

Chapter 8

The phylogeny, ontogeny, causation and function of regression periods explained by reorganizations of the hierarchy of perceptual control systems

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Introduction

The aim of this book is twofold: first, to publish a post-hoc ‘Festschrift’ for Bill Powers, the (grand)father of Perceptual Control Theory (PCT), and, second, to communicate the many scientific advances based on PCT to a wide, multidisciplinary audience by contributions of authors who are well-acquainted with some conventional branch of the life sciences as well as with PCT — who understand why the older theories were persuasive and even useful, and also what has to be changed about them as the realities of perceptual control are to be introduced into them.

My branch of the life sciences is behavioral biology, also called ethology. In the 1970s I studied the behavioral development of free-living chimpanzee infants in the Gombe National Park, Tanzania, East-Africa, and, together with my late wife Hetty van de Rijt-Plooij, the growing independence, conflict and

1. Acknowledgments: My thanks to Lomax Boyd, Jonathan Lombard, Evan MacLean, Warren Mansell, John Richer, Alex Weiss and two reviewers for reading earlier drafts of this chapter and providing useful comments and suggestions for improvement. This research was financially supported by the ‘Netherlands Foundation for the Advancement of Tropical Research’ (WOTRO grant no. W84-66), the ‘Dr. J.L. Dobberke Stichting voor Vergelijkende Psychologie’ at Amsterdam, the ‘Stichting Kinderpostzegels Nederland’ (project no. PH 89/74), and the ‘Fonds Doctor Catharine van Tussenbroek’ in the Netherlands.

learning in mother-infant relations of both Gombe chimpanzees and humans. In this chapter, an overview of this body of work is presented that has never been published before.

The discoveries made in this body of work emerged from the data. It is an example of induction as opposed to deduction. No theory or hypothesis was guiding the data collection. In the tradition of behavioral biology everyday life of free-living chimpanzees was observed directly in a natural setting, taking care of good observational control and making sure the sample size of the monthly observations was large enough to guarantee reliable, quantitative, behavioral measures.

First, I studied the behavioral development of free-living chimpanzee infants (Plooij, 1984). To give an idea of what kind of data were collected, a brief description follows of the observation methods used.

It takes years to get familiar with an animal's behavior (Fagen & Goldman, 1977). In the Gombe Research Center, familiarity with the behavior of chimpanzees was already present and handed over from one researcher to the next. Therefore, my pilot study (to get familiar with the chimpanzees and their environment) only lasted six months, during which time I spent 407 h in the field. First, it took me three weeks before I was able to recognize all the chimps individually. Second, I needed four weeks to follow chimpanzees from all age/sex classes on foot. "It is necessary intellectually to soak in the environmental complex of the animal to be studied until we have a facility with it which keeps us, as it were, one move ahead" (Schneirla, 1950). And third, during the remainder of the pilot study, I followed mother-infant pairs and dictated a running commentary (see Hutt & Hutt, 1970) into a portable cassette-tape recorder. From these running commentaries grew a list of environmental events considered important and behavior categories that were observed repeatedly (Appendix A in Plooij, 1984). The environmental events included all situations in which an infant overtly reacted to: the distance to other chimpanzees, the presence of other species, vegetation noise (a possible danger!), weather variations, and location. Three criteria were used for the definitions of behavior categories. First, the age-dependency criterion: before the age of 5 months it was near impossible to observe discrete behavior patterns that were stereotyped enough to allow definition and quantification; and only after 12 months was it possible to define behavior categories according to consequence (such as 'nestbuilding'). Second, mutually exclusive behavior categories were not used for the whole chimpanzee. The categories were divided into 11 groups, one per body part. Intra-group categories are mutually exclusive, inter-group categories may combine. The continuous stream of behavior was described in terms of a sequence of such combinations.

During the main study I followed the mother-infant pairs monthly for as long as was necessary to get 300 min of good observation, which usually took 1–2 days. The behavior of the baby or infant was recorded *continuously* together with the behavior of the individual it was interacting with.

The main question that dominated the analysis of the data was whether it was possible to find out what type of organization was underlying the developing behavior. In the 20th century there were two opposing lines of thought about the development of behavior (Kortlandt, 1955): differentiation versus ascending development. Differentiation starts with a perfectly integrated unity that expands progressively. Within this unity parts individuate and become more or less discrete. For example, in my own study of newborn human babies (Plooij, 1978) we observed many examples of this total unity, i.e. the movements of one arm mirror the movements of the other or a blink of the eyes is mirrored in a movement of the feet. Other examples are the works of Coghill (1929) on the embryology of behavior in the newt *Amblystoma*; Humphrey (1969) on the ‘total pattern reflex’ in the human fetus involving the organism as a whole, and Condon (1979) on self-synchrony in human newborns.

In contrast to differentiation, “ascending development proceeds through the emergence of isolated units followed by an ascending integration into a hierarchy” (Plooij, 1984, p. 2). Discrete types of behavior emerge, such as walking, flying, twig-quivering or munching fish in cormorants (Kortlandt, 1955), and after a while these become integrated into functional sequences. Good examples are the works of Kortlandt (1955), Kruijt (1964), and Hailman (1967) concerning different bird species; Rosenblatt’s (1976) review of the studies on altricial, non-primate mammals; Baerends-van Roon and Baerends (1979) concerning the domestic cat; and Chevalier-Skolnikoff (1974) on stump-tail macaques.

Neither differentiation nor ascending development covers all observed behaviors however. Therefore, it has been concluded that ascending development replaces differentiation during ontogeny. According to Dawkins (1976) this is only logical if one realizes that the unity of the differentiated parts would be lost if there would not emerge a hierarchically superior system integrating them.

Traditionally, in behavioral biology at the time, discrete behavior patterns were used to find such systems in adult organisms (Baerends, 1956, 1976; Fentress, 1983; Hinde, 1953).² However, such discrete behavior patterns do not exist in chimpanzee infants younger than 5 months, so the search for hierarchically superior systems seemed to have ended in an impasse.

2. This is logical if one realizes that ethology’s presumption at the time was the same as the presumptions of the other behavioral sciences, namely that it is behavior that is controlled, not perception. The behavior was considered to be controlled by a hierarchical system of Innate Releasing Mechanisms (IRMs) on the one hand and a hierarchical system of motor centers on the other hand. Each motor center controls a configurational pattern of muscle contraction (Tinbergen, 1951/1974). (pp. 103–104).

In my efforts to get out of this impasse, I strolled away from the mainstream of ethology and discovered the work of the Estonian biologist [Jakob von Uexküll \(1933\)](#). He focused much more on perception instead of behavior and he came up with the concept of the ‘Umwelt’. The Umwelt is, roughly speaking, the world as it is experienced by a particular organism. Different species all have a different Umwelt because their respective nervous systems have evolved to seek out and respond only to those aspects of the environment that are relevant.³ Over evolutionary time, of course, any persistent long-term change in environmental circumstances can result in selection and adaptation to the new circumstances.⁴ The creature’s Umwelt will change accordingly.

