Embodied Anticipation: A Neurodevelopmental Interpretation

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This article proposes an approach to the brain's role in communication that treats the brain as the vehicle of a multi-scale embodiment of anticipation. Instead of conceptualizing anticipation as something a brain is able to do when circumstances seem to require it, this study proposes that anticipation is continuous and ongoing because to anticipate is an inherent design characteristic of the brain. Correspondingly, there is no anticipation module in the brain, and no focal lesion selectively abolishes the brain's propensity to anticipate. Anticipation is a wager based on previous experience. It readies a response to an event that has yet to occur. First, the anticipation is "embrained" in terms of covert neural representations, and then it is embodied in terms of rudiments of the embrained actions and expressions of feeling. This study applies this concept to conversation and shows that nested anticipations precede the dynamics of the actual encounter and continue at each turn as long as the conversation lasts.

Will you, won't you, will you, won't you, will you join the dance? (Lewis Carroll, *The Lobster-Quadrille*, p. 84)

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Participants in a conversation generate a host of nonverbal anticipatory elements (expressions, gestures, and postures) that foreshadow how the interaction is likely to proceed. Whereas some of these actions have conventional and seemingly arbitrary connotations, many are partial embodiments of the embrained thought or intention. Others can, therefore, interpret these actions without a key to their meaning (Kinsbourne, 2006). These structures enable participants to anticipate each other's actions and meanings. Anticipating, in turn, allows smooth transitions in turn taking, and also enables each participant to continuously confirm emerging interpretations of meanings. It assists participants in cooperating to construct the trajectory of the ongoing interaction.

What role does the brain play in generating these powerfully coordinative projective assets? There is converging experimental evidence that the human brain has properties of an *embodied* anticipatory system. This system enables individuals to continuously *entrain* to one another's actions and meanings. Entrainment means that the participants can generate a context of reciprocating interaction because the movements, postures, gestures, gazes, or languages generated by each can elicit expected similar or congruent movements, postures, gestures, gazes, or languages from the other. These, in turn, can recursively elicit reciprocating movements, postures, gestures, gazes, and languages from the former.

The most fundamental decision open to the most primitive, as well as the most sophisticated, motile organism is whether to approach or withdraw. Among humans, a spectacularly social species, a decision to approach is a frequent preamble to a conversation but predicated on being met by indications of the same decision on the part of the other. Particularly, but not exclusively, when the parties are not well acquainted, the overt approach is preceded by signs that it is intended but is not yet irrevocable. In the initial approach to another with the intention to converse, one's intention is legible in one's body language: forward leaning, with attempted eye contact, and a certain eagerness of expression. These embodiments arise automatically, but they may also be deliberately amplified. They predict and prime a reciprocating response from the other. Before further action, a match–mismatch computation determines whether the expectation was indeed confirmed. If it was, the match encourages the next move, continuing the approach to entrain. If it was not, the mismatch offers the initiator the choice between a slower or an alternative line of approach; or, particularly if the initial approach was formulated so as to be deniable, one might choose to break off the attempt and even to appear not to have intended to converse in the first place. These alternative initiatives have their embodiments, which the other can readily decode (and act accordingly).

Kinsbourne (1989) characterized the laterality of the neural circuitry underlying the activity cycle involved in approach–avoid dynamics—largely left hemispheric for approach and right hemispheric for withdrawal. In the case of

conversation, one would relabel these alternatives as "continue ongoing behav-ior" versus "interrupt ongoing behavior." Successfully accomplished entrainment orients the participants to a common point of view, which they proceed to cooperatively develop. The resultant, recursive, self-sustaining entrainment gives rise to a dyadic space in which the anticipatory structures that conversation analysts and linguists investigate are able to emerge and wield their coordinative influence.

To characterize the anticipatory, entrainment-sustaining activity of the brain, we describe the following: (a) enactive perception, entrainment, and the brain; (b) infant imitation and entrainment; (c) entrainment and the role of approach–withdrawal dynamics; (d) entrainment and embodied reciprocity; (e) the role that these embodied anticipations play in interactions between adults; and (f) multi-scale entrainment and coordinated action.

