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RESEARCH ARTICLE

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Neonatal control of nutritive sucking pressure: evidence for an intrinsic τ-guide

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Abstract Human newborns appear to regulate sucking pressure when bottle feeding by employing, with similar precision, the same principle of control evidenced by adults in skilled behavior, such as reaching (Lee et al., 1998a). In particular, the present study of 12 full-term newborn infants indicated that the intraoral sucking pressures followed an internal dynamic prototype – an intrinsic τ-guide. The intrinsic τ-guide, a recent hypothesis of general tau theory is a time-varying quantity, τ_g, assumed to be generated within the nervous system. It corresponds to some quantity (e.g., electrical charge), changing with a constant second-order temporal derivative from a rest level to a goal level, in the sense that τ_g equals τ of the gap between the quantity and its goal level at each time t. (τ of a gap is the time-to-closure of the gap at the current closure-rate.) According to the hypothesis, the infant senses τ_p, the τ of the gap between the current intraoral pressure and its goal level, and regulates intraoral pressure so that τ_p and τ_g remain coupled in a constant ratio, k; i.e., $\tau_p = k\tau_g$. With k in the range 0–1, the τ-coupling would result in a bell-shaped rate of change pressure profile, as was, in fact, found. More specifically, the high mean r^2 values obtained when regressing τ_p on τ_g, for both the increasing and decreasing suction periods of the infants' suck, supported a strong τ-coupling between τ_p and τ_g. The mean k values were significantly higher in the increasing suction period, indicating that the ending of the movement was more forceful, a finding which makes sense given the different functions of the two periods of the suck.

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Introduction

Control of sucking is perhaps the most precocious purposeful motor skill evident in a newborn infant's movement repertoire. The skill, therefore, provides an excellent opportunity for exploring mechanisms of fine motor control in the neonate. We hypothesized that changes in intraoral sucking pressure, which are the end result of the coordination of different moving components, may reveal similar aspects of motor control to those observed in skilled adult movements.

In order to understand the complexity of the generation and control of intraoral sucking pressure, it is necessary first to describe the main mechanisms involved in a suck cycle. A general theory of movement control will then be presented along with a hypothesis of how this relates to the control of intraoral sucking pressures in neonates. The experiment that was used to test the hypothesis will be subsequently described.

Sucking mechanisms

Successful sucking is dependent on the careful coordination of various oral motor structures so that the ensuing changes in intraoral pressure are controlled, such that the milk flows in a manageable way from the feeding vessel. Previous research into newborn sucking behaviour has tended to focus on the frequencies and pressures generated during nutritive and non-nutritive sucking (Wolff 1968) and how sucking is coordinated with breathing and swallowing (Bu'Lock et al. 1990). Examining the form of a suck, to try to explain how the ensuing changes in sucking pressure are controlled, has largely been ignored. Neonatal sucking behavior can, in fact, be viewed as a precocious motor skill, which requires the careful integration of a complex array of muscle groups via the central nervous system. Injury to or dysfunction of the CNS can have catastrophic effects on sucking coordination (Coulter and Danner 1987). To highlight the complexity of the coordination of the oral motor structures, it is first necessary to briefly outline the movements of the different parts involved in bringing about the increasing suction period and the subsequent decreasing suction period (see Fig. 1).

Following radiographic studies from the 1950s (Ardran et al. 1958) and ultrasonographic studies from the 1980s (Smith et al. 1985), there is now general agreement about the oral motor mechanisms utilized when an infant is sucking. A combination of the peristaltic movement of the tongue and the movement of other related intraoral structures bring about changes in intraoral volume, which directly influences intraoral pressure (Ardran and Kemp 1959; Hayashi et al. 1997).

Increasing and decreasing suction periods

The increasing suction period commences when the labial and facial muscles contract around the nipple, forming an airtight seal, and the tongue surrounds the lateral sides and the bottom of the nipple. Following this the jaw lowers and the tip of the tongue moves forward to the front of the mouth. The central part of the tongue caves in to form a hollow, creating a larger area inside the oral cavity and allowing freer movement of the tongue along the base of the nipple (see Fig. 1A). This enlargement of the cavity causes the intraoral suction pressure to increase (see Fig. 1C), thus causing milk to flow from the feeding vessel into the mouth (Bu'Lock et al. 1990). Once the desired peak suction pressure has been reached, the tongue starts to flatten, the jaw starts to rise, and the mid-frontal part of the tongue lifts to form a bell shape. The tongue consequently moves along the nipple in a peristaltic wave so that remaining remnants of milk are expressed from the nipple, and this milk is propelled to the back of the mouth where it waits to be swallowed (see Fig. 1B). During this time the intraoral pressure becomes less negative (see Fig. 1C).

Precise synchronization between the jaw, tongue, and various other oromotor muscles is therefore essential for effective sucking to take place (Eishima 1991). By subtly changing the coordination of the different moving parts, the newborn infant is able to modulate the amplitude and duration of the intraoral sucking pressures to accommodate changes in milk flow (Mathew 1991) and fat composition, which occur naturally during human lactation (Woolridge et al. 1980). Carefully controlled changes in the intraoral sucking pressures are, therefore, needed to optimize the flow of milk from the feeding vessel into the infant's mouth, and to move the expressed milk to the back of the infant's mouth, where it accumulates prior to being swallowed.

Sucking control

Bernstein (1967) emphasised that the problem for the motor system, when performing controlled movements, lies not in the initiation of the contraction of an isolated muscle fiber, but in the integration of the many different contractions necessary to achieve a desired goal. Since sucking is often described as a reflexive rhythmic behavior, the tendency is to try to explain the origin and control of such a behaviour as being the end product of a neural oscillator, or, in other words, a central pattern generator (CPG) (Finan and Barlow 1996). CPGs are often conceived as discrete groups of interconnected neurons within the CNS that are solely responsible for the generation of one particular behavior. Although CPG theory has often been used to explain how movements, such as locomotion, respiration, and mastication (Grillner 1986; Nakamura and Katakura 1995), are generated, it does not fully account for the versatility observed within these given movement patterns. In fact, Simmers et al. (1995) refutes the idea of a CPG as a discrete entity by discussing how neurons are not invariant, but are in-