Adriaan Kortlandt was a young student and an early pioneer in the field of ethology ([Kortlandt, 1940a; 1940b, 1955](#)) in the 1930s and was influenced by the ideas of Von Uexküll, as he told me himself when I studied in his lab. Kortlandt had observed free-living cormorants. He describes “hierarchically organized appetites” ([Kortlandt, 1955](#)) (pp. 171–172) where an appetite is defined as “either the performance of a specific activity or the presence of a specific external object or situation (consummatory situation) which causes the ending of a variable sequence or series of activities leading to this particular situation.” Because the hierarchically organized appetites are ending activities, Dawkins described them as “hierarchically nested stopping rules” ([Dawkins, 1976](#)). This does not only apply to situations outside the body of the organism, but also to situations inside the body: movement-regulation feedback through proprioception and perception of results outside the body had been shown to be important in primates ([Marsden, Merton, Morton, & Adam, 1978; Polit & Bizzi, 1979](#)), mice ([Fentress, 1976](#)), and some bird species ([Baerends, 1956, 1970; Bastock, Morris, & Moynihan, 1953](#)). Set values play a crucial role in such feedback ([Baerends, 1976](#)); all efforts to restore those values stops as soon as the perception of the situation conforms to the set-values. Kortlandt describes how the appetites and the concomitant consummatory situations are arranged in levels that successively emerge and integrate during ontogeny ([Kortlandt, 1955](#)).

So, it seemed that these appetites and concomitant consummatory situations could be useful in finding the hierarchically superior systems underlying behavioral development. However, these appetites and concomitant consummatory situations appeared not easy to find, if one wants to avoid the trap of using descriptions of behavior for explaining learning and development ([Bickhard, 1992](#)). Furthermore, [Golani \(1976\)](#) had shown that chaos seemed

3. This is in line with findings concerning the selective nature of sensory receptors that act as filters to certain features of the environment ([Kolb & Wishaw, 1990](#)). As a consequence, biologists, trained to focus on differences between species, found that some species would learn a specific task when related species would not ([Hinde & Stevenson-Hinde, 1973](#)).

4. Recently, for the first time the evolution of ‘prepared learning’ was demonstrated experimentally in a population of *Drosophila* over 40 generations ([Dunlap & Stephens, 2014](#)).

present in the observed behavior as long as one did not know what was controlled. As soon as one did know, order appeared in the same overt behavior. Hofer (1978) was talking about ‘hidden, regulatory processes.’

When my thinking had developed thus far, my colleague A.R. Cools pointed out Powers (1973, 1978, 2005) work to me and suggested that Powers’ hierarchical perceptual control theory might be very useful as a lead to detect the appetites and concomitant consummatory situations at different hierarchical perceptual levels.

In addition, three procedures were applied in this search. First, the test for the controlled variable (TCV) by studying the reactions to disturbances (Powers, 1973, 2005). Second, the speed of control systems (the higher the level in the hierarchy, the slower the system according to Powers (1973, 2005) (p. 116). And third, rigidity versus variability of behavior. The third procedure needs some explanation. For his cormorants, Kortlandt (1955) showed that normal variability of behavior occurs mainly at one level below the highest level of the hierarchy. He concluded that this “zone of variability in behavior ascends in the same degree as does the progress in maturation.” (pp. 190–192). From Bingham’s (1928) descriptions of ontogeny in the chimpanzee, Kortlandt suggested that the same rigidity versus variability procedure may apply to behavioral development in this ape.

Using Powers’ hierarchical perceptual control theory and these three procedures, I found major changes in the behavioral development of free-living chimpanzee infants that could well be explained in terms of one level after the other being superposed onto the already existing hierarchy (Plooij, 1984).

Thereafter, my late wife and I analyzed the data further while focusing on the growing independence, conflict and learning in mother-infant relations. The major changes in the behavioral development and the underlying hierarchical organization that I found appeared to be associated with regression periods (van de Rijt-Plooij & Plooij, 1987). The growing independence of the infant appeared not to be a gradual process, but to occur in leaps. With each ‘leap’ in independence comes a sharp decrease in mother-infant body contact. Immediately before each leap a regression period occurred. Regression was expressed by a temporary shift back to mainly staying closer to mother and by a temporary increase in the amount of ventro-ventral contact.

A central role can be assigned to age-related regression periods in the quest for the processes underlying the ontogeny of the hierarchical levels of perceptual control systems. “On the one hand, there is the link with brain changes. On the other hand, each regression period signals the start of a period of developmental progress and the emergence of new skills, task performances, and behaviors. The age-related regression periods stand out as lighthouses to direct the study of developmental change.” (Plooij, 2003).

They will be described following the “Four Why’s” of behavioral biology (Tinbergen, 1963) concerning evolution, development, causation, and function.⁵

Evolution

The regression periods were discovered in 1973 in free-living chimpanzees in the Gombe National Park, Tanzania, East-Africa (van de Rijt-Plooij & Plooij, 1987). Each regression period was followed by a period of mother-infant conflict over body contact together with the sharp decrease in mother-infant body contact.⁶ An example of such mother-infant conflict can be seen in Fig. 8.1A and B.

Evolutionarily speaking, the phenomenon of regression periods in early development turned out to be very old, indeed, and was reported by Horwich in 1974 for twelve monkey species and two non-primate mammals (Horwich, 1974). In those species, regression was expressed as peaks in nipple contact. These peaks are age-linked and occur at similar times in development, if a correction is made for the speed of development of each species. According to Horwich, the peaks are related to emotional states of insecurity.

The next question was whether this phenomenon of regression periods survived during the evolution of our own species *Homo sapiens*. If it is present in non-primate mammals, monkeys and apes, one would expect it to be present in us as well, because we are so closely related. In 1989, Horwich had published promising results on all four ape species (three orangutans, two gorillas, one chimpanzee and four humans) that showed periods of a recurrence of more time spent nursing and in contact with the mother (Horwich, 1989). However, he sampled monthly, and weekly sampling is required to capture the phenomenon completely.

Development

In a study in the Netherlands on human babies, ten age-linked regression periods were found in the first 20 months, covering the sensorimotor stage

5. In 1963 Tinbergen characterized the discipline Ethology as ‘the biological study of behavior’. ‘Behavior’ refers to the fact that Ethology has the inductive description of observable phenomena as a starting point. ‘Biological’ refers to a method of study or the biological method. The latter includes the general scientific method and, in addition, four questions concerning major problems that are studied throughout biology: evolution, development, causation, and function (or survival value). Tinbergen insisted that Ethology gives “equal attention to each of them and to their integration” (Tinbergen, 1963).

6. Trivers argued that, according to parental investment theory, parent and offspring are expected to disagree over the duration and the amount of parental investment that should be given. Interestingly, the periods of mother-infant conflict in chimps are triggered by the regression periods where the infant is demanding extra care (Trivers, 1974).

