters as well as on initial conditions as operationalized in terms of previously performed behaviors or utilized perceptual stimuli. We give explicit examples of our approach and address the emergence of two-handed grasping and catching movements and the emergence of monocular and binocular vision during infant development. In particular, we propose that the emergence of midline crossing movements in 3- to 6-month-old infants involves two independent but interaction control parameters: a body-scaled and a developmental one. Likewise, we argue that the onset of binocularity in infants involves two independent but interaction control parameters: a developmental and an environmental one.* *© 2010 Wiley Periodicals, Inc.* Dev Psychobiol 52: 352–371, 2010.

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INTRODUCTION

Infant development features dramatic changes on the behavioral and perceptual level. On the behavioral level motor milestones such as reaching (Corbetta & Thelen, 1996; Fagard, 2000; Thelen et al., 1993), grasping (e.g., von Hofsten, 1984, 1986; Wentworth, Benson, & Haith, 2000; Wimmers, Savelsbergh, Beek, & Hopkins, 1998), sitting, and bipedal locomotion (Sutherland, Olsen, Biden, & Wyatt, 1988), but also more complex behavioral patterns such as the storage behavior of objects (Bruner, 1973; Kotwica, Ferre, & Michel, 2008) and anticipatory motor activity (Lockman, Ashmead, & Bushnell, 1984; Witherington, 2005), seem to emerge suddenly at particular periods of infant development. The same is true on the perceptual level, with exploitation of qualitatively new information sources such as kinetic information, binocular information (Atkinson, 2000), and pictorial information (e.g., relative size) (see Atkinson, 2000; Kelmann & Arterberry, 2000; Wentworth et al., 2000) that become available to infants at particular ages.

Modeling developmental changes by means of quantitative, explicit models is a crucial step for our understanding of infant development. Theoretical constructs can be illustrated by means of quantitative models and model-based predictions can be made. For example, Thelen, Schöner, Scheier, and Smith (2001) have proposed a quantitative model for Piaget's classical "A-not-B error". In this experimental paradigm, infants

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who have successfully uncovered a toy at location "A" continue to reach to that location even after they watch the toy hidden in the nearby location "B." The model proposed by Thelen et al. (2001) illustrates explicitly how to interpret the A-not-B error from the perspective of embodied cognition. Accordingly, the A-not-B error results from a particular sequential coupling of ordinary processes of goal-directed actions: looking, planning, reaching, and remembering. Thelen et al. used a quantitative model. By means of the quantitative model, novel predictions could be derived. For example, the model motivated to examine the impact of the delay between hiding and searching (see Thelen et al., 2001; Spencer et al., 2006). Van der Maas and Molenaar (1992) have proposed a quantitative model based on catastrophe theory in order to obtain new insights into stagewise cognitive infant development and more specifically the development of conservation in primary school children (see, e.g., Piaget & Inhelder, 1969). The model explains where the criteria (bimodality of test scores, increased variability of responses, etc.) come from that researchers have traditionally used to distinguish between different developmental stages. In doing so, the model provides a theory-driven link between seemingly disconnected criteria obtained in empirical studies. Furthermore, by means of the catastrophe model, it could be demonstrated that connectionist network models perform poorly when they are used for replicating stagewise cognitive processes (Raijmakers, van Koten, & Molenaar, 1996). Wimmers, Savelsbergh, van der Kamp, and Hartelman (1998) used a similar quantitative mode for stagewise *motor* development (see also Newell, Liu, & Mayer-Kress, 2003). In particular, they showed that transitions from reaching without grasping to reaching with grasping during the first 6 months of life also exhibit the characteristic properties of such quantitative stage-to-stage models. That is, the aforementioned catastrophe model performed significantly better in explaining experimental data from reaching and grasping experiments than traditional regression models. Moreover, as a by-product of the model-based data analysis, Wimmers, Savelsbergh, van der Kamp, et al. (1998) could show that arm weight and arm circumference were good predictors for the developmental transition from reaching to grasping as opposed to other body properties such as total body weight that could not be used as predictors (see also Savelsbergh & van der Kamp, 1994). Another set of seemingly disconnected phenomena in infant bouncing, namely, the increase of bouncing amplitude and the decrease in the variability of the bounce periods, could be related to each other by assuming that the key features of development of infant bouncing can be captured by a particular second-order dynamic oscillator model (Goldfield, Kay, & Warren, 1993). Finally, developmental diseases may be addressed. In fact, as far as disease progression is concerned such quantitative modeling approaches have led to the notion that some diseases may be of dynamic nature in the sense that they can be understood as bifurcations of dynamic systems (Friedrich et al., 2000; Glass & Mackey, 1988; Mackey & Glass, 1977). Once the relevant dynamic models have been identified, different types of therapies and medical treatments can be tested in model simulations before applying these therapies and treatments to animal models and patients (see, e.g., Hauptmann et al., 2009; Hauptmann & Tass, 2007; Tass, 1999).

During infant development there is a maturation of the brain, the sensory system, and the muscular-skeletal system. Modeling the physiological details of these systems and the interactions between these systems in order to understand infant development would require models composed of a huge number of interacting components. Mathematically speaking, such systems are defined on high-dimensional generalized coordinate systems. Analytical and computational approaches to examine such interacting component models are mathematically involved and can hardly be carried out due to the complexity of such models. Therefore, the question arises to what extent alternative modeling approaches are available that involve a relatively small number of interacting components. Such alternatives are referred to as low-dimensional modeling efforts because they are defined on low-dimensional generalized coordinate systems. Low-dimensional modeling efforts have indeed been identified in the literature as useful alternatives to high-dimensional approaches. Low-dimensional modeling approaches have been applied frequently in the context of movement coordination (Amazeen, Amazeen, & Turvey, 1998; Beek, Peper, & Stegeman, 1995; Haken, 1996; Haken, Kelso, & Bunz, 1985; Kelso, 1995; Sternad, 2000; Turvey, 1990), posture (Cabrera & Milton, 2002; Collins & DeLuca, 1995; Frank, 2009b; Frank, Daffertshofer, & Beek, 2001; Jeka, Kiemel, Creath, Horak, & Peterka, 2004), muscle force production (Frank, 2005, Frank, Friedrich, & Beek, 2006; Frank, Patanarapeelert, & Beek, 2008; Fuglevand, Winter, & Patla, 1993; Selen, Beek, & van Dieen, 2005; Slifkin & Newell, 1999), and the neural basis of motor control (Frank, Daffertshofer, Peper, Beek, & Haken, 2000; Frank, Peper, Daffertshofer, & Beek, 2006, Jirsa & Kelso, 2004; Grossberg, Pribe, & Cohen, 1997; Uhl, 1999). In particular, motor learning and adaptation has been addressed from this perspective. Accordingly, learning and adaptation are related to parameter changes of low-dimensional systems that are able to capture the essential processes involved in the to-be-learned or to-be-re-learned motor task (Frank, Blau, & Turvey, 2009; Frank, Michelbrink, Beckmann, & Schöllhorn, 2008; Schöner, 1989; Schöner & Kelso, 1988; Stephen, Isenhower, & Dixon, 2009).

Low-dimensional modeling efforts typically involve dynamic system (for definitions of key terms, see Appendix). That is, the focus is on the dynamics of systems: how do systems evolve when time elapses. This is the reason why low-dimensional modeling efforts are also referred to as dynamic systems approaches. The systems are usually defined in terms of differential equations (or difference equations) and exhibit nonlinearities. The nonlinearities in turn reflect interactions between system components. Low-dimensional, dynamic systems approaches have been applied to motor development as well. Key processes that govern motor development have been described in terms of dynamic systems (Corbetta & Vereijken, 1999; Salzmann & Munhall, 1992; Schöner and Thelen, 2006; Schutte, Spencer, & Schöner, 2003; Thelen and Smith, 1994). In fact, it has been argued that nonlinear low-dimensional dynamic modeling is tailored to describe development because nonlinear dynamic systems are those systems in which the emergence of novel system states and transitions between old and new system states can typically be found (Thelen and Smith, 1994; van Geert, 1998a,b). Dynamic systems modeling has the advantage that it provides us with an understanding of how transition processes can occur at all. Accordingly, behavioral, cognitive, and perceptual states can become unstable and other states can emerge or become stable when certain system parameters are changed (Howe & Rabinowitz, 1994; Spencer et al., 2006; Thelen et al., 1993, 2001; van der Maas & Molenaar, 1992). An example of an unstable state is the upright position of a long stick that you may try to balance on your palm. The slightest tremor movement of your palm will make the stick fall down. A simple mechanical illustration of a stable state is the rest state of a spring. If we extend or squeeze the spring such that is becomes longer or shorter as compared to its rest length and release it, then the spring will almost immediately return to its rest state. According to the dynamic systems approach, the stable behavioral and perceptual states are the states that can be performed or experienced. In other words, studying development from a dynamic systems perspective means to study the emergence of stability and studying changes in stability (when stable states become unstable ones).