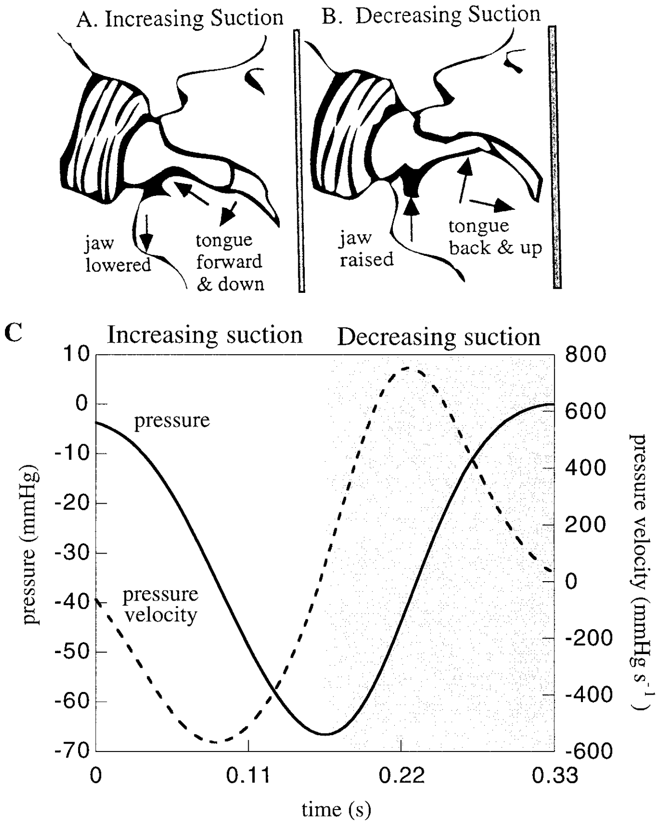


Fig. 1A–C A diagrammatic representation of the different movement processes that take place within an infant's mouth to bring about smooth changes in the intraoral pressure. **A** The increasing suction period, where the tongue moves forward and down as the jaw is lowered. The culmination of these processes brings about an increase in suction, which facilitates the flow of milk from the bottle into the mouth. **B** The decreasing suction period, where the tongue moves upwards and backwards as the jaw is raised. These movements help to propel the milk expressed during the increasing suction period to the back of the mouth, where it waits to be swallowed. **C** Actual recorded sucking pressures from inside the mouth of a feeding infant. The first part corresponds to the increasing suction period and the second part to the decreasing suction period stead subjected to a wide range of neuromodulatory influences. These influences affect the nature of the neurons and the strength of their synapses, which can consequentially change the neuronal output. A central pattern generator alone can not explain the variability of the duration and the amplitude of the movement observed in a rhythmical behaviour such as sucking. It has, however, been suggested that a central rhythm generator (CRG) coexists with a CPG (Nakamura and Katakura 1995), but it has not been made clear how the sensory information from the perceptual systems is integrated into the control of the movement. Oral control needs to be suitably flexible and dynamic so that changing environmental influences exerted by surrounding buccal surfaces and moving air and/or fluids inside the mouth can be accommodated. While engaging in sucking, for instance, it is essential that the infant exercises online control over the duration and subsequent amplitude (pressure) of an *individual* suck cycle, so that the flow of milk from the vessel into the mouth (increasing suction period) is carefully regulated and that the resulting influx of milk is propelled (decreasing suction period) to the back of the mouth in a controlled way. In other words, infants need to control sucking prospectively by using perceptual information about the current pressure inside the mouth, and how it affects the subsequent flow of milk from the breast or bottle, to predict their future course of action. Once an infant can competently control the pressure changes associated within an individual suck cycle, a succession or rhythm of sucks can then be generated.

τ theory – gap closure

For movements to be successfully controlled, it is first important that the approaches of different moving body parts are regulated with respect to desired destinations or goals, and, second that these approaches are guided by perceptual information about the movement of the body parts toward their goals. Since movements often involve changes in angle, distance, and force, and in the first and second time derivatives of these quantities, it might seem that at least nine different perceptual measures are needed. However, a theory that accounts for controlling actions perceptually with respect to a goal using a single perceptual unit of measure is the τ theory of movement control. This ecological theory, proposed by Lee (1976, 1998), emphasizes the importance of using perceptual information to control prospectively the closure of a gap. In keeping with J.J. Gibson's ideas, (Gibson 1966), the tau (τ) theory stresses the need to assimilate internal and external information throughout a movement, so that the closing of the gaps between different body parts and desired goals can be controlled. Lee (1976) proposed a single temporal measure, namely tau (τ) of the gap, that would provide sufficient information about how a gap is closing. τ is the time to closure of a gap at the current closure-rate. Though τ may be calculated as gap size, x, (measured in any unit, e.g., cm, Newton, degree) divided by the rate of change of x, the value of τ could be sensed directly without having to individually perceive x or its rate of change (Lee 1976). Neural utilization of the ubiquitous measure τ across different dimensions would, therefore, help to explain how the CNS overcomes the multi-dimensional problem of dealing with distance, angle, force, and other variables.

τ-coupling – coordination of movement

In the case of sucking, the movements of the lips, tongue, jaw, and cheeks as well as the resulting intraoral pressure changes might all be controlled in terms of τ. However an additional strand to the τ theory, namely τ-coupling (Lee et al. 1995; Lee 1998), needs to be introduced to explain how these different moving parts may be coordinated in space and time, so that the flow of milk from the feeding vessel into the mouth can be controlled. τ-coupling simply involves keeping two different τs continuously coupled together in a constant ratio (i.e. keeping $\tau_X = k\tau_Y$, where k is a constant). Thus, one use to which an animal may put τ-coupling is in making two gaps reach closure together; for as X tends to zero, τ_X tends to zero and so, if $\tau_X = k\tau_Y$,τ_Y and Y will each tend to zero. In a recent experiment, human adults were found to control the speed and direction of movement of hand to mouth when eating, in a manner consistent with their keeping τ of the distance gap (X) between hand and mouth coupled to τ of the angular gap (Y) between the current direction of mouth from hand to the goal direction at final approach (Lee et al. 1998a). Directly similar results have been obtained for echo-locating bats controlling flight speed and direction in order to land on a perch (Lee et al. 1995).

Taking the idea of τ-coupling further, it was hypothesized that, in order to stop at a destination at the same time as a moving object reaches it, a subject would couple the τ of their moving part onto the τ of the moving object. Such coupling was found in a recent experiment where subjects had to move a cursor on a computer screen to catch a moving target within a certain goal zone. In this instance, the perceived τ of the hand-target gap was found to act as an extrinsic τ-guide onto which the subjects coupled the τ of the hand-goal gap (Lee et al. 1998b).

In the above example, coupling the hand movement onto the extrinsic τ-guide provided by the moving target determined not only the timing of the movement, but also relevant aspects of its kinematics (i.e., deceleration to stop at the destination). However, in self-paced movements, such as sucking and reaching, the kinematics and timing of the movement need to be generated within the nervous system. Research on motor imagery suggests that recalling a movement includes having information about its time course (see Jeannerod 1994 for a review). For example, studies have shown that mentally imagined movements occur within the same temporal framework as actual movements (Decety and Michel 1989). Several neural structures have been implicated as being para-