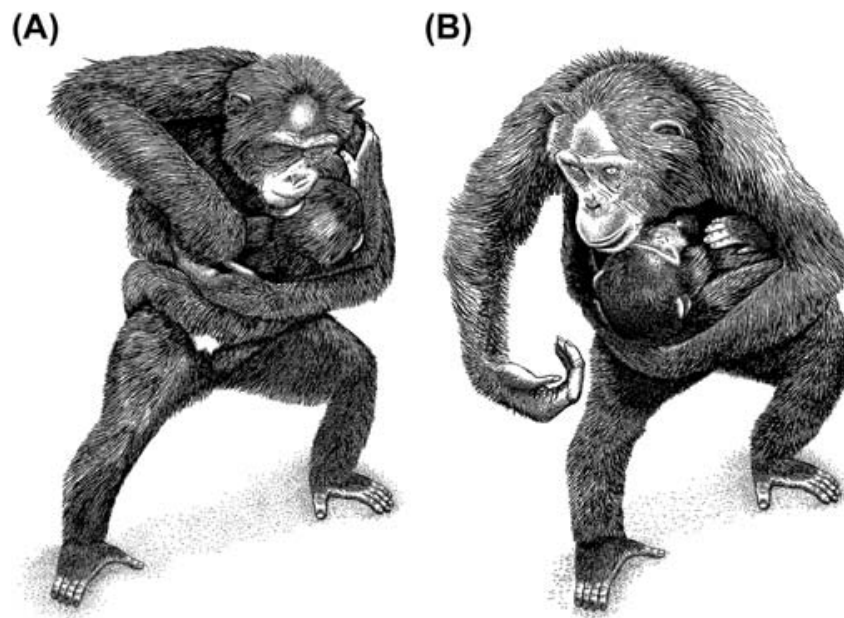


FIG. 8.1 Mother Passion bite-gnawing, pushing, pulling, pinching, and slapping her baby Prof to get him off the belly and off the nipple (A). Here she failed and resumed walking (B). Line drawings Copyright © 2018 by David Bygott.

(van de Rijt-Plooij & Plooij, 1992). These are periods during which the infant was more difficult than usual according to the mother. In such a period the baby is crying more than usual, clinging to the mother more than usual and more cranky or grumpy, than usual. We described these periods as being characterized by the three C's: Crying, Clingy and Cranky.

Direct observations of mother-infant interactions in the homes confirmed the maternal reports. Just to give one example and a feel for the phenomenon, Fig. 8.2 presents the percentage of direct observation time one baby spent in body contact with the mother by age. While the percentage goes down over time, one can clearly see the temporary peaks in body contact superposed onto the downward trend. These temporary peaks represent the regression periods in which the baby is more clingy than usual. The effects of important sources of 'noise' on direct observation measures of regression periods were described using case studies of four infants' adaptations to special parental conditions (Plooij & van de Rijt-Plooij, 2003).

Three independent research groups have replicated the above findings on age-linked regression periods (Lindahl, Heimann, & Ullstadius, 2003; Sadurni & Rostan, 2002, 2003; Woolmore & Richer, 2003).

Just like in the chimps, conflict periods followed the regression periods (van de Rijt-Plooij & Plooij, 1993). These data are based on weekly questionnaires combined with in-depth interviews. At first, mothers were worried that something was wrong with their baby during a regression period. Sometimes they would even pay a visit to the pediatrician, only to find out that nothing was wrong. Then their worry would change into annoyance. In the first

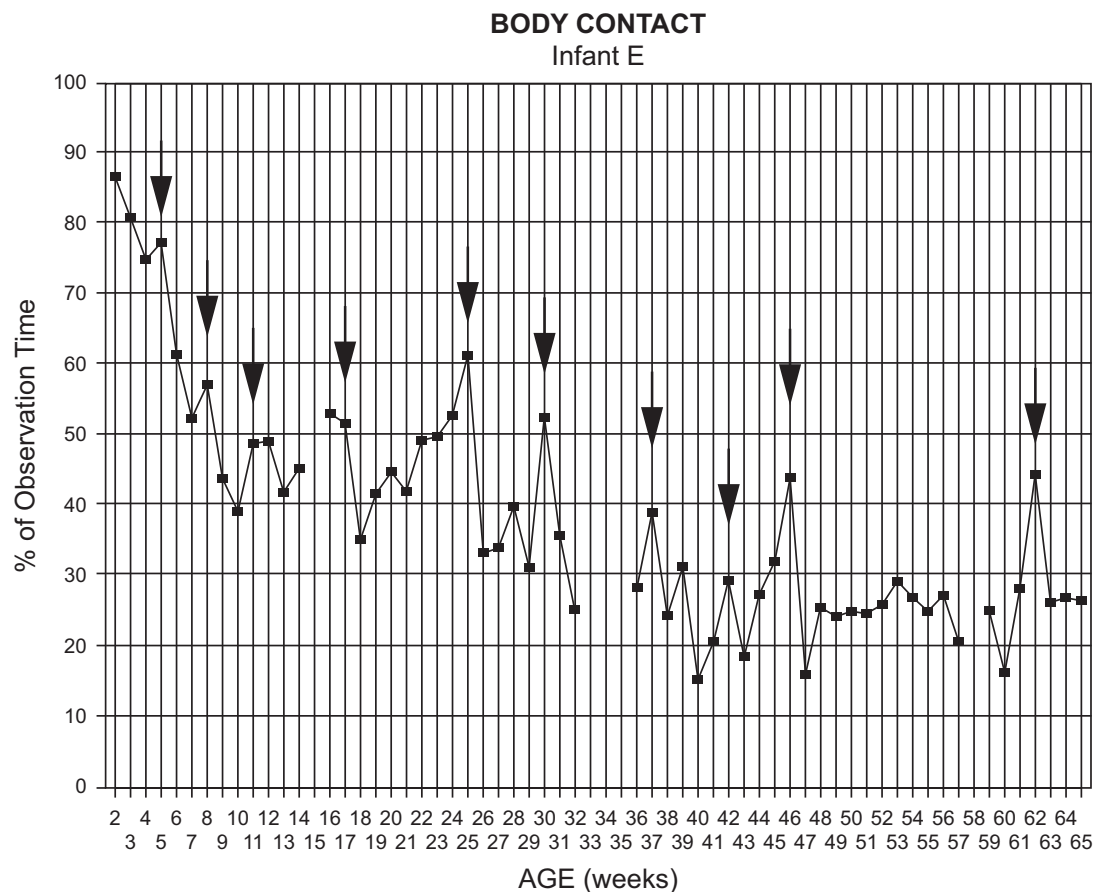


FIG. 8.2 Temporary peaks in body contact superposed on a downward trend. From Plooij, F. X., & van de Rijt-Plooij, H. (2003). *The effects of sources of "noise" on direct observation measures of regression periods: Case studies of four infants' adaptations to special parental conditions*. In M. Heimann (Ed.), *Regression periods in human infancy* (pp. 57–80). Mahwah, NJ: Erlbaum. Copyright © 2003 by Lawrence Erlbaum Associates, Inc. Reprinted by kind permission of Lawrence Erlbaum Associates, Inc.

few months, mothers would not act on their feelings of annoyance. But at later ages, especially the second half of the first year, they would. This was called ‘promoting progress’, because the mothers sensed that their baby was able to do more and they would demand more of their baby. At this age, they would still use mild strategies by diverting the attention of their baby. And the baby would go along with its mother. But soon, and especially during the second year of life, the babies would not go along with their mothers anymore and straightforward ‘clashes’ would result. Around 18 months, all the mothers reported clashes to occur.