In view of these considerations, we might summarize a fundamental scenario in development as follows: there is ''age'' as independent variable on one side and the ''stability'' of a behavioral, cognitive, and perceptual state as dependent variable on the other side, and there is a lawful causal relationship between the dependent and independent variable. However, the emergence of new behavioral patterns and perceptual states related to novel accessible information sources depends in general on many factors such as environmental stimuli and characteristics describing the maturation of an infant's body and brain. For example, it is not the size of an object as such which makes an infant to reach for the object with one hand or two hands. Rather, it is the size of the object relative to the infant's own body scales that determines the reaching and grasping behavior (see, e.g., Newell, Scully, Tenenbaum, & Hardiman, 1989; van der Kamp, Savelsbergh, & Davis, 1998). Therefore, it does not come as a surprise that transitions between one-handed grasping and two-handed grasping depend on both environmental factors and body properties of which only the latter properties are related to maturation. In this context, it has been suggested to distinguish between organismic, task-specific, and environmental factors or constraints (Davids, Button, & Bennett, 2008; Newell, 1986). The aforementioned developmental scenario needs to be generalized such that there are several independent variables affecting the stability of a behavioral, cognitive, or perceptual state. Moreover, frequently, the infant is engaged in a situation where several possible states are available rather than a single state. For example, infants that have developed bimanual grasping movements can grasp not too large and not too small objects either with one hand or two hands. Consequently, more comprehensive developmental scenarios need to discuss the relationship between several independent variables on the one side and multiple stable behavioral, cognitive, and perceptual states on the other side. The question of how to model the emergence and stability of behavioral and perceptual states that become relevant for infants in the presence of multiple (and possibly interacting) constraints and how to deal with multiple coexisting behavioral and perceptual states has not been answered rigorously from a dynamic perspective so far. Therefore, the general goal of the present study is as follows:

(a) To introduce a general dynamic model for the development of multistable behavior and perception that addresses adequately the stability of behavioral and perceptual states and allows to incorporate several independent factors.

In particular, on the behavioral side, the development of grasping movements during infancy has not yet found a satisfactory formulation in terms of dynamic systems theory. It has been observed that the development of crossing the body midline emerges in the context of bimanual reaching (van Hof, van der Kamp, & Savelsbergh, 2002). This experimental study has produced a gap in our knowledge about how development should be understood from a theoretical perspective. More precisely, the study by van Hof et al. (2002) has confronted us with a scenario in which two qualitatively different developmental transitions

Table 1. Flowchart of Haken's (1991) Modeling Approach Applied to Understand the Development of Behavioral and Perceptual Multistability From a Biological Departure Point

1	Infant physiology; organismic factors
2	Environmental factors
3	Self-organization and ecological perspective of perception and action
4	Low-dimensional modeling of behavioral and perceptual states close to developmental transitions by means of Haken's (1991) multistable model
5	Behavioral and perceptual multistability versus organismic and environmental factors

(emergence of bimanual grasping and emergence of midline crossing) are not only related to a developmental factor but also depend on an environmental constraint. Therefore, one of our more applied objectives of the study is to answer the following questions:

(b) How, from a dynamic systems perspective, can we understand the emergence of midline crossing actions in the context of the emergence of bimanual reaching? How do changes of environmental factors such as object size and changes of developmental factors (changes in body properties) results in the emergence of different grasping modes and affect the stability of those modes such that two different types of behavioral transitions can be explained?

As far as perception is concerned, infants in general are exposed to object properties that can be perceived in multiple qualitatively different ways. How can we understand the emergence of this kind of perceptual multistability from a dynamic systems point of view? In particular, in the context of vision, objects provide normally sighted observers both with monocular and binocular visual information. However, infants cannot exploit binocular information until they reach a particular level of maturation (Atkinson, 2000). Binocularity needs to emerge in a perceptual transition. After onset of binocularity infants become less reliant on monocular information, but do not lose the ability to use monocular information (van Hof, van der Kamp, & Savelsbergh, 2006). They exploit monocular information when changes in environmental conditions force them to do so. In view of these findings, we need to address the following issues:

(c) How can we understand the transition from monocular vision to binocular vision during infant development in terms of the emergence of perceptual states with differential stability? How can we understand interactions between environmental factors and maturation factors that result in the disappearance and re-appearance of stable monocular perception?

The aim of the present work is to provide answers to the aforementioned questions. To this end, we will make use of a model for multistable pattern recognition proposed by Haken (1991) that has recently been applied to multistable motor actions, namely, grasping (Frank, Richardson et al., 2009). The multistable model proposed by Haken (1991) is grounded in the theory of self-organization (Haken, 2004) and bridges the gap between high-dimensional modeling approaches and low-dimensional modeling efforts by means of dynamics systems. As illustrated in Table 1, in the context of developmental psychobiology, Haken's (1991) modeling efforts actually start on the physiological level of the infant's brain, sensory system, and muscular skeletal system. This level involves organismic constraints (body properties). A rigorous mathematical analysis shows that such complex biological systems defined on high-dimensional generalized coordinate systems effectively behave like low-dimensional dynamic systems close to stages at which qualitative changes of spatio-temporal patterns can be observed (Haken, 1975, 2004). That is, close to stages of developmental change the biological high-dimensional complexity collapses and psychobiological processes can be described in terms of low-dimensional dynamic systems. In this context, a transition from one spatio-temporal pattern to another, qualitatively different pattern is referred to as a bifurcation. Drawing an analogy between motor control systems and complex systems, low-dimensional modeling approaches are tailored to address qualitative changes that can be observed on the behavioral and perceptual level of human motor control systems. We will consider only one type of model. In doing so, our approach—not to distinguish between a model for behavior and a second model for perception—is motivated by ecological accounts for perception–action systems (Gibson, 1979; Michaels & Carello, 1981) that regard perception–action systems as nonseparable entities. We thus arrive at one low-dimensional dynamic model that can be applied to multistable behavioral and perceptual states alike, see Table 1.

EMERGENCE OF BEHAVIORAL PATTERNS AND UTILIZATION OF INFORMATION SOURCES

In line with earlier studies on dynamic systems approaches to motor control, motor learning, and infant development, we regard states of dynamic systems as counterparts of behavioral patterns and accessible information. Qualitative developmental changes involving the emergence of new behavioral patterns and the utilization of new information sources will be understood as bifurcations of dynamic systems (for terminology, see above and Appendix). Multiple qualitatively different behavioral responses and information sources available related to a given motor task will be considered as states of multistable dynamic systems. In an early work, Haken (1991) introduced a benchmark model for multistable pattern recognition. Classical applications concern the recognition of several different patterns and the recognition of different perceptual interpretations of ambiguous figures (Haken, 1991; Mainzer, 1994) as typically used in Gestalt psychology (Wertheimer, 1912). Further applications of the model concern auditory perception (Ditzinger, Tuller, & Kelso, 1997), settlement behavior (Daffertshofer, 2008), motion-induced blindness (Tschacher & Haken, 2007; Tschacher, Schuler, & Junghan, 2006), and grasping (Frank, Richardson et al., 2009). In Haken's original application for pattern recognition, each perceptual pattern is associated with a time-dependent variable that describes the degree of activation of that pattern. For example, in order to model the perception of figures that offer two different perceptual interpretations two time-dependent activation variables were used. That is, it was postulated that each percept exhibits its own activation variable. The activation variables were also considered as amplitudes. The amplitude or activation variable of a particular mode measures whether the corresponding mode has emerged or not. In line with Landau's theory of phase transitions in physics (e.g., ice–water–gas), vanishing and nonvanishing amplitudes refer to qualitatively different situations (Haken, 2004). According to Haken's multistable pattern recognition model, a perceptual pattern is perceived if the corresponding amplitude becomes finite. At the same time, all other amplitudes become zero due to the competitive pattern recognition dynamics, which implies that all alternative patterns are absent. That is, only one amplitude can be different from zero at a time (note that we refer here to the stationary case only; for details see below). Due to this property, Haken's model is also referred to as a winner-takes-all model.

In line with the multistable competitive model proposed by Haken (1991), we will describe behavioral patterns and different types of visual information in terms of amplitudes or activation variables ξ_i with $i = 1, \ldots, n$. For example, we assign one activation variable (say ξ_1) to one-handed grasping and another one (say ξ_2) to two-handed grasping (Frank, Richardson et al., 2009). In the context of infant development, we will assign these two amplitudes to grasping without midline crossing. Consequently, we will introduce two further amplitudes (say ξ_3 and ξ_4) that describe one-handed and two-handed grasps involving crossing the body midline. That is, following Frank, Richardson et al. (2009), we will draw below an analogy between behavioral patterns and the perceptual patterns originally considered by Haken (1991). Likewise, we will draw below an analogy between information sources and perceptual patterns and link the attendance or utilization to different types of information with amplitude variables that describe the degree to which these different pieces of information are utilized or exploited. We will assign one amplitude variable to monocular perceptual information and another variable to binocular information.