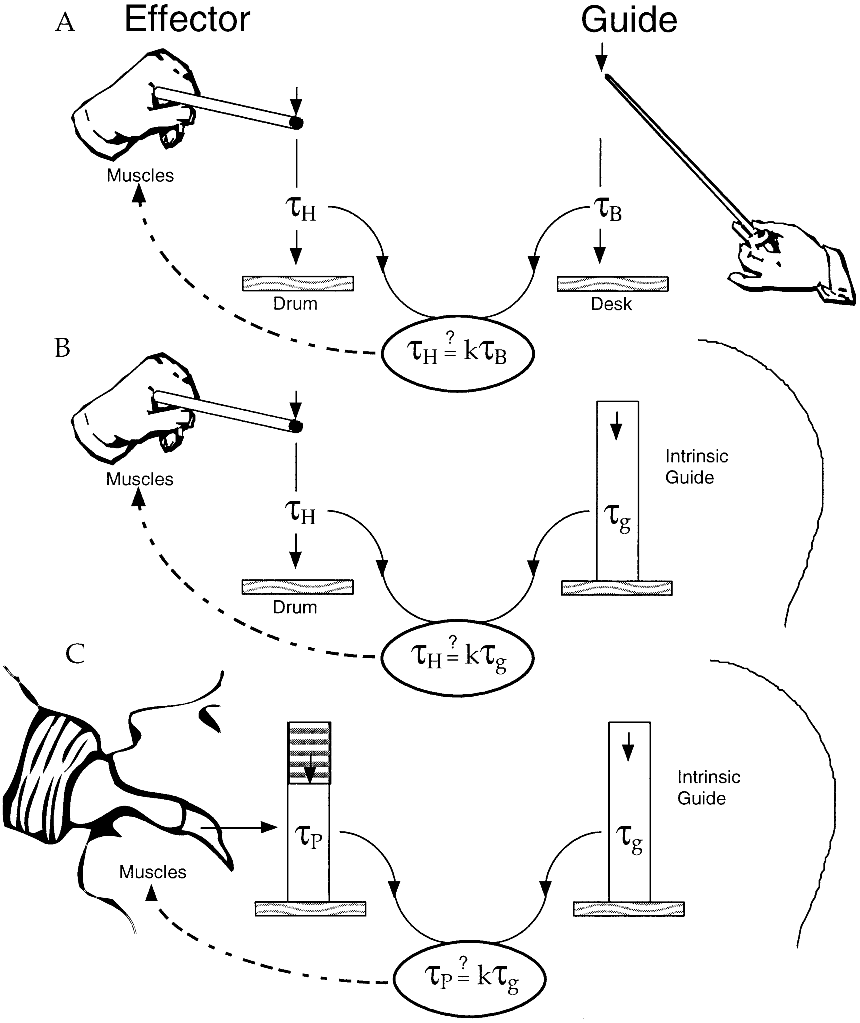


Fig. 2A–C Illustrations of the idea of τ-coupling a movement τ onto a τ-guide. **A** Drummer τ-coupling τ_H, τ of the gap between drumstick and drum, onto the extrinsic τ-guide, τ_B, τ of the gap between baton and desk, so that $\tau_H = k\tau_B$ for constant k. **B** Solo drummer τ-coupling onto intrinsic τ-guide, τ_g, so that $\tau_H = k\tau_g$ for constant k. **C** Newborn infant τ-coupling τ_p, τ of the gap between current sucking pressure and goal pressure, onto an intrinsic τ-guide, τ_g, so that $\tau_p = k\tau_g$ for constant k

mount in the specification of temporal information and the control of timing. The cerebellum, for instance, has been proposed as a basic timing mechanism (Ivry and Keele 1989; Jueptner et al. 1995), with patients suffering from cerebellar degeneration showing a marked deficit when performing perceptual timing tasks (Nichelli et al. 1996). Likewise the apparent slowing of the 'internal clock' observed in patients with Parkinson's disease suggests that the basal ganglia has a key role to play in the regulation of internal time (Meck 1996). However, how this temporal information is neurally represented and utilized still remains a relatively elusive question. A new dimension of τ theory attempts to address this question.

Intrinsic τ-guide

Following the principle of parsimony, it is hypothesized that the timing and kinematics of self-paced movements are controlled by τ-coupling the movement onto an intrinsic τ-guide generated in the nervous system, in much the same way as extrinsically paced movements can apparently be controlled by τ-coupling onto extrinsic τ-guides. An intrinsic τ-guide is simply conceived as a time-varying τ value, τ_g, generated within the nervous system, onto which the τ of a body movement, τ_m may be τ-coupled. (i.e., such that the relation $\tau_m = k\tau_g$ is maintained for some constant k.). τ_g could, for example, be some mathematical function of neural firing rate.

By analogy with extrinsic τ-guides, we may consider putative types of intrinsic τ-guide in terms of the form of motion of a quantity toward a goal level that would generate the changing τ values, τ_g. Thus, it may be said that a τ-guide, τ_g, *corresponds to* a quantity moving toward a goal level, if τ_g equals the value of τ of the gap between the quantity and its goal level at each time t. There are different possible forms of intrinsic τ-guide, that is different possible mathematical functions, τ_g, that correspond to different forms of motion of the quantity to its goal level. In the present study, we considered a simple intrinsic τ-guide, τ_g, that corresponds to some quantity changing with a constant second-order temporal derivative from a rest level to a goal level (τ_g being equal to τ of the gap between the quantity and its goal level at each time t). If the quantity has zero rate of change at time t=0 and reaches its goal level at time t=T, then it can be

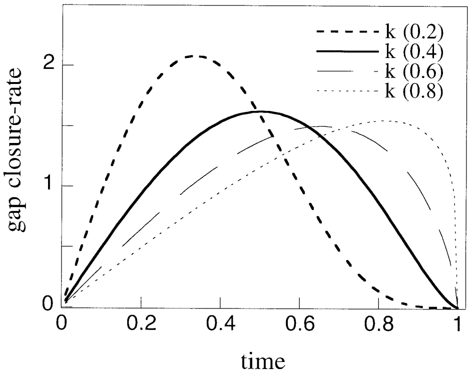


Fig. 3 Examples of gap closure-rate (”velocity”) profiles that would result if τ_X, τ of gap *X*, were τ-coupled onto an intrinsic τ-guide, τ_g, keeping $\tau_X=k\tau_g$, for a constant k. (See Appendix A for derivation of the formula used.) Gap *X* could, for example, be the distance-gap between a drumstick and a drum or a pressure-gap between current intraoral pressure and goal pressure. The gap closure-rate profiles, normalized so that the extent and duration of the movement are unity, are shown for four different values of k. The profiles are generally bell-shaped, like the distance-gap closure-rate profiles of a skilled reaching movement. In general, peak closure-rate is attained relatively later in the movement, and the rate of change of closure-rate is relatively more abrupt, the higher the value of k (for $0<k<1$)

shown that $\tau_g = 0.5(t-T^2/t)$ (see Appendix A for derivation of the formula). Thus, the intrinsic τ-guide has a single parameter that can be set, namely its duration, T.

An intrinsic τ-guide, or something akin to it, would appear to be necessary to explain much skilled behaviour. Consider, for example, a solo drummer playing a complex rhythm that has been learned and internalized. Two crucial aspects of the sequence of drumming movements are their relative timings and their velocities and accelerations at impact with the drum. The impact velocities and accelerations determine the stress pattern in the music and so are as integral to the rhythm as the timing of the movements. The timings and kinematics of the movements could be controlled by coupling the movements onto a sequence of intrinsic τ-guides that had been assembled by the drummer when learning the rhythm. The durations, T, of the guides would control the timings while the coupling constant would control the kinematics. The point is illustrated in Fig. 2B. There the drummer is using an intrinsic τ-guide, τ_g, to keep the τ of the gap between the drumstick and drum, τ_H, coupled onto the τ-guide, such that $\tau_H = k\tau_g$ at each time t. The value of the coupling constant k can be set according to how the drummer wishes to approach the drum, since the value of k determines the kinematics of the gap closure.

Contrary to what one might think, the constant second-order intrinsic τ-guide does *not* produce a movement across a distance gap that has constant acceleration. Instead the kinematics that emerge from τ-coupling the τ of given gap *x* onto an intrinsic τ guide are generally bell-shaped gap closure-rate (”velocity”) profiles, as illustrated in Fig. 3 (see Appendix A, Eq. 10 for the derivation of the formula). The different forms of the profiles are determined by the k values. For instance, a k value of 0.2 produces a short rise to peak closure-rate, with a long gradual deceleration to the drum. In contrast, a k value of 0.8 produces a longer rise to peak closure-rate with a shorter, more abrupt decelerative approach to the drum. In general, as the value of k increases, peak closure rate occurs relatively later in the motion and the approach to the target becomes more curt.