Comparing what babies could understand before and after a regression period, we found that they had made a leap and were able to perceive a new order of phenomena. In terms of PCT (Powers, 1973, 2005), we assumed that with each regression period a new type of perception had emerged, and a new perceptual world had opened up for the baby to explore. Following that assumption, we should expect the baby to develop new skills. In collaboration

with my colleagues in Spain, we tested the hypothesis that following each regression period, a cluster of new skills should emerge (Sadurni, Burriel, & Plooij, 2010). We asked the mothers of the babies each week what new skills they had observed that week and the results are shown schematically in Fig. 8.3. The blue line stands for the occurrence of new skills and the red line represents the regression periods and it is clear that the peaks in new skills follow the regression periods.

Our original findings having been replicated by independent research teams and validated by direct observation, we moved on to search for convergent evidence of a different kind. The line of argument was as follows. The relation between regression (or disorganization) on the one hand and progression (or reorganization) on the other hand has been considered for almost a century by scientists from various backgrounds (Bever, 1982; Kortlandt, 1955; Kozulin, 1990; Mahler, Pine, & Bergman, 1975; McGraw, 1945/1974; Mounoud, 1976; Peterfreund, 1971; Schore, 1997; Scott, 1986; Smotherman & Robinson, 1990; Thelen, 1989; Werner, 1948). The ethologist Kortlandt even invented the term ‘reprogression.’ Being disorganized, the whole organism is ‘off balance.’ So, the disorganization should not only show in the behavior within the phenomenon of regression periods, but in other aspects as well. The progress in the discipline psychoneuroimmunology over the last few decades has brought to light the complex interactions between behavior, the CNS, the endocrine system, and the immune system (Ader, Felten, & Cohen, 2001). If the organism is disorganized, this should also show in the immune system and the health of the organism, among other things.

We approached this question by studying the distribution of illnesses over early age and predicted we should find peaks in illness around the ages at which we had found the regression periods. And so we did (Plooij, van de Rijt-Plooij, van der Stelt, van Es, & Helmers, 2003).

Consequently, we did a similar study on peaks of death in infants that died of Sudden Infant Death Syndrome (SIDS) and found small peaks superimposed on the one large peak reported until then in the literature (Plooij, van de Rijt-Plooij, & Helmers, 2003). McKenna, (1990a, b); McKenna and Mosko (1990) has suggested a connection between the one large peak in SIDS and the shift from reflexive to speech breathing with its neurological control system errors. In similar vein there might be more sudden changes in the brain that underlie the other, superimposed peaks in SIDS.

These suggestions that sudden brain changes might underlie the regression periods and the peaks in illnesses and SIDS bring us to the third of the Four Why’s: the question concerning immediate causation.

Causation

Trevarthen and Aitken (2003) conducted an extensive literature review on the pre- and post-natal development of the central nervous system. There is clear

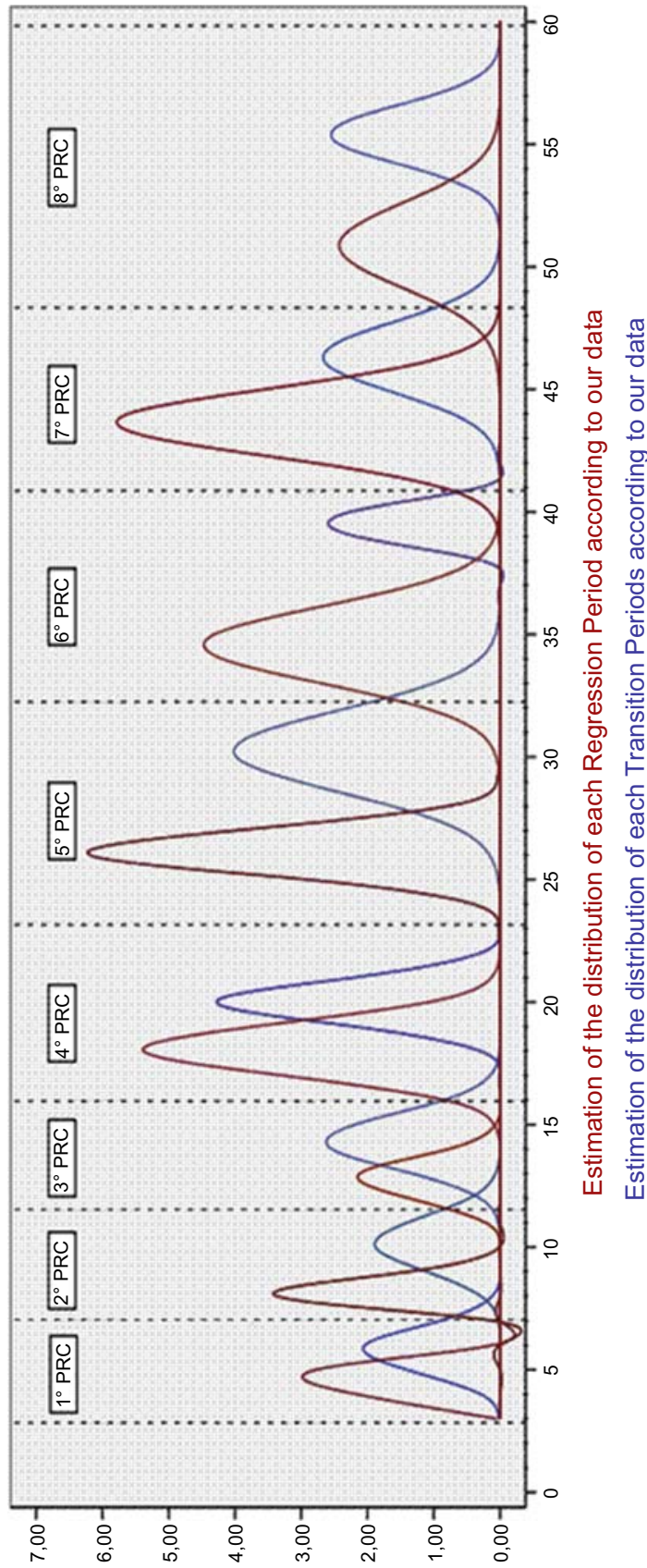


FIG. 8.3 Each regression period is followed by a cluster of new skills. From Sadurni, M., Burriel, M. P., & Plooij, F. X. (2010). *The temporal relation between regression and transition periods in early infancy*. Spanish Journal of Psychology, 13(1), 112–126. Reprinted by kind permission of the publisher.

evidence for sudden, gene-regulated, age-linked brain changes. For instance, sudden increases in the skull circumference were found in the first few months shortly before or at the beginning of regression periods. Sudden age-linked brain changes occur shortly before or at the beginning of most regression periods.