Haken's model for n amplitude variables is given by (Haken, 1991)

$$\begin{aligned}
\tfrac{\mathrm{d}}{\mathrm{d}t}\xi_1 &= \lambda_1\xi_1 - B(\xi_2^2 + \cdots + \xi_n^2)\xi_1 - C(\xi_1^2 + \cdots + \xi_n^2)\xi_1 \\
&\vdots \\
\tfrac{\mathrm{d}}{\mathrm{d}t}\xi_n &= \lambda_n\xi_n - B(\xi_1^2 + \cdots + \xi_{n-1}^2)\xi_n - C(\xi_1^2 + \cdots + \xi_n^2)\xi_n
\end{aligned} \tag{1}$$

In our context, the model describes the *evolution* of amplitudes that describe the activation of behavioral or perceptual states (where the exploitation of a particular kind of information source will be considered as a perceptual state). Note that the amplitudes ξ_i are functions of time t: $\xi_1(t), \ldots, \xi_n(t)$. It can be shown that for any $B, C > 0$ model (1) eventually relaxes to a stationary (i.e., time-independent) state (Haken, 1991). Mathematically speaking, a stationary state is a n-dimensional vector $(\xi_1, \ldots, \xi_n)$ that corresponds to a particular location in the model space spanned by the coordinates $\xi_1, \ldots, \xi_n$. These locations reflect activated behavioral patterns or utilized information sources when amplitudes are finite (i.e., different from zero). In doing so, each behavioral or perceptual state becomes its own position or point in the n-dimensional model space $\xi_1, \ldots, \xi_n$. The model space is an example of a low-dimensional generalized coordinate system. The number of coordinates n is typically small as compared to the number of components involved in high-dimensional modeling approaches (e.g., networks of 10,000 units or multijoint biomechanical models). As mentioned above, it can be shown that for $B, C > 0$ model (1) eventually relaxes to a stationary state. The stationary case is characterized by points in the n-dimensional model space at which the dynamic system does not change with time. Such points are called fixed points.

Stationary states can be stable or unstable. It is this stability issue that can only be understood in the context of a dynamic system. This is, although we will focus on the fixed points (reflecting the behaviors and percepts as such) of the model given by Equation (1), we need to bear in mind that the model is a dynamic model that describes variables that evolve with time. In line with our comments in the Introduction Section, a stationary state (fixed point) is called stable if any (sufficiently small) perturbation that drives the dynamics out of the state will decay and vanish such that the dynamics eventually will relax back to the state. Conversely, we are dealing with an unstable state if perturbations increase with time (see also Appendix). How does this concept of stability relate to behavioral and perceptual states? Roughly speaking, a stable behavioral or perceptual state is unaffected by disturbances. That is, the behavioral or perceptual state can emerge even in the presence of disturbing stimuli (Corbetta & Thelen, 1996)—stimuli not related to the state. In contrast, unstable behavioral and perceptual states are crucially affected by any kind of disturbing influences. Any such perturbation will immediately destroy the behavioral and perceptual states, which makes it impossible for such a state to emerge at all. In theory, unstable behavioral and perceptual states can only be performed or perceived if we would be able to switch off all disturbing influences.

The parameters λ_i occurring in Equation (1) are real numbers that can assume both positive and negative values. They determine, roughly speaking, the stability of stationary states described by the model (Haken, 1991; Frank, Richardson et al., 2009) and in our context reflect negative and positive feedback. If a parameter is positive, then the corresponding behavioral or perceptual state receives positive feedback such that there is a tendency that the state becomes activated (i.e., there is a tendency that the activation variable increases). In contrast, a negative parameter indicates that the corresponding state receives negative feedback such that the activation of the state decays to zero. The parameters B and C are positive and determine the interaction between different behavioral or perceptual modes as well as the saturation dynamics. In order to separate these two properties, it is useful to introduce the parameter $g = 1 + B/C$ which for B, $C > 0$ satisfies $g > 1$. Then Equation (1) becomes

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t}\xi_1 &= \lambda_1\xi_1 - Cg(\xi_2^2 + \cdots + \xi_n^2)\xi_1 - C\xi_1^3 \\ \frac{\mathrm{d}}{\mathrm{d}t}\xi_n &= \lambda_n\xi_n - Cg(\xi_1^2 + \cdots + \xi_{n-1}^2)\xi_n - C\xi_n^3 \end{aligned} \tag{2}$$

Equation (2) reveals that g occurs as coefficient of the mixed terms that describe mode–mode interactions. Consequently, g is a measure for the strength of the interactions between different behavioral patterns or perceptual states. As mentioned above, we are concerned with mutually exclusive modes. Accordingly, the mixed term (term involving the g parameter) describes competition between different behavioral and perceptual states. The behavioral and perceptual states inhibit each others as indicated by the minus sign in front of the mixed term. The larger the g the stronger the competition and inhibition. The degree of competition is minimal if the parameter B tends to zero, which corresponds to the case $g = 1$. It can be shown that C primarily determines the scale in which stationary values of the activation variables are measured (see, e.g., Frank, Richardson et al., 2009, for $n = 2$). That is, C does not change qualitatively the relationship between the locations of behavioral and perceptual states in the n-dimensional model space $\xi_1, \ldots, \xi_n$. Increasing (decreasing) C implies that all locations shift further away (come closer) to the origin $\xi_1 = \cdots = \xi_n = 0$.

As mentioned above, we distinguish between stable and unstable states of infant behavior and perception. In fact, in the context of multistability there is a need for discussing this issue in a slightly more sophisticated way, see Table 2. First of all, if a feedback parameter λ_i is negative, then we have in general $\xi_i = 0$ and the corresponding behavioral or perceptual state has neither a stable nor an unstable representation in the model. If a feedback parameter is

Table 2. Interpretations of Zero and Nonzero Amplitude Variables

Feedback λ	State i	Ampl. ξ	Interpretation
Negative	Does not exist	$\xi_i = 0$	It is physically impossible to perform the behavior i. The information i is not provided to the infant
Positive	Unstable	$\xi_i = 0$	The behavioral or perceptual state is unstable because it is inhibited by another behavioral or perceptual state. As a result, the infant is not able to perform without assistance the behavior i although it is physically possible to make the infant performing the behavior i. Likewise, the infant cannot exploit the information variable i although the environment provides the information i to the infant
Positive	Stable	$\xi_i = 0$	This case occurs only in the multistable domain. The infant does not exhibit the behavioral or perceptual mode i although the infant could perform or exploit the mode i. Instead of performing the behavioral or perceptual mode i, the infant is engaged in a behavioral or perceptual mode k (which has a nonvanishing amplitude $\xi_k > 0$)
Positive	Stable	$\xi_i > 0$	Behavior i is performed. Perceptual state i is experienced

positive then this does not necessarily imply that its corresponding behavioral or perceptual state is stable. The state can be unstable due to the inhibition by other states. If a feedback parameter is positive and there is no inhibition by other states or the inhibition by other states is not sufficiently strong, then the corresponding state is stable. Still this does not necessarily imply that the infant performs that behavioral pattern or attends to the corresponding information source. There might be multiple stable behavioral or perceptual states. Since we consider mutually exclusive states, the infant can only select one of these states. In line with the notion of a dynamic model, the initial conditions will determine which state will be selected out of all stable states. In an experimental context, the initial conditions describe the pattern of activation which exists right at the beginning of the experimental trial. Since the model exhibits multistability and sensitivity to initial conditions, the model can account for history-related phenomena such as hysteresis (see, e.g., Frank, Richardson et al., 2009). Let us exemplify the aforementioned three different cases of positive feedback in the context of grasping during infant development (see also Tab. 2). In general, as long as a performance pattern can physically be performed, we assume that there is a positive feedback for that pattern. According to the model defined Equation (1) exhibits a location or state different from the origin which represents the behavioral pattern. For example, relative small objects can be grasped with one hand by infants. Consequently, the lambda parameter of one hand grasping is positive and a point in the model space exists that reflects the behavior. If an object is relatively larger (e.g., a ball whose diameter exceeds the hand span of an infant), then the infant is not able to grasp the object with one hand. The aforementioned location disappears (or merges with the origin). Adults tend to grasp relatively small objects with one hand. In this case one-handed and two-handed grasping can be performed but the two-handed grasping mode is inhibited by the one-handed mode as a result of the competition processes between the unimanual and bimanual modes. In the model the feedback parameters of both modes are positive but only the one-handed mode corresponds to a stable state. The two-handed model corresponds to an unstable state.

For $n = 2$ the model has been used to study the emergence of transitions between one-handed and two-handed grasps (Frank, Richardson et al., 2009). In this context, it has been shown that the model predicts hysteresis, which has indeed been found in experimental work on grasping (Cesari & Newell, 1999, 2000; Lopresti-Goodman, Richardson, Baron, Carello, & Marsh, 2009; Newell et al., 1989; Richardson, Marsh, & Baron, 2007; van der Kamp et al., 1998). Moreover, it has been shown that for model (1) with $n = 2$ bifurcation lines can be computed from (Frank, Richardson et al., 2009)

$$\lambda_1 = \frac{\lambda_2}{g}$$
$$\lambda_2 = \frac{\lambda_1}{g} \qquad (3)$$

Each equation defines one bifurcation line (we will depict these lines below when discussing monocular and binocular vision). For example, the first relation of Equation (3) defines the straight line $\lambda_1 = \lambda_2/g$ when λ_1 and λ_2 are plotted on the horizontal and vertical axes of a two-dimensional parameter space. The line defines the conditions for the parameters at which a bifurcation occurs (hence the name "bifurcation line"). This implies also that the line can be used to separate between subspaces of the parameter space in which fixed points are stable or unstable. One can show that for $\lambda_1 > \lambda_2/g$ the mode ξ_1 is stable and ξ_2 is unstable. Likewise, for $\lambda_2 > \lambda_1/g$ the mode ξ_2 is stable and ξ_1 is unstable. For lambda parameters that fall in between these two cases both modes are stable and the dynamic system exhibits bistability (which is a special case of the multistability mentioned in the Introduction Section).