Hypothesis on control of sucking

We now apply the intrinsic τ-guide hypothesis to the control of sucking. As mentioned previously, sucking is a self-paced action that is dependent on the coordination and integration of the different moving parts to bring about changes in intraoral pressure that will facilitate milk flow. It is hypothesized that the sucking pressures are controlled by τ-coupling τ_p (the τ of the gap between the current intraoral pressure and the desired end pressure) onto τ_g (a τ-guide generated within the nervous system), by keeping $\tau_p = k\tau_g$, where k is a constant (Fig. 2C).

Materials and methods

Subjects

Twelve healthy bottle-feeding term infants, six males and six females, aged between 28 and 82 h, were tested in the post-natal wards of the Simpson Memorial Maternity Pavilion, Edinburgh. All infants were uncomplicated spontaneous vaginal deliveries. Ethical approval was granted and maternal consent was given before subjects were included in the study.

Pressure recording apparatus

Intraoral sucking pressures were measured via a modified twist-on disposable teat, normally used in the nursery. The alteration involved the insertion of a reasonably non-compliant catheter (5 French), through a small incision at the base of the teat. The tube was then threaded into the inside of the teat and out through one of the three manufactured feeding holes at the top. To be able to measure the intraoral sucking pressures the tube was positioned so that it protruded about 2 mm through the end of the teat. The catheter was then connected to the open end of the plastic pressure dome (the other end was closed to the outside world). The disposable pressure dome screwed on top of a pressure transducer (see Fig. 4), which was connected to the pressure terminal on a Hewlett Packard 78342A. These analogue pressure readings were sampled at 200 Hz and converted to digital output via a DAS 800 analogue-to-digital conversion board in a PC 486. Pressures ranging from +50 to –300 mmHg were calibrated using an external pressure generator.

Procedure

Prior to the testing session, the newly modified feeding teat was sterilized, and the catheter and the pressure dome were primed with sterile water to make the pressure readings more robust and less sensitive to artifactual fluctuations. The Hewlett Packard pressure monitor was then zeroed and calibrated using the in-built calibration. The corresponding application program used to collect the data was opened on the PC.

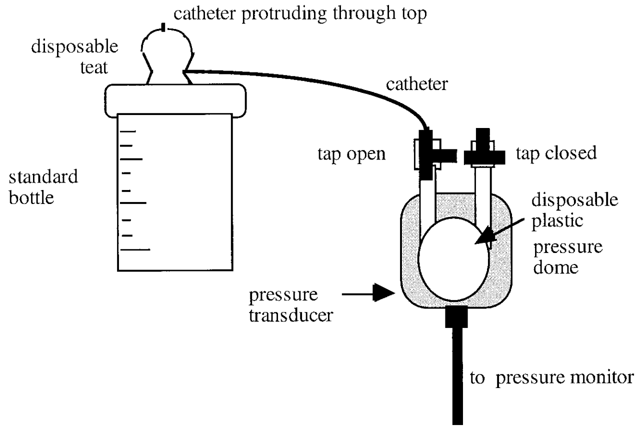


Fig. 4 Diagram of the apparatus used to measure intraoral sucking pressures. The modified disposable teat is connected to the pressure transducer via a non-compliant catheter. The catheter protruded through the top of the teat so that the pressure changes inside the infant's mouth could be measured during nutritive sucking

Following informed maternal consent, the mother brought her baby to the postnatal nursery when the baby was alert and demanding its next feed. A standard bottle of milk normally used in the nursery was attached to the modified disposable teat. Recording started as soon as the bottle entered the baby's mouth. The mother was encouraged to feed the baby normally so as not to disrupt the infant's natural rhythm. If, however, winding was required mid-recording, data collection was stopped at that point and restarted as soon as the infant was ready to begin feeding again. This seldom occurred, since limitations in the software meant that data collection was automatically stopped after 40 s. In these instances, recording was restarted as soon as physically possible. All files were saved in an ASCII format.

Results

The sucking durations and the corresponding pressures for the increasing and the decreasing suction periods differed markedly between infants (see Fig. 5A and B). The relatively large standard deviations also indicate a high degree of variablility within subjects.

Sucking pressures

The intraoral pressure traces recorded were cyclical in nature, with sucks being characterized by pressure becoming increasingly negative (i.e., increasing suction), followed by a change in pressure in the opposite direction (i.e., decreasing suction; see Fig. 1C).

The corresponding velocities (i.e., rates of increase) of sucking pressure were calculated using finite differences. It was found that the pressure-velocity profile of a suck had two different turning points: a trough during the increasing suction period and a peak during the decreasing suction period. Thus, the pressure velocity profile for each period was bell-shaped, resembling the (distance) velocity profile obtained for a swift reaching movement (Jeannerod 1988). To test the intrinsic τ-guide hypothesis, analysis was carried out using the following procedure.

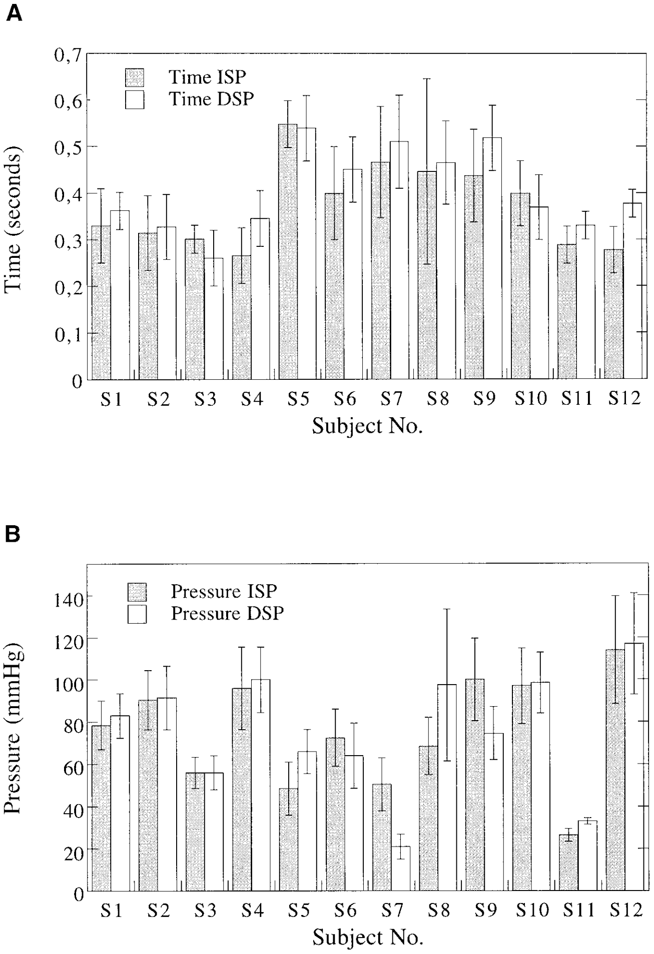


Fig. 5 The mean sucking times (**A**) and the mean sucking pressures (**B**) for the increasing suction period (*ISP*) and the decreasing suction period (*DSP*) for each of the 12 infants tested

Suck selection

Sucks for analysis were selected from the 200-Hz pressure recordings. In order to reduce the effects of noise, all of the recordings had previously been smoothed using a Gaussian filter with time-constant sigma, corresponding to the standard deviation of the Gaussian, of 20 ms. The Gaussian filter spanned the range ±2.575 sigma, thus 99% of the area of the full Gaussian. A suck was classified as having a pressure greater than –10 mmHg and was of a form similar to the other surrounding sucks. In order to get a good representation of sucks from the entire feeding session, all sucks meeting the above criteria were numbered. A random-number sequence, generated by the computer, was then used to select 12 sucks by each infant for detailed analysis. (A combination of infants tending to pause during the data collection and the limitations of the software meant that there wasn't an abundance of data for some of the subjects.)