Knowing this, one might approach the question of immediate causation of regression periods from another angle, taking purpose into account experimentally by testing for controlled variables (TCV; Marken, 2013), based on PCT. If a living organism is able to control a certain perception, so the theory goes, any deviation from the reference value of that perception should be met with resistance, counteracting the deviation from the reference value caused by the disturbance. If the organism is not able to perceive that type of perception, the disturbance is met with indifference. It is simply not perceived. This is called the test for the controlled variable or quantity (Powers, 1973, 2005). Also in developmental studies this test can play an important role, as we will see shortly.

The PCT model of the sensorimotor stage specifies what type of perception is emerging at the beginning of or shortly before each regression period (Plooij, 2003). This is shown in Fig. 8.4. The types of perception that are supposed to emerge are the perception of:

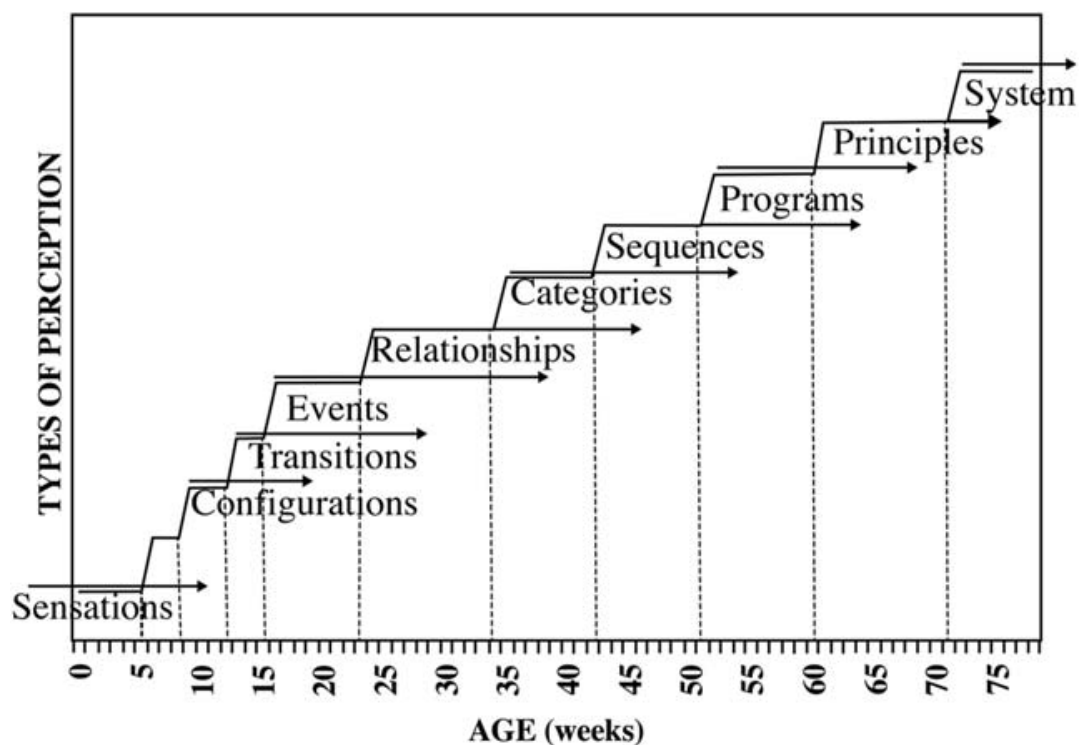


FIG. 8.4 The Hierarchical Perceptual Control Theory model of the sensorimotor stage. From Plooij, F. X. (2003). *The trilogy of mind*. In M. Heimann (Ed.), *Regression periods in human infancy* (pp. 185–205). Mahway, NJ: Erlbaum. Copyright © 2003 by Lawrence Erlbaum Associates, Inc. Reprinted by kind permission of Lawrence Erlbaum Associates, Inc.

Configurations, Smooth transitions, Events, Relationships, Categories, Sequences, Programs, Principles, and System concepts.

We conducted some preliminary studies testing this PCT-model with a variant of the TCV. The emergence of the perception of Events and the perception of Sequences were chosen to be tested first for two reasons. First, by combining ethological and experimental, neurophysiological techniques, Aldridge and coworkers (Aldridge, Berridge, Herman, & Zimmer, 1993) have shown that the neostriatum is involved in the perception and control of sequences of behavior and determines the syntax of grooming in rats. Lesions in the neostriatum affect only the serial order of behavior but not the behavioral elements or events. This may show that the perception and control of events is ruled by another hierarchical level than the perception and control of sequences. Second, Diamond and coworkers (Bell, Wolfe, & Adkins, 2007; Diamond & Goldman-Rakic, 1989; Diamond, Werker, & Lalonde, 1994) have shown for human infants that the perception of, or memory for, temporal order is a potential that underlies the development of the whole list of skills, behaviors or task performances.

For each type of perception, a battery of some 20 to 30 tasks was developed that were based on that type of perception. Two of my students (Ten Horn & Paro, 1995) then followed individual babies weekly for four months, two months before and two months after the age of onset of a regression period and the supposed emergence of a particular type of perception. Every week we presented the battery of task items to the babies. The prediction was that a baby should not perform well with the battery of tasks before this age of onset, but thereafter should quickly master one after the other.

Fig. 8.5 concerns the perception and control of events. In this graph the cumulative number of task items that was finished successfully is plotted against age (in weeks). Weeks 14–17 concern the regressive period as reported

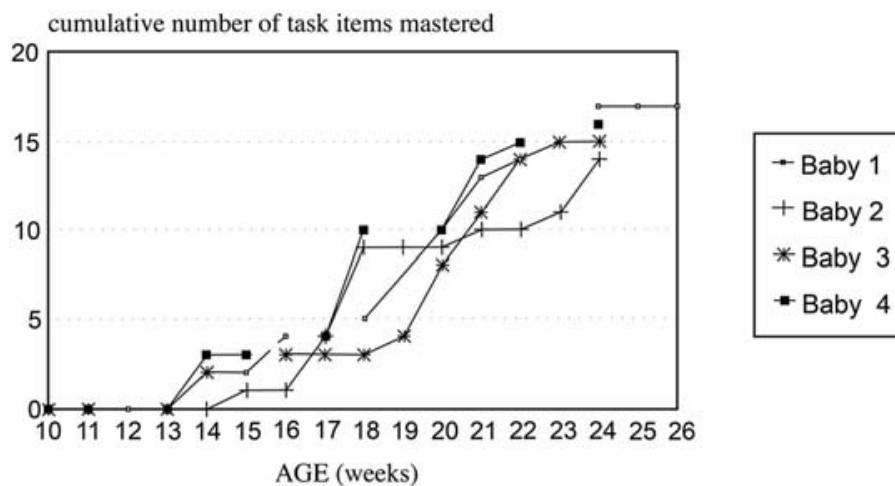


FIG. 8.5 The successfully finished, cumulative number of task items concerning ‘Events’ over age (in weeks). From Ten Horn, J., & Paro, I. (1995). *Mentale ontwikkeling bij baby’s: Try-out taakbatterijen*. *Heymans Bulletin Psychologische Instituten. Scriptie. Ontwikkelingspsychologie. Rijksuniversiteit Groningen. Groningen. Reprinted with kind permission of the authors.*