For $n > 2$ a similar analysis as in Frank, Richardson et al. (2009) yields the following result (for mathematical details see also Frank, 2009a). Let $\lambda_{max} > 0$ denote the maximal lambda parameter (or the value of one of the maximal lambda parameters if two or more parameters are maximal simultaneously; e.g., $\lambda_1 = \lambda_2 = \lambda_{max}$). Then, all states i are stable for which $\lambda_i > \lambda_{max}/g$ holds. That is, all behavioral and perceptual modes are stable and can be performed or exploited that exhibit feedback parameters $\lambda_i > \lambda_{max}/g$. It is useful to illustrate this result graphically. To this end, we plot all positive feedback parameters in a

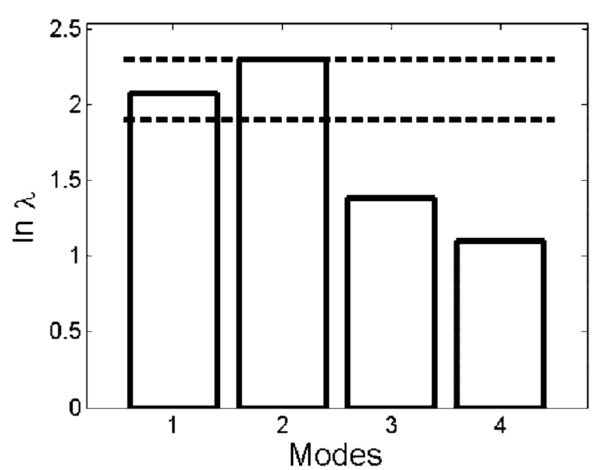

FIGURE 1 Graphical stability analysis of Haken's model (1). Behavioral and perceptual states i with feedback parameters λ_i that fall in between the dashed lines are stable (here $i = 1$ and 2). All others states are unstable (here $i = 3$ and 4). Illustration for $g = 1.5$, $\lambda_1 = 8$, $\lambda_2 = 10$, $\lambda_3 = 4$, and $\lambda_4 = 3$.

logarithmic scale, see Figure 1. The domain of stable modes is then bounded by two horizontal lines. The upper line is just at the top of $\ln(\lambda_{\max})$. From this upper line we subtract the distance $\ln(g)$ in order to obtain the position of the lower line. All feedback parameters that fall in between the upper and lower lines are associated with states or modes that are stable at the same time. Feedback parameters that fall below the lower line are related to unstable states. Note that the negative feedback parameters do not show up in this graph because the corresponding behavioral and perceptual states cannot affect the states with positive feedback. In sum, by means of the parameters λ_i, we can distinguish between stable and unstable behavioral and perceptual modes. Consequently, transitions between different behavioral modes and transitions between utilization of different information sources can be induced by changes of feedback (lambda) parameters. This is the reason why we will assume that feedback parameters depend on experimentally accessible control parameters.

FROM UNIMANUAL TO BIMANUAL GRASPS AND MIDLINE CROSSINGS

Infants begin to reach and grasp between 3 and 6 months of age (Thelen et al., 1993; von Hofsten, 1984). During this period different kinds of grasping patterns occur. Young infants tend to reach and grasp with one hand (Corbetta & Thelen, 1996; Fagard, 2000). At about 4 months of age infants begin to reach and grasp with two hands and to cross the midline during reaching movements (Morange & Bloch, 1996; Provine & Westerman, 1979). For an illustration see Figure 2.

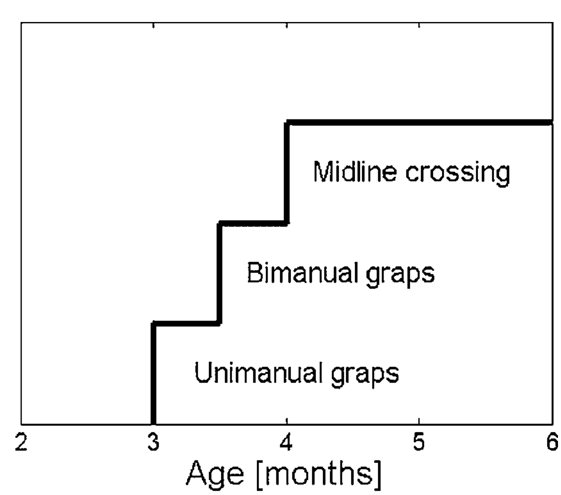

FIGURE 2 Bifurcations of a dynamic system describing the development of grasping patterns.

In terms of the dynamic systems approach we say that there are bifurcations from the unimanual grasping patterns without midline crossing to bimanual grasping patterns without midline crossing and reaches involving midline crossing. It has been argued that the developmental factors leading to bimanual grasping and midline crossing depend on each other (van Hof et al., 2002). That is, midline crossing develops in the context of bimanual grasps. Only if infants have developed the ability to perform bimanual grasping then midline crossing can emerge as a new performance pattern. Consequently, there is a bifurcation from a monostable motor control system featuring only one-handed grasps without midline crossings to a bistable motor control system featuring both one-handed and two-handed grasps without midline crossing. Subsequently, there is a secondary bifurcation related to the emergence of midline crossing movements. In order to describe these two types of bifurcations, we introduce a developmental parameter which will be denoted by β and is a real positive number. β is strongly correlated to age but in general does not correspond to age as such. We distinguish between small, medium, and large values of β. As an example we may relate these parameter domains to the age groups (12-, 18-, and 26-week-old infants) of the study by van Hof et al. (2002). We propose to use β as a control parameter. Accordingly, for small values of the developmental parameter β, we can only observe one-handed reaching and grasping movements in infants. There is only one stable state: the state of one-handed grasps without midline crossing. Other states exist but are unstable. At a critical value of β a bifurcation occurs such that for medium values of β we can observe that infants both grasp with one or two hands. Still they do not cross the body midline during grasping. In line with our comments made earlier concerning stability (see Tab. 2), infants at that stage of development maturity exhibit perception–action systems with two stable behavioral patterns: one-handed (1H) grasping and two-handed (2H) grasping. Both grasping modes do not involve midline crossings. Increasing the developmental control parameter β even further, another bifurcation occurs such that for larger values of β one-handed grasping with midline crossing (1HC) and two-handed grasping with midline crossing (2HC) become stable as well. This is summarized in Table 3.

In addition, it has been found that infants who are able to perform both unimanual and bimanual grasping patterns preferably grasp small balls with one hand and large balls with two hands (van Hof et al., 2002). This finding is in line with several studies both on children and adults which showed that there are body-scaled transitions in grasping such that relatively small objects are preferably grasped with one hand, whereas relatively large objects tend to be grasped with two hands (Cesari &

Table 3. Partial Bifurcation Diagram for Infant Grasping

	Stable Behavioral States	Unstable Behavioral States
β large	1H, 1HC, 2H, 2HC	
β medium	1H, 2H	1HC, 2HC
β small	1H	1HC, 2H, 2HC

Note. Only the developmental control parameter β is considered.

Newell, 1999, 2000; Lopresti-Goodman et al., 2009; Newell et al., 1989; Richardson et al., 2007; van der Kamp et al., 1998). That is, we have a body-scaled parameter, the size of an object in relation to the hand size of a person, which determines whether an object is grasped preferably with one or with two hands. We will denote this parameter with α which again is a real positive number. α is another control parameter (Frank, Richardson et al., 2009). From studies on children (age of 6 years and older) and adults, it is known that there is a hysteretic domain in which both one-handed or two-handed grasps are performed depending on particular experimental manipulations (Cesari & Newell, 1999, 2000; Lopresti-Goodman et al., 2009; Newell et al., 1989; Richardson et al., 2007; van der Kamp et al., 1998). A quantitative discussion of these hysteretic domains can be found in Frank, Richardson et al. (2009). Just as for the parameter β, we consider next three parameter domains for the parameter α in which the relative object size assumes small, medium, and large values. Let us scale the parameter α such that all objects for which it is physically impossible to grasp them with one hand we have $\alpha > 1$. In line with our previous discussion and in view of the experimental and theoretical results reported in previous studies we can construct the bifurcation diagram shown in Table 4.

The study by van Hof et al. (2002) revealed that there is an interaction between the control parameters α and β. If β is small, then there is no impact of α. If β is medium or large, then there is an impact of α. Taking this interaction between α and β into account, we can merge Tables 3 and 4 and arrive at the result shown in Table 5. Only the stable behavioral states are shown and also the case $\alpha > 1$ is neglected.