τ-guide analysis

The following manipulations were performed on the individual sucks. Each suck was divided into the increasing suction period and the decreasing suction period. The increasing suction period was considered to be the period during which the pressure trace progressed from the least negative point (a peak) to the most negative point (the subsequent trough). The decreasing suction period followed from the increasing suction period and was taken from the trough where the increasing suction period ended to the next immediate peak (see Fig. 1C). In both these cases, the start and the end of the period was characterized by a zero crossing point in the pressure velocity.

Each period of the suck was treated separately in the analysis, as it was characterized by different movements of the tongue, jaw, etc. For each period, a time series was created, running from zero at the start of the period, in increments of 0.005 s (the sample interval), to the end of the period. Durations of a period varied from 0.15 s to 0.6 s. The pressure data were then normalized by adding or subtracting (whichever was appropriate for the increasing suction period or decreasing suction period), the last value in the pressure data set from each of the other pressure values in that data set. In the case of the increasing suction period, the normalized pressure values were positive going to zero, and, for the decreasing suction period, the normalized pressure values were negative going to zero. The rate of change of the normalised pressure at each sample time, t, were then calculated using finite differences (see Fig. 6 for examples of the traces). Finally, the τ of normalized pressure, τ_p at each sample time, t, was calculated by dividing the normalized pressure values, p, at each time t by the rate of change of the normalized pressure, $\dot{p}$, at that time. That is:

$$\tau_p = p/\dot{p} \tag{1}$$

For each period of the suck, τ_g, the value of the constant second-order τ-guide at sample time t, was then calculated using the formula:

$$\tau_g = \tfrac{1}{2}(t - T^2/t), \tag{2}$$

where T represents the duration of the sucking period (see Appendix A for the derivation of the formula).

The hypothesis is that, during each period of the suck,

$$\tau_p = k\tau_g \tag{3}$$

for some value k that is constant throughout the period. The best-fit value of k was determined by the following procedure. First, values that corresponded to pressure velocities below 10% of the peak pressure velocity were removed. The reason for this being that, when the pressure is just beginning to change, the estimations of the pressure velocity are noisy and, since the pressure velocity appears in the denominator of the formula for calculating τ_p, this noisy element is accentuated in the resulting values of τ_p. Table 1 gives the mean durations of the data that were excluded at the start and end of the movement, together with the mean total duration of the movement. The top graphs in Fig. 6 show examples of the pressure traces and the corresponding proportion of points that were excluded (masked parts at the beginning and the end of the graphs).

Table 1 Mean durations of the sections of data, at the beginning and end of a sucking period, that were excluded from analysis on the criterion that the rate of change of intraoral pressure was less than 10% of the peak value during the sucking period. For the increasing suction period, more data were excluded at the start of the movement as the suck cycle was being initiated and, for the decreasing suction period, more data were excluded at the end of the movement as the suck cycle was being terminated. It is worth noting that subject 3, who had the greatest amount of data excluded, actually had the lowest r^2 values in both the increasing and the decreasing suction periods

Subject no.	Increasing suction			Decreasing suction		
	Start (s)	End (s)	Total (s)	Start (s)	End (s)	Total (s)
S1	0.015	0.012	0.332	0.005	0.025	0.362
S2	0.021	0.014	0.314	0.014	0.031	0.327
S3	0.047	0.012	0.301	0.007	0.040	0.260
S4	0.017	0.011	0.265	0.008	0.037	0.345
S5	0.029	0.018	0.548	0.010	0.048	0.539
S6	0.030	0.015	0.399	0.005	0.060	0.450
S7	0.036	0.014	0.466	0.006	0.043	0.510
S8	0.019	0.016	0.446	0.010	0.028	0.465
S9	0.027	0.015	0.437	0.007	0.035	0.518
S10	0.030	0.015	0.399	0.009	0.019	0.369
S11	0.026	0.014	0.288	0.012	0.042	0.334
S12	0.012	0.013	0.277	0.008	0.022	0.377
Mean	0.026	0.014	0.373	0.008	0.036	0.404
S. D.	0.01	0.002	0.089	0.003	0.012	0.089

The best-fit value of k was found using the standard criterion of minimizing the sum of squares of the deviations of the data values, τ_p, from their predicted values, $k\tau_g$, and the corresponding r^2 for the fit was calculated (see Appendix B for details).

r^2 values

As can be seen from Fig. 7A, the mean r^2 values of the 12 sucks for each individual infant, for the increasing and decreasing suction periods, are all above 0.950 (apart from one extraneous value), indicating a strong coupling between the τ of the pressure and the τ of the guide. Looking at the results for the different periods in more detail, the box plot shows that the mean r^2 values for the increasing suction period for all 12 subjects range from 0.955 to 0.996, with a median value of 0.982. The overall mean for all 12 infants for this period was found to be 0.981, with a standard deviation of 0.01. The decreasing suction period, however, had a wider spread of mean r^2 values, ranging from 0.901 to 0.992 (see Fig. 7A). The median value in this case was, at 0.975, lower than the increasing suction period. Again the overall mean for all 12 infants was lower at 0.967, and the respective standard deviation was higher at 0.025. It is worth noting that the outlier values (represented by a circle) in both boxplots corresponded to the same infant (subject number 3).