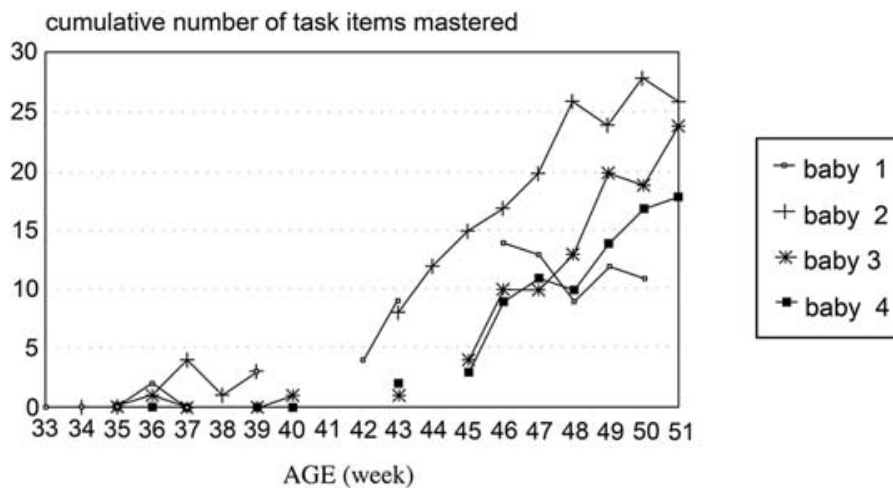


FIG. 8.6 The successfully finished, cumulative number of task items concerning ‘Sequences’ over age (in weeks). From Ten Horn, J., & Paro, I. (1995). *Mentale ontwikkeling bij baby’s: Try-out taakbatterijen*. *Heymans Bulletin Psychologische Instituten. Scriptie. Ontwikkelingspsychologie. Rijksuniversiteit Groningen. Groningen*. Reprinted with kind permission of the authors.

by the mothers. The individual graphs of four babies are depicted. Before the regression period, the babies did not master a single item, and thereafter the graphs clearly show improvement.

Fig. 8.6 concerns four other babies and the perception of sequences. Weeks 40–44 concern the regressive period as reported by the mothers. A similar picture is shown.

Function

Regression periods are difficult on the parents who would sometimes rather do without them. However, they do have a function. For instance, Marten de Vries (1984) studied the survival of Masai children in East Africa with and without a ‘difficult temperament’ in times of famine. A greater number of difficult children survived because they were better able to elicit care from their mothers.

Another example concerns data that support the hypothesis that difficult infants activate special family resources, which stimulates intellectual development over the years. Using three temperamentally different subgroups from a large birth cohort, Maziade and coworkers (Maziade, Côté, Boutin, Bernier, & Thivierge, 1987) undertook a longitudinal study of the association between temperament measured in children at 4 and 8 months and IQ assessed at 4.7 years. The data suggested a strong effect of extreme temperament traits on IQ development in middle and upper socioeconomic classes and in families with superior functioning in terms of communication. The temperamentally difficult group unexpectedly displayed higher IQ’s, and the well-replicated effect of socioeconomic status on IQ development was observed mainly in this

group. According to [Belsky and Pluess \(2013\)](#) difficult babies are more open to experience and do better if parents can cope, but worse if they can't.

We ourselves developed a parental support and education program called 'Leaping Hurdles' for a group of single mothers who were at risk of abusing their infants ([van de Rijt-Plooij, van der Stelt, & Plooij, 1996](#)). In it we made parents aware of the regression periods, showed them that their babies could not help being difficult and how they could comfort their babies in these difficult periods and facilitate the new type of perception and consequent learning.

In an evaluation study we compared an experimental group receiving the program 'Leaping Hurdles' with a control group following a comparison program.

The effects of the program Leaping Hurdles on the parents were as follows: the parental judgment of the temperament of their baby changed in the sense that it was based on different information, specifically, on the behavior of the infant instead of their own, parental rules and restrictions. Their judgment of the development of their baby was based more on information concerning the mental development instead of the motor development. Finally, the program gave parents a greater sense of control.

The effects of the program Leaping Hurdles on the infants were as follows: First, the infants scored much higher on the mental Bayley scales. Second, the program removed gender differences in developmental test scores, the girls did not get lower scores on the Bayley. Third, the program children were socially more accepting and open toward strangers and not fearful and reserved as the control children were. No differences were found in the type of attachment, although this may have been an artifact of the Strange Situation scoring protocol failing to pick up differences. Finally, the program had positive effects on the health of the infants, specifically the girls.

So, it is likely that regression periods have the function of activating family resources and thus promoting intellectual and social development as well as physical health (at least as long as the demands of the infant do not exceed parent's capacity to meet them, a capacity which can be enhanced by appropriate knowledge and support). The improved physical health would promote survival directly, whilst the improved intellectual and social development are likely to do so in the longer term.

Discussion

Summarizing our explanation of the findings, the following picture emerged. At gene-regulated ages, a new type of perception emerges intrinsically and is superposed onto the already existing hierarchy of levels of perception, resulting in a disruption in the behavioral organization. Consequently, the baby is stressed and gets closer to the parent, and the next regression period has started. Regression facilitates a trial-and-error process that is aimed at

reducing the stress. This process is called reorganization. However, the baby has very little control over the outer world and needs his carer to reduce the stress and restore homeostasis. The resulting, more intensive caretaking period and parent-infant interaction can involve parent-infant conflict which pushes the baby toward more independence and exploration of the new perceptual world within the boundaries of its maturational abilities. A new type of learning results in a new set of skills apt for controlling the new perceptual world. There are individual differences in the age at which babies master a particular skill, depending on the personal preferences of the baby and the prevailing circumstances of the (social) environment. When the next level of perception emerges, the whole process starts all over again.

The findings bring up a number of questions or statements that will be dealt with in the remainder of this chapter.

The field of ethology is ready for a paradigm shift toward PCT

Without being exhaustive, the following few examples concerning some major branches of research in ethology suggest the field of ethology is ready for a paradigm shift toward PCT.