We have indicated with (!) the cases that have been addressed in experiments so far. With (?) we have denoted predictions that can be drawn from the model and have not yet been verified in experimental studies. In order to show qualitatively that the behavioral modes listed in Table 5 are predicted by the multistable dynamic model (1), we need to discuss how the parameters λ_i depend on the control parameters α and β. Let us first present a qualitative discussion that involves both control parameters α and β using the graphical approach illustrated in Figure 1. To begin with, we assign the amplitudes $\xi_1, \ldots, \xi_4$ to the different grasping modes 1H, 2H, 1HC, 2HC, see Table 6.

In Figure 3 it is shown how the lambda parameters depend qualitatively on the control parameters α and β. For example, for β small and all kinds of α parameters and for β medium and α small we have qualitatively the same ordering of the lambda parameters. λ_1 is maximal which implies that ξ_1 can assume a stable stationary activation value. This in turn reflects that the 1H mode can be performed. All other feedback parameters are smaller than λ_1 and there is a gap of at least $\ln(g)$ between λ_1 and the other lambda parameters. Consequently, the amplitudes ξ_2, ξ_3, ξ_4 can only assume unstable stationary activation levels. The infant does not perform either of the 2H, 1HC, 2HC modes. The panel shows qualitatively the ordering of the feedback or lambda parameters. The exact order of the parameters λ_2, λ_3, λ_4 is irrelevant for our purposes. We have plotted them like $\lambda_3 > \lambda_2 \sim \lambda_4$. However, any other order would yield qualitatively the same result as long as the lambda parameters λ_2, λ_3, λ_4 do not exceed the lower line indicating the multistability domain. Similar considerations can be carried out for all other panels shown in Figure 3. For example, for β large and α medium all four lambda parameters have values that fall into the multistability domain. This implies that infants exhibit perception–action systems with four stable states in the four-dimensional model space spanned by the coordinates ξ_1, ξ_2, ξ_3, ξ_4. These stable states describe the activation of the four behavioral modes 1H, 2H, 1HC, 2HC. Any of these modes can be activated and performed.

In order to illustrate the transitions predicted by our model more quantitatively, we need to relate the feedback parameters λ_1, λ_2, λ_3, λ_4 to the control parameters α and β. To this end, we linearize the relationship between feedback parameters and the relative

Table 4. Partial Bifurcation Diagram for Infant Grasping

	α Small	α Medium	α Large But $\alpha < 1$	$\alpha > 1$
Stable states	1H	1H, 2H	2H	2H
Unstable states	2H		1H	
Behavioral states without fixed point representations				1H

Note. Only the control parameter α is considered.

Table 5. Bifurcation Diagram for Infant Grasping Involving Two Control Parameters α and β

	α small	α medium	α large
β large	1H(!),1HC(!)	1H(!),2H(!) 1HC(?),2HC(?)	2H(!), 2HC(!)
β medium	1H(!)	1H(?), 2H(?)	2H(!)
β small	1H(!)	1H(!)	1H(!)

object size α as suggested earlier (Frank, Richardson et al., 2009). We put $\lambda_1 = s_1(1-\alpha)$, $\lambda_3 = s_1(1-\alpha)$, $\lambda_2 = s_2\alpha$, $\lambda_4 = s_2\alpha$. The parameter s_1 measures how fast the feedback to one-handed modes (with and without crossing) decrease when we increase relative object size. Likewise, the parameter s_2 measures the slope of the increase of the feedback to the two-handed modes when object size is increased. Note that (as opposed to Frank, Richardson et al., 2009) we neglect a possible offset of the two-handed lambda parameter and in order to reduce the number of parameters assume that for vanishing relative object size the feedback parameters tend to zero. In order to reduce further the number of parameters, we point out that only the difference between the slopes s_1 and s_2 determines transitions points (see Frank, Richardson et al., 2009). Therefore, we put $s_2 = 1$ and $s_1 = s$. The slope parameter s should be regarded as a measure of how strong feedback variations to the one-handed modes are relative to feedback variations to the two-handed modes. The linear approximations used above and in earlier work (Frank, Richardson et al., 2009) should be considered as first-order approximations to any kind of nonlinear relationship that might hold between the feedback parameters λ_i and the control parameter α. In the absence of experimental evidence and theoretical arguments for the role of nonlinearities, the linear approximations are the most parsimonious and plausible choice. As far as the age-related control parameter β is concerned, we are inclined to postulate that β has only an impact in a relatively small range of its possible values. More precisely, in the pretransition and posttransition parameter domain (e.g., for ages long before and long after the typical ages at which transition to midline crossing occur) the parameter should not induce changes in the feedback parameters λ_i.

Table 6. Mapping Between Grasping Modes and Activation Variables (Amplitudes) of the Dynamic System Defined by Equation (1)

Activation Variables	Feedback Parameters	Grasping Modes
ξ_1	λ_1	1H
ξ_2	λ_2	2H
ξ_3	λ_3	1HC
ξ_4	λ_4	2HC

In line with this reasoning, we assume that the impact of β can be described in terms of a sigmoid function. Such sigmoid functions are widely used in neural network theory (Haykin, 1994; Murray, 1989) for the same reason as mentioned above: the ability to describe a threshold-type functional behavior. As discussed earlier, the feedback parameters $\lambda_1, \ldots, \lambda_4$ are subjected to an interaction between α and β. Therefore, we multiply the relationship obtained so far with particular functions $f_1, \ldots, f_4$ depending on β. In doing so, we obtain: $\lambda_1 = s(1-\alpha)f_1$, $\lambda_3 = s(1-\alpha)f_2$, $\lambda_2 = \alpha f_3$, $\lambda_4 = \alpha f_4$. Again, what matters is only how these functions vary relative to each other when β increases. Therefore, we can neglect one of these functions. We put $f_1 = 1$. Alternatively, we may say that we neglect the impact of the developmental control parameter on the grasping mode, which usually emerges first during development: the one-handed grasping mode without midline crossing. As argued above, we describe all other functions f_i reflecting the impact of β by means of sigmoid functions that increase from zero to particular saturation levels w_i. The sigmoid functions are characterized by a parameter b_i that describes at which developmental state the sigmoid functions reach 50% of their saturation levels. At these points the slope is maximal and the curvature changes its sign. That is, we have an inflection point. The slope of the increase at the inflection point will be denoted by $1/\sigma_i$. If σ_i is small then the slope is large and there is a rapid transition from zero to the saturation value. That is, the transition region is small. Therefore, the parameters σ_i describes the size (or width) of the transition region. In short, the functions f_i are given by $f_i(\beta) = h(\beta, w_i, b_i, \sigma_i)$, where h is a standard sigmoid function defined by $h = w/(1+\exp(-(\beta-b)/\sigma)$. From our qualitative discussion related to Figure 3 it follows that the inflection points b_3 and b_4 for midline crossing should be larger than the inflection point b_2 of the 2H grasping mode without midline crossing. Accordingly, we put $b_3 = b_4 = b_c > b_2 = b_{2H}$. Likewise, we assume that the sigmoid function parameters for grasping involving midline crossing are approximately the same across the one- and two-handed conditions such that we put $w_3 = w_4 = w_c$, $\sigma_3 = \sigma_4 = \sigma_c$ and likewise we use the notations $w_2 = w_{2H}$ and $\sigma_2 = \sigma_{2H}$. Then, the lambda parameters depend explicitly on the control parameter like

$$\begin{aligned} \lambda_1 &= s(1-\alpha) \\ \lambda_3 &= s(1-\alpha)h(\beta, w_c, b_c, \sigma_c) \\ \lambda_2 &= \alpha h(\beta, w_{2H}, b_{2H}, \sigma_{2H}) \\ \lambda_4 &= \alpha h(\beta, w_c, b_c, \sigma_c) \end{aligned} \tag{4}$$

The domains in which the different modes are stable (or multistable) are shown in Figure 4 for a particular set of parameters with $w_c = w_{2H}$. The parameters were chosen such that transitions from one-handed to two-handed grasping occur at relative object sizes of .7. The inverse

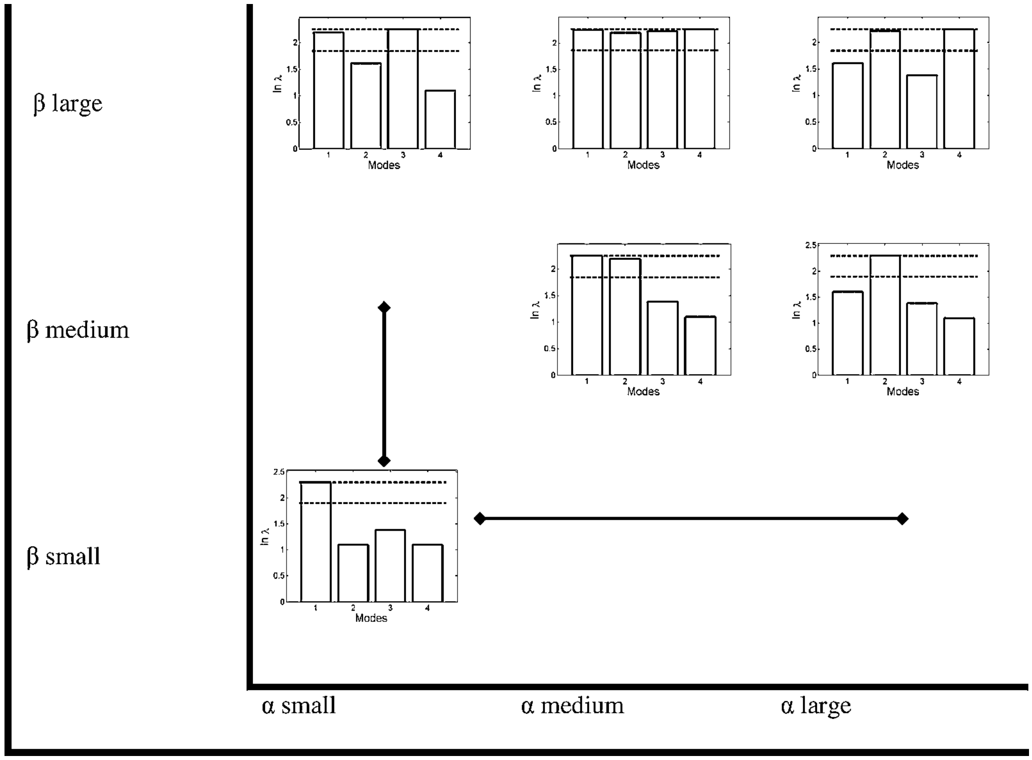

FIGURE 3 Dependency of the feedback parameters $\lambda_1, \ldots, \lambda_4$ of the dynamic model (1) on the control parameters α and β.