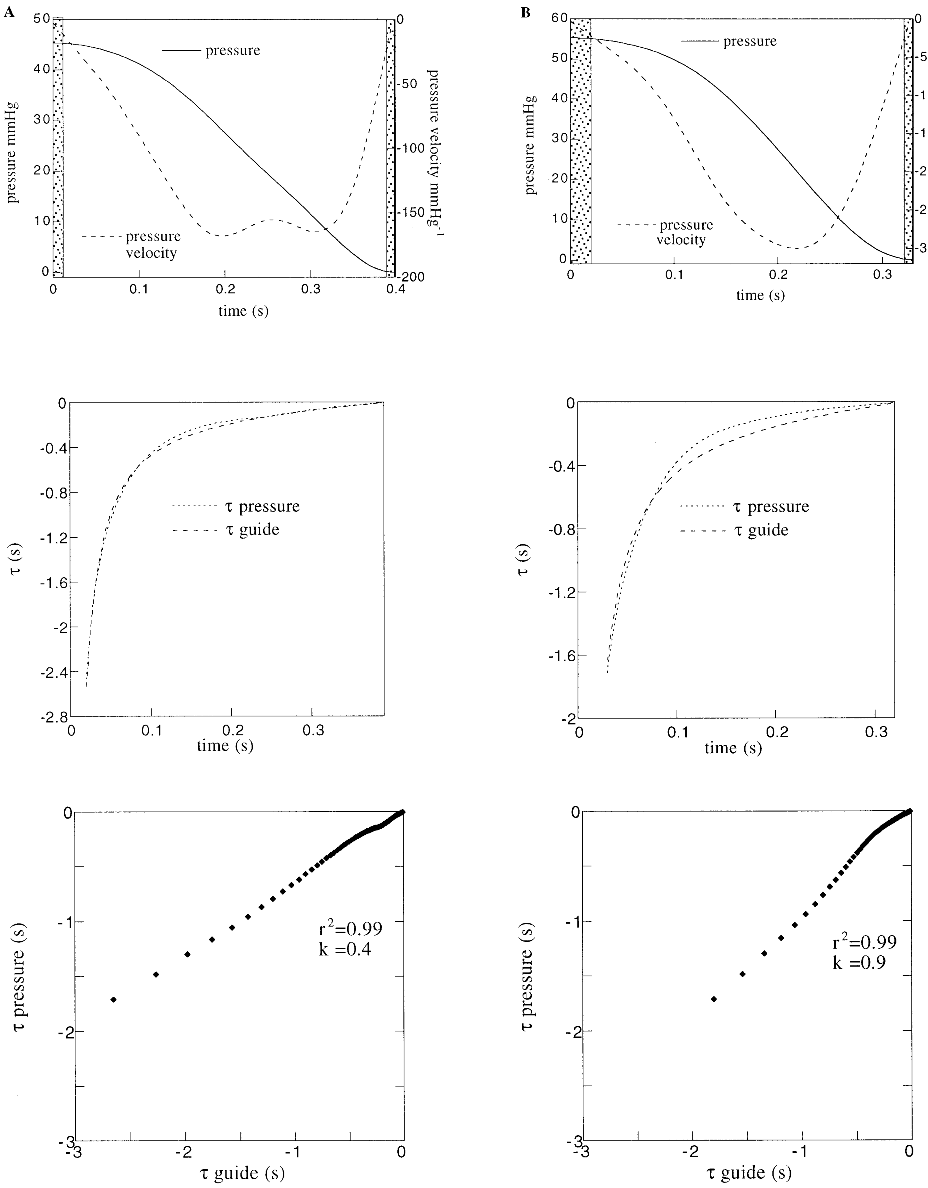
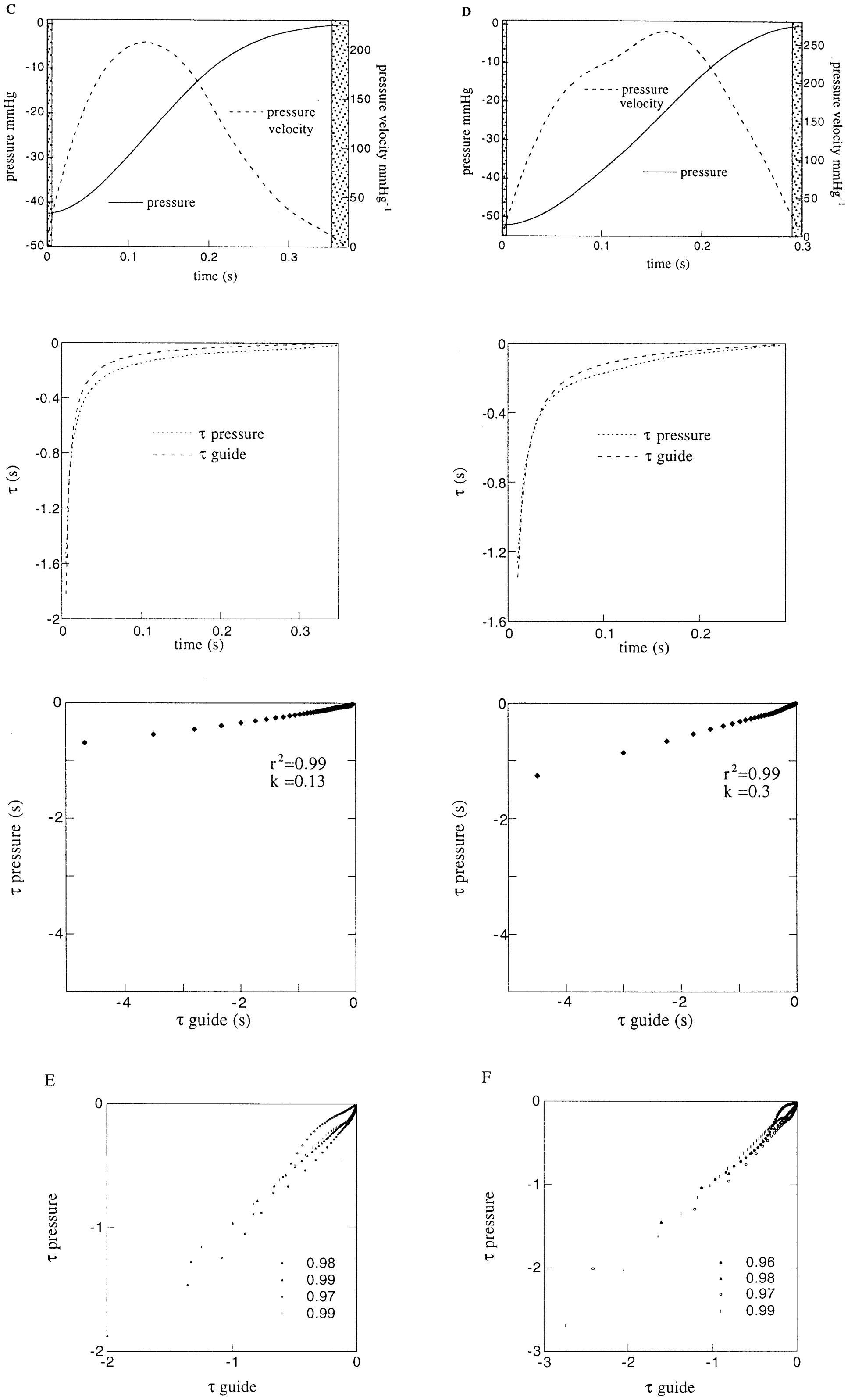


Fig. 6 Examples of profiles of intraoral pressure and the corresponding rate of change of pressure (pressure ”velocity”) for both the increasing suction period (**A** and **B**) and the decreasing suction period (**C** and **D**). The *masked areas* at the start and the end of the pressure traces indicate the data that were excluded from analysis because the pressure velocity was below 10% of the peak value attained during the suck period. The τ_p and τ_g values plotted against time in the *middle graphs* were calculated using the data in the graphs directly above. The *bottom graphs* illustrate the strength of τ-coupling between τ_p and τ_g, as indicated by the degree of linearity. For each graph, the r^2 value is the proportion of variance in τ_p, accounted for by the predicted τ-coupling equation, $\tau_p = k\tau_g$, and measures the strength of the coupling; the k value is the best estimate of the k in the τ-coupling equation (see Appendix B). It is worth noting that, although the durations are similar for each period, the k values obtained and the corresponding shape of the pressure-velocity profiles differ markedly for each suction period. **A** Example of a low k value (0.4) during an increasing suction period, while **B** is an example of a high k value (0.9). Conversely, for the decreasing suction period, an example of a high k value is 0.3, shown in **D**, whereas an example of a low k value is 0.13, shown in **C**. **E** and **F** show more examples of the τ-coupling and the resulting r^2 values between τ_p and τ_g for the increasing and decreasing suction periods, respectively