ENACTIVE PERCEPTION, ENTRAINMENT, AND THE BRAIN

Attention is preparatory for action (Allport, 1987) and, consequently, attended percepts are encoded enactively (Varela, Thompson, & Rosch, 1991). Perceiving an attended object (thing or person) is enactive in that the percept's encodings include the response possibilities that the perceived object affords. Gibson (1979) remarked: "The observer . . . cannot help seeing the affordances for behavior in whatever he looks at" (p. 223). To an extent, the perceptual encoding activates the motor programs that would be in use were the afforded action actually to be carried out. It follows that perception incorporates an element of anticipation (Jordan, 1998) of one's own prospective actions. Research indicates such antic-ipatory, prospective perception is evident in infant behavior. Rochat and Hespos (1997), for example, found that the rooting response is not so much a reflex response as it is a prospective (i.e., anticipation-driven) behavior. Specifically, infants do not make the rooting response if they touch their cheek themselves. Craig and Lee (1999) found newborns prospectively control the flow of milk while sucking. In addition, van der Meer (1997) found that newborn infants are able to track a moving beam of light by prospectively controlling the position, velocity, and deceleration of their arm. In a summary of such results, von Hofsten (2007) stated:

> Adaptive behavior has to deal with the fact that events precede the feedback signals about them. . . . The only way to overcome this problem is to anticipate what is going to happen next and use that information to control one's behavior. (p. 54)

Within the framework of enactive perception, such *anticipation* is provided by the activation of the motor codes that would be needed to act toward the

perceived entity. The research of Craig and Lee, Rochat and Hespos, and van der Meer indicated such prospective activation is evident in perception as early as birth.

This prospective, anticipatory aspect of infant perception plays an important social role. For in a dyadic interaction, one's movements, postures, or gestures potentially anticipate those of the other and prime them to be congruent (e.g., imitative). Each action takes a further step toward dyadic entrainment and to continued entrainment. Just as the rhythmical activity of an individual has an inherent momentum in that single acts are actually rhythmic movement sequences cut short (Miall & Ivry, 2004), so the reciprocal entrainment of conversing participants has its own momentum (independent of meanings conveyed) and continues until it is brought to a halt by a deliberate act of withdrawal (disengagement) by one or both participants.

The physiology of imitation and entrainment was brought center stage by the discovery of two types of neurons that are involved in the perception of actions: canonical and mirror (Gabarini & Adenzato, 2004). Canonical neurons in motor planning areas of area F5 become active when a macaque monkey perceives an object, such as a peanut, which implies that seeing the peanut entails aspects of the motor plan that the monkey would use to act on the peanut (the peanut's affordance as perceived by the monkey). Mirror neurons are also located in area F5, and have even more pronounced motor qualities in that they become active when an agent actually acts on the object, regardless of whether the agent is the monkey itself or another agent. The activity of mirror neurons (Rizzolatti, Fadiga, Fogassi, & Gallese, 2002) reveals that not only perceiving objects but also perceiving actions is enactive—that is, perceiving the actions of another entails representing aspects of the motor planning one would use were one to generate that action oneself. Recent neuroimaging experiments with humans have revealed mirroring systems in Broca's area, the human homologue of macaque area F5 (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Ramnani & Miall, 2004).

The mechanism by which one's mirror neurons respond indifferently to a perceived action, and to the same action when one intends it oneself, is not necessarily a tailor-made adaptation for integrating a first- and third-person perspective, as is often suggested in attempts to infer the origins of empathy and language. Mirror neurons were first described in macaque monkeys who are not known to empathize or converse or even, in the strict sense, imitate. The most parsimonious account of mirror activity is that the action as such is represented in certain cortical fields, and the identity of the agent, self or other, is concurrently represented in a different cortical field (for differential hemisphere localization of "self" and "other" markers, see Decety, Chaminade, Grèzes, & Meltzoff, 2002) The mirror neurons respond indifferently in both conditions because they cannot by themselves tell the conditions apart (Kinsbourne, 2005).

The perceptual representation does double duty for perceiving and for forming an afference copy (Hershberger, 1976) of an intended goal state. An afference copy prespecifies the content of the feedback to be expected should the goal be attained. It represents the goal to be attained. Specifying the goal is the first step in forming an intention to act. Perceptually, the end point of another's completed action is the same as the beginning of an intended action.

The degree of mirror-system activation depends on one's level of expertise with the perceived motor skill were he or she to imitate the perceived action. Calvo-Merino et al. (2005) found that ballet dancers manifested more mirroring activity while watching ballet than while watching *capoeira* dancing. Mirroring activity in non-dancers was significantly lower than in ballet dancers, and did not differ in relation to dance type.