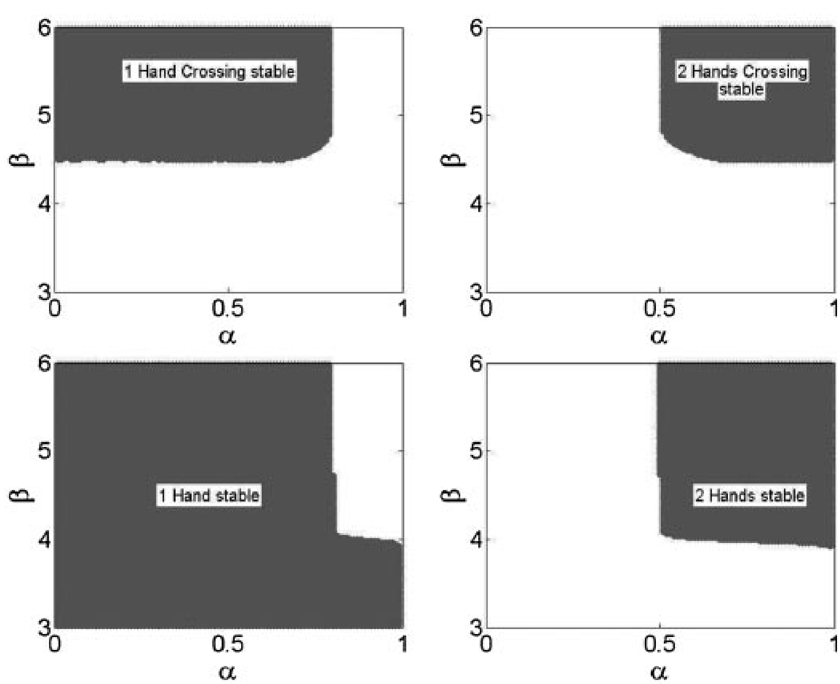

FIGURE 4 Bifurcation diagrams computed from Equation (4) and the graphical solution method illustrated in Figure 1. The stability domains (shaded gray) of the four different grasping modes are shown as functions of α and β. Bottom-left: ξ_1 (1H). Bottom-right: ξ_2 (2H). Top-left: ξ_3 (1HC). Top-right: ξ_4 (2HC). Parameters: $g=2$, $s=2$, $w_{2H}=w_c=1$, $b_{2H}=4.5$, $b_c=4.0$, $\sigma_{2H}=.02$, and $\sigma_c=.1$.

transitions occur at about $\alpha = .5$. The developmental parameter β was assumed to reflect age in months. For the parameter set used to generate Figure 4, two-handed grasping becomes stable at about 4 months. Midline crossings can be found at an age of about 4.5 months. A detailed analysis of the parameter space involving the parameters g, s, w_c, w_{2H}, b_c, b_{2H}, σ_c, σ_{2H} is beyond the scope of our study. Here, we only would like to mention that the model predicts a so-called reentrant bifurcation—a type of bifurcation known in the theory of multiplicative stochastic processes (Frank, 2005). For a particular parameter set with $w_c > w_{2H}$ the stability panels shown in Figure 5 were obtained. The two-handed grasping mode without midline crossing becomes stable for medium-sized objects at the age of about 4 months. However, when midline crossing emerges, the two-handed noncrossing mode for that particular range of object sizes becomes unstable again.

FROM USING MONOCULAR TO USING BINOCULAR INFORMATION

In our second example we discuss the emergence of the use of binocular perception during infant development. At birth the visual system is not fully functional which implies that the visual system can exploit monocular information but it cannot use binocular information (Atkinson, 2000). At the age of 8–24 weeks the visual system has reached a state of maturity such that binocular information becomes available, see Figure 6.

In the context of dynamic systems theory, the development to binocularity can be described by a bifurcation from a monostable to a bistable system. Before the onset of binocularity the system exhibits only one stable perceptual state: the exploitation of monocular information. After onset of binocularity the system exhibits two stable modes of perception: one reflecting the utilization of monocular sources of information and the other reflecting the use of binocular sources of information. Accordingly, we introduce the amplitudes ξ_1 and ξ_2 that describe attention to or the exploitation of monocular and binocular information, respectively, see Table 7. In this context it is useful to consider visual information as a measurable entity to which we can assign a real positive number. If the amount of visual information is relatively close to zero, the corresponding visual information is absent. In contrast, the visual information is present if there is a relatively large amount of visual information. In this sense, exploited visual information variables can be introduced that have both a qualitative and quantitative aspect. For example, monocular information is qualitatively different from binocular information. In addition, the detection of monocular information involves a sensory input that has a quantitative aspect. It is plausible to relate in the context of perception the different types of visual information to different activation variables or amplitudes. Each activation variable or

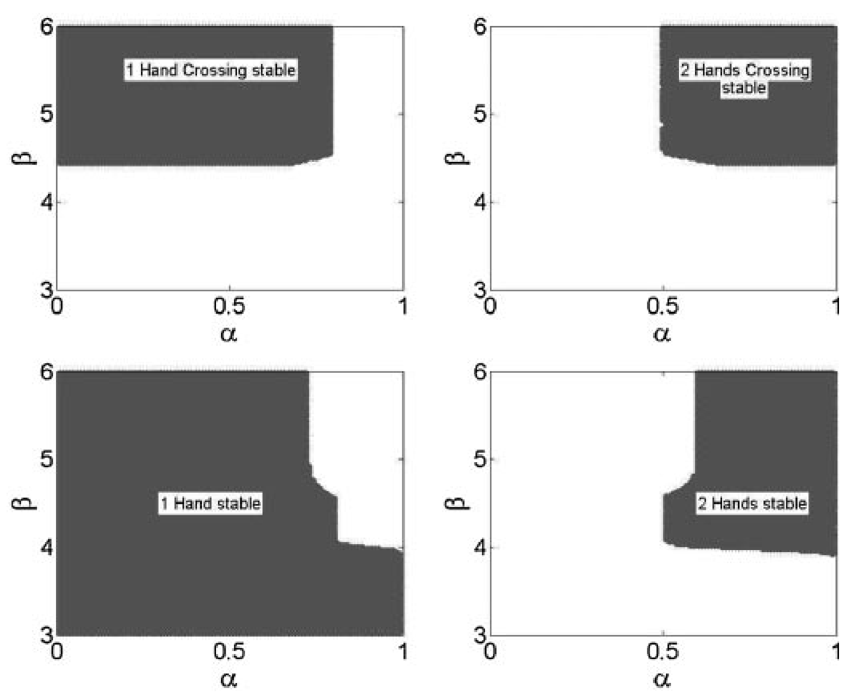

FIGURE 5 As in Figure 4 but for $w_{2H} = 1$ and $w_c = 1.5$.

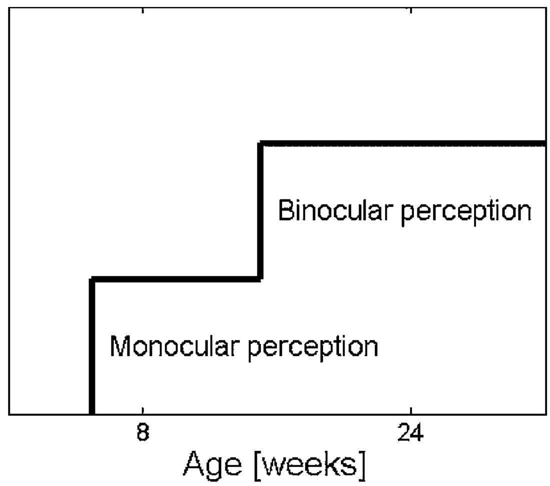

FIGURE 6 Developmental bifurcation from a monostable monocular visual system to a bistable system involving both monocular and binocular vision.

amplitude describes the degree to which its information source is utilized or the degree to which attention is directed toward the corresponding information source. If ξ_2 is zero but ξ_1 is larger than zero, then monocular information is exploited. If ξ_1 is zero but ξ_2 is larger than zero then binocular information is used (see Tab. 7).