k values

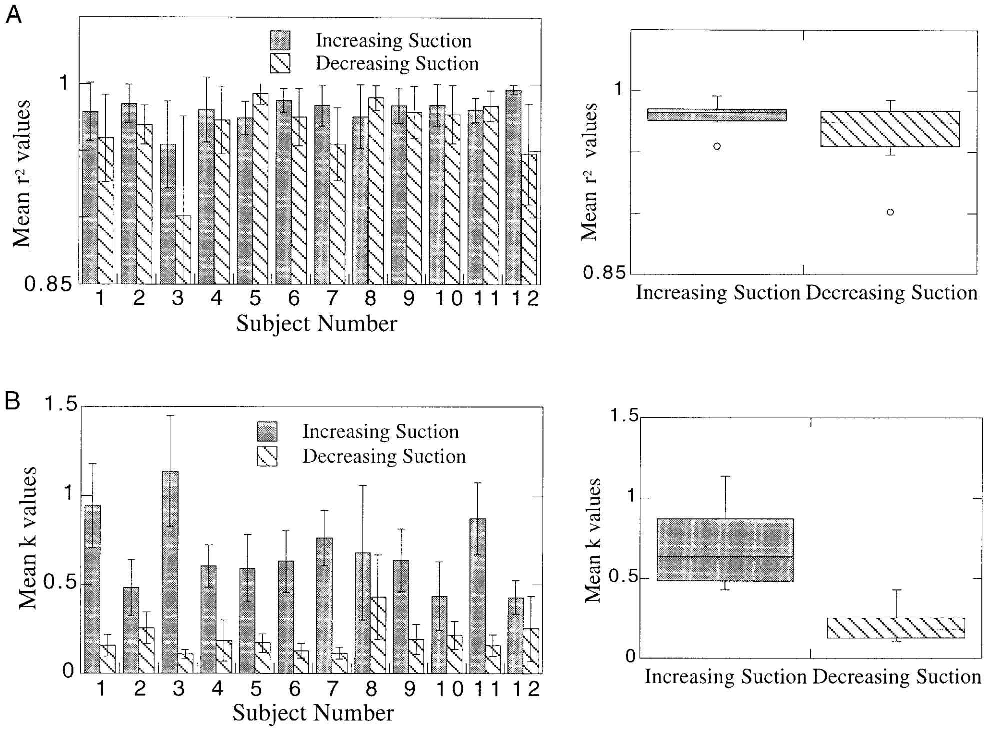
In Fig. 7B, the bar chart and the boxplot both show that there is something very different about the approach to the goal value for the increasing suction period, when compared with the decreasing suction period. The mean k values for the increasing suction period vary quite considerably, from 0.427 to 1.13, whereas the mean k values for the decreasing suction period range from 0.11 to 0.42. However, it should be noted that the lower the value of r^2, and hence the higher the variance of the data points about the regression line, the less reliable is k (the regression slope) as an indicator of how the movement is controlled. If r^2 is above 0.95 – meaning that over 95% of the variance in τ_p, tau of the intraoral pressure, is accounted for by the model – then the k values may be taken to provide reasonably reliable information about how the intraoral pressure is approaching its goal value. A k value ranging from 0 to 0.4 indicates that peak pressure

Fig. 6C, D (see legend page 378)



velocity was reached during the first half of the suction period, with a gentle decreasing deceleration to the goal value. A value greater than 0.4, but less than 1, indicates a more abrupt approach to the goal value, with peak pressure velocity being reached during the second half of the suction period (see Fig. 3 for examples). For the increasing suction period, the infants appeared to adopt a forceful approach to the peak negative pressure (mean k value 0.68), whereas a more gentle approach (mean k value 0.2) was used during the decreasing suction period.

Fig. 7 The histograms on the *left* show the mean r^2 values (**A**) and the mean k values (**B**) with respective standard deviation bars, obtained for each of the 12 infants tested, for both the increasing and the decreasing suction periods, testing the hypothesis that $\tau_p = k\tau_g$ for constant k. The *boxplots* on the *right* group all the infants together to show more clearly the range and median of all the mean values for the different suction periods



The difference between the two periods was found to be statistically very significant [($t_{(11)} = 6.39$; $p = 0.0001$].

Discussion

The results indicate that, while bottle feeding, jaw, tongue, lip, and buccal movements are coordinated in such a way that they bring about smooth pressure changes within a newborn infant's mouth. The pressure changes have similarly precise kinematics to those found in skilled adult movements, such as reaching. In contrast, the kinematics of neonatal infant reaches are much more erratic. Thus, neonatal sucking would appear to be a precocious fine perceptuo-motor skill. In particular, the results on sucking (like those on reaching: Lee et al. 1998a), indicate that intraoral pressure (or adult hand movement) follows an internal kinematic prototype in the form of an intrinsic τ-guide. The hypothesized τ-guide is a time-varying quantity, τ_g, assumed to be generated within the nervous system. It corresponds to some quantity (e.g., electrical charge) changing with a constant second-order temporal derivative from a rest level to a goal level, in the sense that τ_g equals τ of the gap between the quantity and its goal level at each time t (τ of a gap is the time-to-closure of the gap at the current closure-rate). The neural embodiment of the quantity could be a mathematical function of neural firing rate. According to the hypothesis, the infant senses τ_p, the τ of the gap between the intraoral pressure gap and its goal level, and regulates intraoral pressure so that τ_p and τ_g remain coupled in a constant ratio, k; i.e., $\tau_p = k\tau_g$.

The high mean r^2 values obtained for the 12 newborn infants when plotting τ_p against τ_g indicated strong constant-ratio coupling between τ_p and τ_g. This pattern was evident for both the increasing and the decreasing suction periods. The decreasing suction period did show more variation in the r^2 values and the mean r^2 values were significantly less than the mean r^2 values for the increasing suction period [$t_{(11)} = 2.15$; $P = 0.055$]. This finding might be due to the movement of the milk to the back of the mouth during the decreasing suction period, thereby perturbing the intraoral pressure.

The mean k values for each period also provide interesting information about how the pressure changes in the mouth are controlled. Although the duration of each suction period is similar (see Table 1), the mean k values obtained are markedly different, reflecting the divergent purposes of each movement period. The increasing suction period is concerned with optimizing the flow of milk from the feeding vessel into the mouth. This purpose is reflected in the mean k values, which were significantly greater than 0.4 [$t_{(10)} = 4.2$: $P = 0.0007$], highlighting a longer period of acceleration and a more forceful approach to the destination (see sample velocity curves in Fig. 3). The opposite was found for the decreasing suction period, where a more gentle approach was found with the mean k values significantly less than 0.4 [$t_{(10)} = -7.43$: $P = 0.0001$]. This strategy is definitely more advantageous for the infant, as the danger of expressed milk coming into contact with the infant's airway is minimised. Instead, the milk is collected in a controlled way at the back of the mouth, where it awaits swallowing.

In order to control sucking pressures, the infants must have some means of sensing the changing intraoral pressures. It is known that Pacinian corpuscles found deep in the skin provide the nervous system with sensory feed-back about the changes of pressure exerted on the surface of the skin (Schauff et al. 1990). However, with regards to pressure sensors in the intraoral environment, experiments have shown that afferents in the oral mucosa, innervated by the infraorbital nerve, increase their firing rate in response to an increase in the intraoral pressure caused by subjects blowing (Furusawa et al. 1992). Likewise, during phonation, significant differences have been found in the responsiveness of the receptors supplying the oral mucosa when producing a /pa/ sound compared with the responses when producing /ta/ and /ka/ sounds (Furusawa 1994). Sucking control involves similar oral motor structures to those required for coherent speech production. Articulating words is dependent on the control of the flow of air pressure through the mouth as the tongue and lips move to produce the desired sounds. However, the outcome of the two activities are very different. Sucking control has two very distinct periods within a cycle. The second period of a suck will be dependent on the outcome of the first period, that is, the amount of milk that flows into the mouth as a result of the increase in suction pressure. In order for the infant to build up a sucking rhythm, it is necessary to get the control right within an individual suck cycle. The generation of successive sucks will therefore be dependent on good control within an individual suck. Findings with very preterm infants, tested using the same set-up outlined in this paper, have shown that irregularities within an individual suck cycle can prevent a rhythm or succession of sucks from being generated.