Collectively, these findings are consistent with the enactive approach to perception. Whereas *object* perception entails activation of aspects of the motor plans that the perceiver would have to generate to interact with a perceived object, *action* perception activates aspects of the motor planning the perceiver would have to generate to imitate the action that he or she observed.

INFANT IMITATION AND ENTRAINMENT

Interpersonal entrainment both enables conversation and constitutes it. The reciprocal moves of the entrained parties are most obvious in infants in whom the innate motivation to "converse" is most evident and the displeasure when the interaction fails to materialize or is abruptly concluded is most clearly expressed. The infant and mother engage in a precursor, called interactional synchrony, which, like conversation, has affective coloring and also predictive value for the mother–child relationship—that is, for mother–child attachment (Isabella, Belsky, & von Eye, 1989; Stern, 2000). The entrainment may not always involve the use of the identical motor patterns, but the rhythmic aspect is maintained. For instance, the mother speaks, but the pre-verbal child blinks in time with her speech rhythms. The mother and child are "on the same wavelength." The entrainment consists of sequences of imitation and anticipation. Trevarthen (1977), who first described this phenomenon as "intersubjectivity," remarked:

> Both partners express complex purposive impulses in a form that is infectious for the other. It is difficult to perceive any content in the communication except for the exchange itself. (p. 75)

The conversation in the infant–mother dyad is largely phatic (Malinowski, 1923)—that is, the medium is the message. We suggest that adults conversing are often not so different from infants in these respects and that an interchange

largely for its own sake describes most everyday conversations. Although what is said can be important, it is the nonverbal accompaniments that sustain and drive the act (and may also be most likely to be remembered). Small talk may not reduce informational uncertainty, but it does reduce affective uncertainty. It is about social exchange. Each act of communication, thus, might have a future in a gain in information, a gain in affiliation, or a gain in both. This concept puts the nonverbal components of conversation into focus.

In light of the enactive quality of perception, many researchers have proposed that the mirror system constitutes the neural substrate of imitation (see Meltzoff & Prinz, 2002). Meltzoff and others (e.g., Meltzoff & Moore, 1997) described the infant's propensity to imitate the caretaker's gestures and facial expressions, such as protrusion of the tongue (cf. Jones, 2006). This act on the part of infants may be best understood as being neither reflexive nor volitional. Kinsbourne (2002) conceptualized infant imitation as "infant perception on the fly." "Imitation is inherent in the organization of the central nervous system and may have to be restrained for non-imitative responses to occur" (Kinsbourne, 2002, p. 314). Were one to routinely respond to perceived objects with the relevant actions, that would generally be seen as maladaptively impulsive. The mature nervous system has sufficient inhibitory power to hold the actual response that any percept affords in abeyance, until it is called for in the broader context of the moment. Moreover, relevant to our proposal that participants in conversation signal their meanings and intentions involuntarily, even in the mature brain, the inhibitory barrier is often not totally effective. Some incipient embodiments of the action-coded percept leak from the covert representations[1] in the brain so as to cause overt postural adjustments and corresponding facial expressions, which betray the suspended intention. Maintaining a "poker face" to block the leaking information is notoriously difficult. What seems to be an imperfection in the capability of the infant brain for inhibitory control has obvious costs but also benefits. The tendency for one's thoughts to be inadvertently revealed in one's actions is at a maximum in infants, whose inhibitory capacity is yet to emerge,

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[1]At first glance, referring to neural activity as a "representation" may seem at odds with the notion of "embodied anticipation," for many theorists have been drawn to the "embodiment" position precisely because of its opposition to traditional computational assumptions regarding the relation between brain, body, and world (A. Clark, 1997). Although we are sympathetic with this position, we argue there is still quite a bit of disagreement in the embodiment community as to just what embodiment means (for a thorough review of the issues at stake in the debate between internalist and radical-interaction approaches to cognition, see Jordan, this issue, as well as Jordan, 2008). Thus, for the purpose of this article, we utilize the concept of representation as an efficient means of referring to neural activity. We do so, however, in a manner consistent with current embodiment theory in that, while discussing brain dynamics, we focus on the recursive, multi-scale contingent contingencies that exist between brain dynamics, body dynamics, and world dynamics. These continuous, multi-scale, contingent interactions lie at the heart of the embodiment critique of computationalism and constitute the theoretical thrust of this article.

and whose thoughts have therefore not yet differentiated from their actions. At that stage of development, the infant has no use for secrecy and deception, and yet cannot express his or her needs in words. Under these circumstances, the overt embodied indications of the infant's state of body and mind can only be helpful to the caretaker.