A necessary condition for the amplitude of a perceptual state to be finite is that the corresponding dynamic state is stable. As mentioned earlier, the stability of the perception–action system described by Equation (1) depends on the relationship between the lambda parameters occurring in Equation (1). The two bifurcation lines defined by Equation (3) are shown in Figure 7 for a strong and weak competition between monocular and binocular sources of information. In the parameter domains labeled "Monocular" only the amplitude ξ_1 can assume stable stationary values. That is, only monocular information can provide the basis for an emerging stable perceptual state. Therefore, an infant characterized by lambda parameters λ_1 and λ_2 falling into this domain picks up monocular information. Likewise, in the domains "Binocular" only ξ_2 exhibits a stable state in the two-dimensional model space spanned by ξ_1 and ξ_2. An infant with corresponding feedback parameters exploits binocular information. In the domains between the bifurcation lines both monocular and binocular information provide a basis for stable perceptual states. Consequently, an infant exploits either monocular or binocular information. Note that this bistability domain shrinks if the degree of interaction g between the perceptual modes decreases. That is, for large g the bistability domain is larger. If g approaches unity (minimal mode–mode interaction), then the two bifurcation lines collapse and the bistability domain vanishes.

Table 7. Mapping of Visual Percepts or Different Types of Visual Information to Amplitude Variables of the Dynamic Model Defined by Equation (1)

Amplitude Variables	Feedback Parameters	Percepts/Types of Information
ξ_1	λ_1	Monocular
ξ_2	λ_2	Binocular

We will use Figure 7 to identify the relevant control parameters for the development of the use of binocular information. First, we see that the parameter λ_2 depends on an infant–environment parameter α which describes whether visual information is provided to one or two eyes. For example, in the study by van Hof et al. (2006) infants were tested while one eye was covered with an eye patch. In this experimental condition, the infant's perception was basically monocular. For the sake of convenience, we put λ_2 equal to the infant–environment parameter α: $\alpha = \lambda_2$. In particular, α is negative if visual information is provided only to one eye. On the contrary, we have $\alpha > 0$ when information is provided to both eyes. As mentioned earlier, the amplitude dynamics subjected to a negative feedback decays to zero as a function of time. Consequently, for $\alpha < 0$ the amplitude of binocular information ξ_2 equals zero. Second, we propose that λ_1 depends on the developmental control parameter β which measures the degree of development of an infant and (as mentioned above) is highly correlated to age but not identical with age. From Figure 6 we see that there is a transition to the use of binocular information at a certain threshold value of β. In view of the results presented in Figure 7, we assume that λ_1 decreases when β increases. In this case, the multistable model (1) yields the experimentally observed transition from monocular to exploiting binocular information. In order to model this reciprocal relationship between λ_1 and β, we put

$$\lambda_1 = \frac{L_0}{L_1 + \beta} \qquad (5)$$

where L_1 and L_2 are positive constants. Note that any other reciprocal relationship would yield qualitatively similar results. Using Equation (5), the bifurcation diagrams shown in Figure 7 can be transformed into the bifurcation diagrams shown in Figure 8. The two panels illustrate the bifurcation diagrams in the parameter space spanned by the infant–environment parameter α and the developmental control parameter β.

The parameters α and β are independent control parameters because they describe qualitatively different scenarios of infant development. They describe infants who are at various stages of development and live and act in environments providing information to either one or two eyes. There is an interaction between the impacts

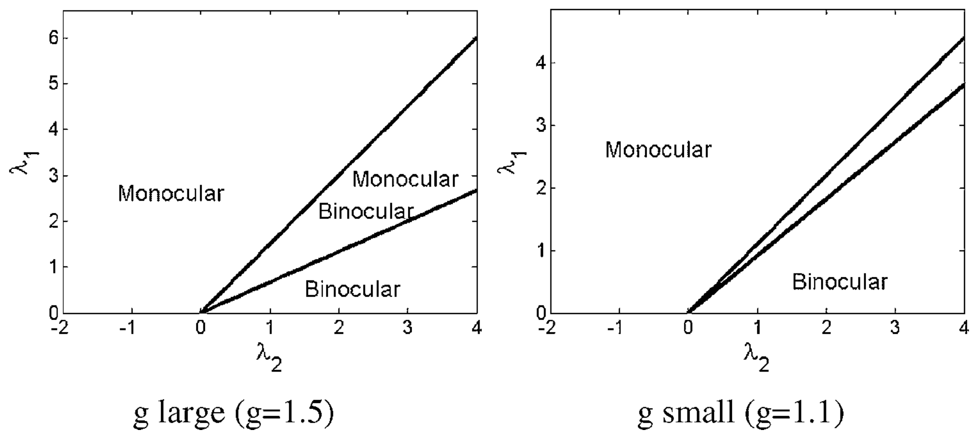

FIGURE 7 Bifurcation diagrams computed from Equation (3) and plotted in the two-dimensional space spanned by the feedback parameters λ_1 and λ_2.

of the control parameters α and β. If α is negative (one-eyed viewing mode), then β has no impact at all. Only if α is positive, then the two control parameters in combination determine whether the perception–action system is monocular monostable, binocular monostable, or bistable.

Previous experimental studies have explored to a certain extent the bifurcation diagrams shown in Figure 8. As indicated with the symbol (!) previous studies demonstrated that in general the utilization of monocular and binocular information by infants depends on the degree of development (see, e.g., Atkinson, 2000). In such studies the bifurcation diagram was typically explored along a vertical line for a fixed positive value of λ_2. That is, stimulation of both eyes was assumed to hold for at all ages and different age groups were considered (i.e., β was varied), see Figure 9a. In particular, van Hof et al. (2006) used a data analysis technique introduced earlier (Caljouw, van der Kamp, & Savelsbergh, 2004; van der Kamp, Savelsbergh, & Smeets, 1997) in order to determine whether infants exploited monocular or binocular information for the purpose of reaching and grasping. This technique takes advantage of the observation that time-to-contact estimates based on monocular information are subjected to object size, whereas time-to-contact estimates based on binocular information are not. Van Hof et al. showed that the development of reaching and catching movements during infancy involves a transition from monocular to binocular information. That is, van Hof et al. explored the bifurcation diagram shown in Figure 9 along the vertical line in the context of reaching and catching.

Moreover, in the study by van Hof et al. (2006) eye patches were used in order to provide visual information

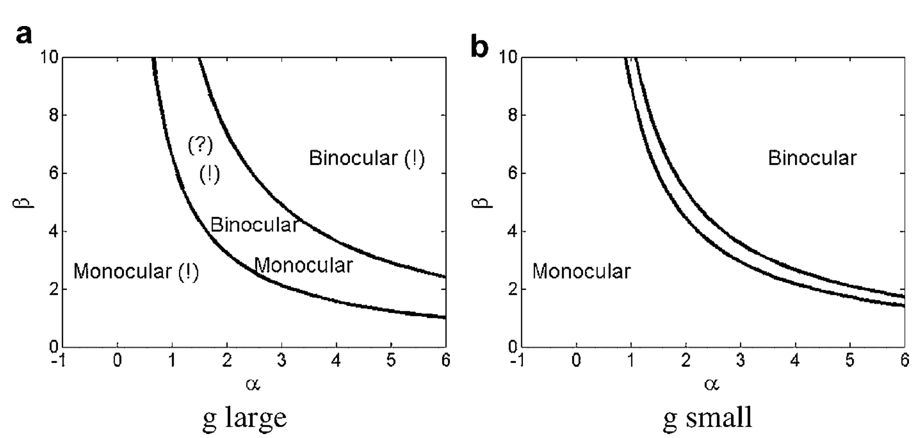

FIGURE 8 Bifurcation diagrams computed from Equations (3) and (5) and plotted in the two-dimensional space spanned by the infant–environment control parameter $\alpha = \lambda_2$ and the developmental control parameter β. Panel a): Bifurcation diagram exhibiting a large bistability domain induced by a large parameter g (here: g = 1.5). Panel b): Bifurcation diagram with a relatively small bistability domain related to a parameter g close to 1 (here: g = 1.1).

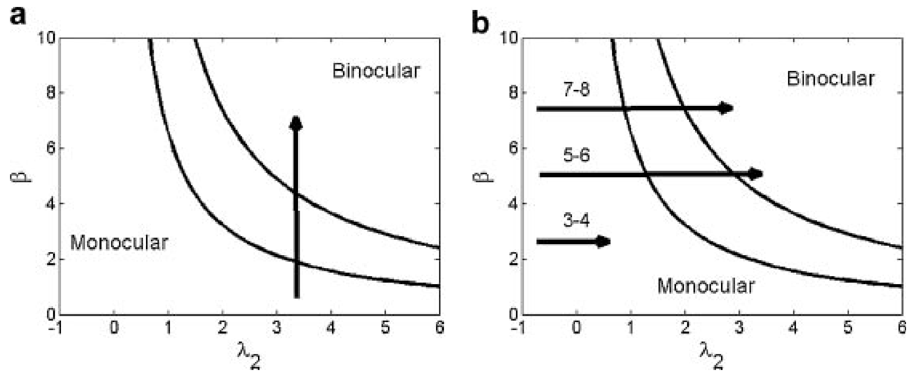

FIGURE 9 (Panel a) Manipulation typically realized in experimental studies on perceptual infant development. (Panel b) Manipulations and results reported in van Hof et al. (2006).

only to one eye. Consequently, the study by van Hof et al. also explored the bifurcation diagram (Fig. 8) along horizontal directions. Three age groups were investigated involving 3- to 4-month-old infants, 5- to 6-month-old infants, and 7- to 8-month-old infants. For the age group of 3- to 4-month-old infants manipulating the control parameter α did not result in a transition to binocularity. In contrast, for the two other age groups transitions from using monocular information to using binocular information were observed. These results are schematically illustrated in Figure 9b.