Cools (1985) tested the PCT model experimentally through chemical stimulation of the brain of adult rats, cats, and monkeys and argued that it is the perception that is controlled through behavior and a hierarchy of feedback systems in the nervous system. This is quite the opposite of classical ethology's presumption that it is behavior that is controlled, not perception. The behavior was considered to be controlled by a hierarchical system of Innate Releasing Mechanisms (IRMs) on the one hand and a hierarchical system of motor centers on the other hand. Each motor center controls a configurational pattern of muscle contraction. The IRM was supposed to remove a block preventing continuous discharge of a motor center (Tinbergen, 1951/1974) (pp. 103–104). Since Cools' publication, not much has changed in ethology. If one looks at the box diagrams of the 'hunger system' (Fig. 2) or the 'dustbathing system' (Fig. 3) in a paper in 2005 reviewing the trends since Tinbergen (Hogan & Bolhuis, 2005), there is still a hierarchy of perceptual mechanisms on the one hand and a hierarchy of motor mechanisms on the other hand, and there is still a linear causation from stimuli to behavior. The paradigm shift toward PCT was then already long overdue.

The latter notion is supported by the work of Pellis and coworkers (Pellis, Gray, & Cade, 2009) on crickets. These authors posit that a PCT view of behavior is applicable to the kinds of actions often labeled as 'Fixed Action Patterns' (FAPs) or 'Modal Action Patterns' (MAPs), that are core concepts of classical ethology. They have shown that such action patterns are not that fixed after all and that the variability serves to maintain some constancy or invariance. "Variability in individual movements by different body parts can be accounted for as compensatory actions that are enacted to preserve the

invariant features.” Examples of such invariant features are “some fixed relationship between body parts, or of some body part to an environmental cue (animate or inanimate), or to some dynamic aspect of the pattern performed (e.g., displacement, velocity, etc.)” Pellis and coworkers give examples of such invariances for many other species. They explain such invariances in PCT terms: “there is a reference signal that sets the value that the system maintains as constant, and variable behavioral output is what the system does to protect against deviation from the reference signal (Powers, 1973).”

PCT may explain the fascinating pattern in the foraging and grouping behavior of social insects and of primates and in the co-ordination in swarms of insects, of fish, and of birds in a small flock by assuming that each individual simply controls its own perceptions according to a reference value or target value. Most astonishing are the complex maneuvers in flocks of tens of thousands of European starlings over the sleeping site at night before they settle in the trees. And yet, explanation of these complex phenomena does not need the assumption that the perception of the complete flock or any leadership or complex cognition is needed. Hemelrijk and coworkers (Hemelrijk, van Zuidam, & Hildenbrandt, 2015; Hildenbrandt, Carere, & Hemelrijk, 2010) have shown that the flocking maneuvers of starlings result from local interactions only. These are the following: “Individuals avoid those that are too nearby, they align with those at intermediate distance, and are attracted to those further away.” In addition, they interact with only six to seven of their nearest neighbors, they remain above their sleeping site at a certain height, and they follow the simplified aerodynamics of flight. Unfortunately, Hemelrijk and coworkers claim that these complex phenomena can be understood with the help of ‘complexity science’ and models of self-organization. But what is complexity science, really? Phelan (2001) has tried to answer this question and concluded that “While it has been relatively simple to show high-level resemblances between the emergent properties of computer models and real-world phenomena, it has proven extremely difficult to calibrate these models to produce correlations or confirmable regularities of real-world systems.” PCT may provide such models, as shown by McPhail and coworkers (McPhail, 2000; McPhail, Powers, & Tucker, 1992; Tucker, Schweingruber, & McPhail, 1999). Their models simulated collective action, arcs and rings in temporary gatherings of humans. While Hildenbrandt et al. (2010) (p. 1350) admitted that “social co-ordination depends on internal motivations,” they built their model in terms of (social) forces. In contrast, Bourbon (1995) suggested that the actions of animals in social groups such as flocks, schools, or swarms “might simply become coordinated with those of their immediate neighbors when each of them controls its own perceptions (p. 165).” In the simulations of McPhail and coworkers each individual simply controls its own perceptions according to a reference value or target value.

In PCT, purposive behavior is a core issue. In classical ethology it was not seen as appropriate to “point to the goal, end, or purpose of behavior, or of any

life process.” (Tinbergen, 1951/1974) (p. 4). Barrett (p. 100) states that PCT is an attractive theory because it helps us to work out what perceptions of the world an animal is trying to keep stable (Barrett, 2011).

To give one more example, the field of birdsong learning would be appropriate to apply PCT. The diagrams researchers in this field draw are very much like the PCT diagrams; the feedback loop from moment to moment contains the comparator function comparing the song model (reference signal in PCT) with the perception (perceptual signal in PCT) of the young bird’s own emerging song via auditory feedback. If there is a mismatch between the bird’s current song and the song model, an error-signal is produced that results in distinct events of vocal change in the song production (output signal in PCT). This in turn changes the perception of the bird’s own song via auditory feedback. Some changes in the song production only take hours or days, others may take weeks. In the end, the song motif fully crystallizes and the bird rarely changes its song motif. Without mentioning PCT, Adret (2004) is searching for the reference signal (the template) when he says: “Moreover, songs of early-deafened birds were highly degraded regardless of the amount of prior auditory exposure to conspecific models, suggesting that (1) central motor programs are not sufficient for fully normal song development and (2) self-generated auditory feedback is essential for the conversion of memorized songs into produced songs.” And Deregnaucourt et al. (2004) are searching for the error signal. In a recent review article (Bolhuis, Okanoya, & Scharff, 2010) this overall picture is confirmed: “during birdsong ... learning ... vocal motor output must be monitored continually through auditory feedback and if errors are detected the output should be adjusted.” Furthermore, recent findings are reviewed of how and where this happens. Three interconnected neural networks are mentioned. First, secondary auditory regions have to do with song perception and the recognition of tutor song. Second, the song motor pathway (SMP) has to do with song production and part of song learning. And third, the anterior forebrain pathway (AFP) is crucial for sensorimotor learning and adult song plasticity. The latter two neural networks are called the ‘song system’. In the AFP, a comparator function (in PCT terms) is postulated to be present that compares auditory feedback with the song model and sends an error signal to the motor system, if a difference is found between the desired outcome and the actual performance. The AFP originates in the nucleus HVC that has a functional position at the top of a sensorimotor hierarchy for song, and auditory-vocal ‘mirror neurons’ have been shown to be present in this nucleus (the so-called HVCx cells) (Mooney, 2014). This author concluded that “... the singing-related activity of HVCx cells can encode syntactic information about song in a hierarchical fashion, spanning from the identity of individual syllables to the number of repeated syllables and the nature of inter-syllable transitions.” As for the observation related activity of HVCx cells, “the auditory properties of mirror neurons in HVC are well suited to extract features that are important to song perception at multiple levels of acoustical

complexity,” including categorical perception of learned vocalizations (Mooney, 2014). There is clear potential for the perceptual hierarchy in PCT to be applied to these findings, potentially providing a more robust model.

PCT informs human developmental studies beyond the sensorimotor stage

One may wonder what regressions might be occurring beyond 80 weeks of age - the time span of sensorimotor development - given the huge amount of development that still happens thereafter, especially in terms of language and social interaction. Potentially, regression periods will be found at later ages to mark later steps in development.