Kinsbourne (2002) suggested that by virtue of the enactive property of uninhibited perceptual encoding when perceiving and thereby imitating the actions of another, the infant gains knowledge of and control over his or her body movements. When an infant observes an action, the motor planning that accompanies the perception of the action is uninhibited, due to the maturational immaturity of the infant's developing brain. As nothing is holding back the motor realization of the action plan, the infant expresses this uninhibited motor plan, given of course that the perceived action is within the infant's limited motor repertoire (synergisms of flexion vs. extension, exploration vs. startle, interactional synchrony vs. disengagement). The execution of the action makes the infant's perception of the action publicly available and allows others to "see" what the infant has seen on the fly. The infant engages over and over in repetitive reciprocal imitation. This is presumably because the resulting entrainment has evolved to be innately and intrinsically motivating for the infant. The entrainment then becomes secondarily motivating also because it facilitates bonding with a caretaker and, later in development, bonding with a group.

Although they are far more differentiated, the adult's corresponding thought processes exhibit in their embodiment the imprint of the infant's innate action patterns. Brain damage reveals the imitation found in the infant, but held covert by the intact brain. Clinical data that is consistent with the view that infant imitation constitutes infant "perception on the fly" reveals that adults who experience damage to prefrontal inhibitory centers have difficulty inhibiting the generation of perceived action. As a result, they occasionally engage in uncontrollable imitation. The brain basis of the inhibition that normally conceals the inner workings of perception is the relatively late-myelinating prefrontal cortex. Patients with bilateral prefrontal lesions have been observed automatically to imitate the clinician's movements, described as echopraxia (Luria, 1973) and to handle objects within reach according to their affordances but automatically and to no purpose. This is called utilization behavior. Lesions elsewhere in the left hemisphere cause patients with "transcortical aphasia" to repeat, involuntarily and without understanding, another's spoken words. This is called echolalia. The brain damage appears to reveal the otherwise covert imitation that occurs in the intact brain.

The enactive nature of both infant and adult perception makes it possible for the infant's actions to entrain those of a caregiver. Specifically, if the infant produces an action, and the caregiver does not inhibit the expression of the motor plans activated in his or her brain by the infant's action, the caregiver will also

produce the enactively perceived action. This action on the part of the caregiver will, in turn, recursively activate the enactive perceptual systems of the infant. As a result, the infant–caregiver dyad will find itself locked in a self-sustaining loop of reciprocal enactive perception. In short, the two will be entrained. Unlike other primates who do not converse, the parent–child dyad generates cycles of reciprocity that allow the infant to learn to expect reciprocity during interaction. The infant confirms that the caretaker is taking care of him or her and embeds a trusting anticipation of continuing positive interaction in his or her physical states. Iterative reciprocity is inherently enjoyable and engenders an anticipation of support (Stern, 2000).

ENTRAINMENT AND THE ROLE OF APPROACH– WITHDRAWAL DYNAMICS

The enactive nature of perception provides a mechanism for humans to entrain with one another. Both infants and caregivers normally take great pleasure in engaging in entrainment episodes, whereas chronic lack of opportunity to entrain, as in "hospitalism" and certain orphanages, is known to lead to disorders of attachment, with severe consequences for emotional development. That adults, in turn, take pleasure in sustained entrainment with infants is evidenced by the caregiver's efforts to bring about an entrainment episode. The caregiver keeps him- or herself aligned within the infant's visual field, so as to maximize the infant's entrainment potential, makes eye contact to fix the coordinates of confrontation, positions his or her own face closely to the infant's, and holds the infant directly in front of him or her during entrainment. For his or her part, the infant sustains this behavior, by expressing pleasure in the cycle of interaction. The interaction must be intrinsically rewarding to the infant because it is sustained, although it is not associated with food or another tangible reward.

The impulse to entrain dyadically seems to be specifically human. Non-human primates have not been observed to engage in sustained reciprocal face-to-face interaction with their offspring. For sure, the primate mother observes and cares for the non-human primate infants. However, she does not make sustained eye contact "for its own sake." The innate motivation of the human infant to interact may lay the foundation for the intensely social group behavior for which the human species is remarkable, as well as for sophisticated means of sustaining such interactions at all ages, notably by conversation, which itself is often carried out for its own sake.