Although fetuses have shown mouthing movements in utero as early as 15 weeks gestation (Ianniraburto and Tejani 1981), the neural mechanisms needed to coordinate sucking, swallowing, and breathing when feeding nutritively are not functionally mature until at least 32 weeks gestational age (Medoff-Cooper 1991). A recent study (Craig et al. in preparation), using the same procedure as presented in this paper, found that, for four very preterm infants (born at less than 26 weeks gestational age), the coupling between the τ-guide and the τ-pressure improved systematically from the first test during the first week of oral feeding (varying from 33–35 weeks gestational age depending on the individual infant) to the fourth test (3 weeks after the first test). This suggests that either the neural mechanisms needed to generate a τ-guide mature over this time or that the ability to integrate the perceptual information from the τ-pressure and to couple this onto a τ-guide improves. In contrast, two other very preterm infants, which were also tested in the above study, failed to show any coupling between the τ-guide and the τ-pressure over the 4-week period. In these cases, the lack of coupling may be indicative of neurological deficits, as preterm infants born at a low gestational age and/or birthweight are at a much greater risk of developing neurological and subsequent motor problems (Volpe 1994). Perhaps identification of these neural deficits that cause motor difficulties when coordinating intraoral sucking pressures may help to elucidate the neural mechanisms involved in sucking control.

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Appendix A. Intrinsic τ-guide

The hypothesis is that, at any time t during a self-paced movement, such as sucking, τ_p, the (changing) τ of the gap between current intraoral pressure and the goal pressure, is τ-coupled onto an intrinsic τ-guide, τ_g, by keeping

$$\tau_p = k\tau_g \tag{A1}$$

where k is a constant. The τ-guide – the time-varying quantity, τ_g – is assumed to be generated within the nervous system. The particular form of intrinsic τ-guide considered in this paper corresponds to some quantity (which might be, e.g., electrical charge) changing with a constant second-order temporal derivative from a rest level to a goal level, in the sense that τ_g equals τ of the gap between the quantity and its goal level at each time t (τ of a gap is the time-to-closure of the gap at the current closure-rate).

If, at time $t=0$, the quantity starts changing with constant second-order temporal derivative, A, from its rest level and reaches its goal level after time T, then the initial gap to the goal level will be $x_g(0)={}^1\!/_2AT^2$. After time t, the gap will have reduced by ${}^1\!/_2At^2$ and so will be equal to

$$x_g = {}^1\!/_2A(T^2-t^2) \tag{A2}$$

The gap closure-rate then will be equal to –At. Therefore, τ_g, the τ value of the τ-guide at time t, will be ${}^1\!/_2A(t^2-T^2)/At$ (τ is conventionally taken as being negative during closure of a gap). Thus, simplifying,

$$\tau_g = {}^1\!/_2(t-T^2/t) \tag{A3}$$

for $t_0 < t \leq T$, where t_0 is a small positive time ($t=0$ is excluded because τ_g is infinite then). Note from Eq. A3 that τ_g has a single adjustable parameter, its duration T.

Therefore, from Eqs. A1 and A3, the hypothesis predicts that, at each time t, during all or most of the time interval (t_0, T)

$$\tau_p = {}^1\!/_2k(t-T^2/t) \tag{A4}$$

for a constant k.

The equations giving the pressure-gap, x_p, the gap closure-rate, $\dot{x}_p$ and the rate of change of the closure rate, $\ddot{x}_p$, as a function of time are obtained by first noting that if, $\tau_p = k\tau_g$ (Eq. A1), then

$$x_p = Cx_g^{(1/k)} \tag{A5}$$

where C is a constant. This follows from the τ-coupling theorem (Lee 1998). Substituting $x_g = {}^1\!/_2A(T^2-t^2)$ from Eq. A2

$$x_p = C[{}^1\!/_2A(T^2-t^2)]^{(1/k)} = D(T^2-t^2)^{(1/k)} \tag{A6}$$

where D is a constant. Differentiating Eq. A6 successively with respect to time

$$\dot{x}_p = -2D(1/k)t(T^2-t^2)^{(1/k-1)} \tag{A7}$$

$$\ddot{x}_p = 2D(1/k)[(2/k-1)t^2-T^2](T^2-t^2)^{(1/k-2)} \tag{A8}$$

Finally, we may normalize Eqs. A6–8 without loss of generality by setting the duration $T=1$ and the initial gap size $x_g(0)=1$ for the intrinsic τ-guide. Since $D=x_p(0)/T^{(2/k)}$ (shown by setting $t=0$ in Eq. A6), in the normalized equations $D=1/1=1$. Thus substituting $T=1$ and $D=1$ in Eqs. A6–8, the normalized forms of these equations are

$$X_p = (1-t^2)^{(1/k)} \tag{A9}$$

$$\dot{X}_p = -2(1/k)t(1-t^2)^{(1/k-1)} \tag{A10}$$

$$\ddot{X}_p = 2(1/k)[(2/k-1)t^2-1](1-t^2)^{(l/k-2)} \tag{A11}$$

where uppercase Xs designate the normalized values. The gap closure-rate profiles shown in Fig. 3 were generated using Eq. A10.

Appendix B. Measuring fit of data to intrinsic τ-guide

To test the intrinsic τ-guide hypothesis, it is necessary to determine how closely the pressure data satisfy Eq. A4, viz. $\tau_p = k\tau_g =$ 8 pt k(t-T^2/t). The value of the constant k that yields the best fit over the time interval (t_s, t_e) on the least sum of squares criterion is computed as follows. Let S be the sum of the squares of the deviations of the intraoral pressure data, τ_p, from the values, $k\tau_g$, predicted by the hypothesis. Thus,

$$S = \sum_{t=t_s}^{t=t_e} \left[\tau_p - \frac{1}{2}k\left(t - T^2/t\right)\right]^2 \tag{A12}$$

S is minimum when $\frac{ds}{dk} = 0$, i.e., when

$$-\sum_{t=t_s}^{t=t_e} \left[\tau_p - \frac{1}{2}k\left(t - T^2/t\right)\right]\left(t - T^2/t\right)$$

$$= -\sum_{t=t_s}^{t=t_e} \tau_p\left(t - T^2/t\right) + \sum_{t=t_s}^{t=t_e} \frac{1}{2}k\left(t - T^2/t\right)^2$$

$$= 0 \tag{A13}$$

Thus, solving for k,

$$k = \frac{\sum_{t=t_s}^{t=t_e} \tau_p\left(t - T^2/t\right)}{\sum_{t=t_s}^{t=t_e} \frac{1}{2}\left(t - T^2/t\right)^2} \tag{A14}$$

The formula for calculating the r^2 of the linear relationship between τ_p and $k\tau_g$, using the least sum of squares model (Hays 1970, p. 498), is computed as follows:

r^2=1- sample variance of estimate for standard scores

$$= 1 - \frac{\sum\left[\tau_p^* - k\tau_g^*\right]^2}{N} \tag{A15}$$

where

$$\tau_p^* = \frac{\tau_p - \text{mean}\left(\tau_p\right)}{\text{s.d.}\left(\tau_p\right)},$$

$$k\tau_g^* = \frac{k\tau_g - \text{mean}\left(k\tau_g\right)}{\text{s.d.}\left(k\tau_g\right)}, \quad \text{and}$$

n = number of samples

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