Although the buildup of the hierarchy ends when human development is far from complete at the end of the sensorimotor stage, the usefulness of the PCT model does not end there. As Barton (2012) clarified, the “key aspect of human cognition is... the adaptation of sensorimotor brain mechanisms to serve new roles in reason and language, while retaining their original function as well.” (p. 2098) Because of extended connectivity between the neocortex and the cerebellum, essentially the same kinds of computation appear to underlie sensorimotor and more ‘cognitive’ control processes including speech (p. 2101). Barton (2012) gives examples of computation and control processes at hierarchically different levels concerning events, spatial relationships, sequences and programs. More recently, Barton and Venditti (2014) have even shown that humans and other apes deviated significantly from the general evolutionary trend for neocortex and cerebellum to change in tandem. Humans and other apes have significantly larger cerebella relative to neocortex size than other anthropoid primates. This suggests that the current, almost exclusive emphasis on the neocortex and the forebrain as the locus of advanced cognitive functions may be exaggerated. Instead the cerebellum may play a key role in human cognitive evolution. Recently, Verduzco-Flores and O’Reilly presented a cerebellar architecture “allowing the cerebellum to perform corrections at various levels of a hierarchical organization spanning from individual muscle contractions to complex cognitive operations” (Verduzco-Flores & O’Reilly, 2015). In human adults there is growing evidence that the cerebellum is not limited to sensorimotor control (Manto et al., 2012), but plays important cognitive roles as well (Koziol et al., 2014; Stoodley, 2012; Timmann, Richter, Schoch, & Frings, 2006), including social cognition (Van Overwalle, Baetens, Mariën, & Vandekerckhove, 2014), emotion (Schmahmann, 2010), language (Argyropoulos, 2015; Highnam & Bleile, 2011), and even music and timing (E, Chen, Ho, & Desmond, 2014). In addition, there is evidence that “the cerebellum takes an early role in processing external sensory and internally generated information to influence neocortical circuit refinement during developmental sensitive periods” and thus influences cognitive development (Wang, Kloth, & Badura, 2014).

The latter authors propose the ‘developmental diaschisis hypothesis’ that states that “cerebellar dysfunction may disrupt the maturation of distant neocortical circuits.”

The above account indicates that the perceptual levels within the PCT hierarchy may form more complex functional processes where the same kinds of computation that have developed during the sensorimotor stage are used time and again to “serve new roles in reason and language, while retaining their original function as well,” (Barton, 2012) (p. 2098). The latter option is in line with the notion of embodied modes of thought (Barrett, 2011) and with the identification of “the origins of narrative in the innate sensorimotor intelligence of a hypermobile human body” (Delafield-Butt & Trevarthen, 2015). The latter authors “trace the ontogenesis of narrative form from its earliest expression in movement.” In light of this it is interesting to note that *Homo sapiens* is the only species that has language and the only species that has a life history with a childhood (Locke & Bogin, 2006). Childhood is the interval between infancy and the juvenile period. A great deal of language learning occurs during childhood. Bruce Nevin elaborates on a PCT view of language in Chapter 12.

PCT and understanding the evolution of human cognition

PCT fulfills the need for a theory that incorporates the following elements: a complex interplay between biological evolution of new brainstructures enabling more complex hierarchical, domain general information processing and perceptual control on the one hand, and the discovery during the lifetime of an individual (through reorganization of the hierarchy) of new ways of producing cultural products on the other hand.

This need was expressed by the new view about the evolved human mind (Heyes, 2012): “This new thinking about the evolution of human cognition (i) takes a longer historical perspective and therefore a more comparative approach, (ii) highlights the importance of co-evolution and cultural evolution in generating gradual, incremental change and (iii) suggests that humans are endowed with uniquely powerful, domain-general cognitive-developmental mechanisms, rather than with cognitive modules⁷.” Many of the articles in the ‘New Thinking’ theme issue (Heyes, 2012) suggest that humans are born with extraordinarily powerful cognitive-developmental mechanisms. These mechanisms are domain-general—they use a common set of computations to

7. The type of evolutionary psychology called the ‘Santa Barbara school’ or ‘high church evolutionary psychology’ (Cosmides & Tooby, 1987; Tooby & Cosmides, 2005) suggested that, in contrast to our primate relatives, we have a range of distinctive, special-purpose cognitive gadgets or modules, each responsible for thinking about a particular kind of technical or social problem that confronted our Stone Age ancestors. Experience was assumed to play a limited role in the development of these modules.

process information from a broad range of technical and social domains— and they use experience, especially sociocultural experience, to forge new, more domain-specific cognitive-developmental mechanisms of the kinds that control tool-making, mentalizing, planning and imitating the actions of others. The genetically inherited cognitive-developmental mechanisms use computational processes that are also present in other animals, but they are uniquely powerful in their range, capacity and flexibility. The work in these articles shows a complex interplay between biological evolution of new brainstructures that enable more complex hierarchical information processing on the one hand, and the discovery of new ways of producing cultural products on the other hand. The various authors of that work express the need for a theory that accounts for both.

PCT provides a useful functional model of these uniquely powerful, domain-general cognitive-developmental mechanisms suggested by the ‘new thinking’. And reorganization in PCT may explain co-evolution and cultural evolution in generating gradual, incremental change (Cloak, 2014; Powers, 2009/2014). According to Powers (personal communication) this is possible because the perceptual control hierarchy is the product of two reorganization systems, each operating by trial and error. The first, evolution, has produced variants over a very large number of generations of autonomous control systems, of which only some succeeded in bringing progeny to reproductive maturity. In consequence, a neonate begins life with many biologically inherited control systems in place and others emerging in the developmental process. The second reorganization system, an important form of learning, makes slight adjustments to synapse weights, amplification (gain), etc. around the loop in perceptual input functions, error output functions, and reference input functions until intrinsic error is decreasing (Powers, 2008).

Summary of the discussion

The field of ethology is ready for a paradigm shift toward PCT. This is illustrated with a few examples concerning some major branches of research in ethology such as experimental neuro-ethology, fixed action patterns or modal action patterns, the fascinating pattern in the foraging and grouping behavior and in the co-ordination in swarms, purposive behavior, and birdsong learning.

Although the build up of the hierarchy ends when human development is far from complete at the end of the sensorimotor stage, the usefulness of the PCT model does not end there. The perceptual levels within the PCT hierarchy may form more complex functional processes where the same kinds of computation that have developed during the sensorimotor stage are used time and again to serve new roles in reason and language, while retaining their original function as well. The cerebellum plays a much more important role in cognitive development than previously thought and the current, almost

exclusive emphasis on the neocortex and the forebrain as the locus of advanced cognitive functions may be exaggerated.

PCT fulfills the need for a theory that incorporates the following elements: a complex interplay between biological evolution of new brain structures enabling more complex hierarchical, domain general information processing and perceptual control on the one hand, and the discovery during the lifetime of an individual (through reorganization of the hierarchy) of new ways of producing cultural products on the other hand.

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