In a longitudinal experiment reported in the same study some evidence for the existence of the bistable domain depicted in Figure 8 was found. For most infants the object size effect diminished at the age of 5–6 months indicating that they used binocular information. However, for some infants the object size effect was still present at the age of 5–6 months. In sum, infants that belonged to the same age group (i.e., exhibited the same β parameter) of about 5–6 months relied both on monocular and binocular information, which is consistent with the existence of a multistable parameter domain. However, the multistable dynamic model (1) makes an even stronger claim regarding the bistability domain. According, multistability exists within individual infants. That is, while the results of van Hof et al. may be interpreted as some evidence for multistability within a group of infants, the multistable model (1) actually describes multistability within individual infants. Equation (1) and Figure 8 predict that an infant may exhibit a multistable perception–action dynamics such that if the infant for a single catching event is deprived of binocular information (via eye-patch) and forced to use monocular information then in the subsequent catching event the infant will continue to use monocular information even if binocular information is provided and even if the infant has matured enough to exploit binocular information. More precisely, let us consider a hypothetical experimental with a group of infants that are provoked to catch balls and wear an eye patch during every second catching trials. If the infants fall in the critical age group of 5- to 6-month-old infants, then our considerations predict that infants of that group more frequently use monocular information in trials in which binocular information is provided (eye patch removed) as compared to infants of a control group in which binocular information is available all the time. This stronger prediction of multistability within individual infants has not yet been tested—as indicated by the symbol (?) in Figure 8a.

SUMMARY

We discussed the emergence and selection of behavioral patterns and information sources during infant development from a modeling perspective. We used a low-dimensional modeling approach involving a dynamic system composed of relative small number of interacting components. Behavior and perception in general and motor performance and perceptual information in particular were treated on a similar basis. The fact that our modeling approach does not principally distinguish between behavioral and perceptual state reflects the ecological stance that action and perception are two closely related phenomena (Gibson, 1979; Michaels & Carello, 1981; Turvey, 1990).

We mapped qualitative and quantitatively developmental changes related to the emergence of new behavioral patterns and information sources to bifurcations in appropriately defined low-dimensional dynamic systems. In doing so, we considered bifurcations involving two control parameters. Such bifurcations have previously been studied in the context of detuning of coupled rhythmic movements with the detuning parameter and movement frequency as control parameters (Amazeen, Amazeen, Treffner, & Turvey, 1997; Kelso, 1995; Schmidt & Turvey, 1994; Treffner & Turvey, 1996).

We argued that the development of reaching and grasping is subjected to at least two qualitatively different control parameters. One parameter accounts for the fact that an infant develops in an environment. That is, infant development depends on object properties of the environment in which infants act and live. Importantly, object properties as such are not of primary relevance. Rather we are concerned with object properties relative to the infant. Accordingly, we did not consider the absolute size of objects as control parameter, but the relative size of objects when measured in terms of body scales of an infant (e.g., Cesari & Newell, 2000; Newell et al., 1989; van der Kamp et al., 1998). Likewise, we did not consider binocular information provided by objects as such. Rather at issue was whether or not binocular information is actually provided to infants (i.e., whether an experiment involves visual information of one or two eyes). As a second control parameter, we used a rather unspecific developmental parameter β that is assumed to be highly correlated to age but not necessarily identical with age. The parameter β in general accounts for a plentitude of developmental factors that for the purpose of clarity may be considered and studied in isolation. For example, it has been argued that the maturation of the postural system (Hopkins and Rönnqvist, 2001) and the physical and social environment of an infant (Lynch, Lee, Bhat, & Galloway, 2008) affect the development of reaching. Moreover, it has been suggested that the development of perception during infancy is closely linked to the motor development of infants (van Hof, van der Kamp, & Savelsbergh, 2008). Roughly speaking, the control parameters α and β are used to capture different types of constraints such as organismic constraints, task specific constraints, and environmental constraints (Newell, 1986). While in the examples discussed above, explicit interpretations of α were given, the parameter β may be considered as a summary factor that includes all other factors except those captured by α. A more comprehensive modeling approach however would require to increase the number of control parameters such that we would have a set of parameters α, β, γ, δ and so on at our disposal. Using this enlarged set, we could in more detail examine (or speculate about) the relationship between the control parameters and the feedback parameters (lambda parameter) that primarily determine—according to our model—developmental transitions. In this context, it should be mentioned that transitions in gaits have frequently been related to control parameters that measure energy efficiency or energy costs (Alexander, 1989; Hoyt and Taylor, 1981; Minetti, Ardigio, Reinach, & Saibene, 1999; Newell, 1986; Sparrow, 2000). As suggested by Thelen (1986) the disappearance of newborn stepping at about 2 months of age may result from an increase of body fat that outranges the increase in muscle strength. In the context of our dynamic systems approach, we may say that newborn stepping becomes unstable because a control parameter related to biomechanical constraints and energetic costs crosses a critical value.

We pointed out that in general there is an interaction between the impacts of different control parameters. In the context of grasping, the impact of the relative object size parameter α is eliminated if the developmental parameter β is small. Only for medium and large values of the developmental control parameter β relative object size α affects grasping. Irrespective of this interaction, we argued that α and β should be regarded as independent parameters. Let us dwell on this point. The independence of α and β can be best illustrated by Table 5 and Figure 3. Each parameter has three levels: small, medium, and large. Consequently, the parameters can be used to code 9 qualitatively different cases. If the parameters were not independent (i.e., if they would collapse to a single parameter), then we would have only one parameter that could code at most three different cases. In Table 5 as well as Figure 3 we clearly distinguished between six qualitatively different cases. Since one independent parameter with three levels is not sufficient to code these cases, we conclude that the developmental parameter β and the relative object size α correspond indeed to a pair of independent parameters. In the context of the development of visual perception of infants, we showed that the onset of binocularity can be understood as a bifurcation involving an infant–environmental parameter α and a developmental control parameter β. Again, we argued that these parameters constitute a pair of independent but interacting control parameters.

Our modeling approach yields predictions that can be used as test-beds in future experiments. The development of grasping was modeled quantitatively in terms of four behavioral modes. The stability of these grasping modes was related to experimentally accessible parameters. More precisely, four feedback parameters were linked to the infant–environment parameter α and a developmental control parameter β via Equation (4). Equation (4) features various additional parameters. While for a particular parameter set the model is qualitatively and quantitatively consistent with experimental results reported in the literature, we might explore predictions that can be obtained for other parameters. As an example, we showed in Figure 5 that infant development may exhibit the so-called reentrant bifurcations. Abilities emerge during development at particular ages but disappear when the developmental process continues. We could also think of the opposite scenario: a behavior or ability emerges, disappears and then reemerges permanently. This kind of analysis shows us what type of phenomena we could expect to observe during infant development provided that the multistable dynamic systems perspective is valid. Likewise, by means of the bifurcation diagrams given in terms of Table 5 and Figure 8 we were able to identify conditions that have not yet been explored in experimental studies. For example, the multistability of grasping movements that involve crossing of the body midline has not yet been discussed, see Table 5. Moreover, multistability of monocular and binocular perceptions within individual infants has not been examined so far, see Figure 8. Finally, it is well known that bifurcations are accompanied by critical phenomena such as critical fluctuations and critical slowing down (Haken, 2004). Therefore, critical phenomena should be observable in the aforementioned developmental bifurcations. In fact, critical fluctuations have been discussed in studies on coordinated movements (Schöner, Haken, & Kelso, 1986), movement-related neural activity (Frank, Daffertshofer, Beek, & Haken, 1999; Wallenstein, Kelso, & Bressler, 1995), and learning (Stephen et al., in press).

APPENDIX: DEFINITION OF KEY TERMS

Dynamic system: System that evolves with time. In our context, a system described by a relatively small number of interacting components that evolve in (developmental) time.

Fixed point: Point or position in a generalized coordinate system at which a dynamic system does not change with time.

Stable: A stable state of a system is a state to which the system returns when it is pushed away from that state (e.g., rest state of spring).

Unstable: An unstable state of a system is a state that is abandoned by the system as soon as the system is slightly pushed out of that state (e.g., upright position of a long stick balanced on your palm).

Multistable: When several stable states coexist.

Bifurcation: (in our context) Transition to a new stable state from a state that becomes unstable.

Bifurcation line: Line in a parameter space that indicates all combinations of parameters at which bifurcations can be observed.

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