Enactive perception affords entrainment but does not compel it. However, whether the entrainment is undertaken and if so, whether it is sustained, will be shaped by its consequences (i.e., whether to do so is reinforcing or punishing)

and involves approach–withdrawal dynamics. Appearances that are repeatedly associated with positive consequences, such as the face of the caregiver, will lead to approach dynamics, such that the infant will initiate entrainment when it sees the caregiver, whereas repeated negative consequences will result in withdrawal dynamics. In terms of enactive perception, this means that approach behavior is more than the act of moving toward something positive. Rather, social approach entails the willing exposure of one's enactive perception systems to the influence of another. Put simply, it is a primitive embodied form of trust (Erikson, 1994). Evolution has tilted the odds toward interaction. The opportunity to approach is sought after because its consequence, entrainment, is intrinsically enjoyable. Evolution has made it so.

These valence-driven decisions (i.e., approach–withdrawal dynamics) constitute embodied anticipations of the consequences of entrainment. They need not be conscious. In delayed imitation (Meltzoff & Moore, 1994), an infant who had engaged in reciprocal imitation with an adult (e.g., an investigator) greets the adult with the same facial gesture when he or she next reappears, even several days later. We see this as an invitation to resume what is for the infant a pleasurable activity. It may be taken as an instance of embodied anticipation of approach. Such embodiments are useful because they afford both adults and infants a means of selectively allocating their entrainment potential in ways that are cognitively efficient; and they come to be embodied in the brain via the persistent pairing of valence-laden consequences with the entrainments that emerge spontaneously, with a little help from the caregiver, out of the enactive perceptual properties of the brain.

ENTRAINMENT AND EMBODIED RECIPROCITY

Although the recursive reciprocity of infant–caregiver entrainment might start out as an unintended consequence of enactive perception, at least as far as the infant is concerned, it seems to work as a scaffold for both learning about the world, as well as supporting eventual entrainment with others. Striano, Reid, and Hoehl (2006), for example, measured EEG activity in 9-month-old infants observing an object they had seen before. If the infant's previous encounter with the object occurred during a dyadic interaction in which an adult looked back and forth between the infant's face and the object, there was an enhanced negative component in the infant's neural activity in response to the later presentation of the stimulus. This enhanced negativity is an index of attentional processes (Richards, 2003), and it did not appear in stimulus observations that were not preceded by entrainment episodes. This indicates that entrainment might provide a scaffold from which joint attention can be extended to events beyond the dyad to help the infant's developing understanding of the world.

Regarding extending entrainment to others, at 18 months, toddlers who are provided identical toys entrain with one another in ways that reveal deliberate turn taking (Nadel, 2002). If the toys are not identical, the entrainment is not nearly as robust. In addition, this nonverbal entrainment drops off at roughly 30 months, yielding to language as it emerges as the dominant form of entrainment. Nadel proposed that the turn taking expressed in entrained play behavior at 18 months constitutes a behavioral precursor to the cooperative reciprocity required for sustained dialogue. The question for this discussion is how the deliberate reciprocity demonstrated at 18 months develops out of the spontaneous reciprocity expressed in infant–caregiver entrainment.

One avenue for the transformation from spontaneous to deliberate reciprocity may be the emerging sense of body ownership that infants develop during the early months of life (Kinsbourne, 2002). This sense of body ownership develops dynamically over time, as the correlated feedbacks from receptors located on the same limb are differentiated from the often uncorrelated feedbacks arriving from receptors on different limbs (S. A. Clark, Allard, Jenkins, & Merzenich, 1988; Montague, Gally, & Edelman, 1991).

Infants themselves catalyze this differentiation process. As well as engaging in entrainment with others, they also entrain themselves. Self-entrainment is mediated by the same dynamic as self–other entrainment; that is, by the enactive nature of perception. Specifically, as the infant moves a body part, the infant perceives his or her own movement. Given the motor-planning nature of enactive perception, as well as the infant's lack of inhibition, the "perceived" action is initiated; and this action, in turn, recursively activates a similar action. This sequence of events explains the recursively self-sustaining pattern of body movements that Piaget (1952, p. 171) referred to as circular reaction and which Meltzoff and Moore (1997) referred to as "body babbling."

As the infant engages in entrainment episodes, be they episodes of self- or other-entrainment, the resulting differentiation of body parts comes to be embodied in the structure of the brain, and the body parts come to feel "owned" (Kinsbourne, 2002). This sense of owned body parts may constitute an initial phase in the development of the self–other distinction. To be sure, we know of no neurophysiological research that reveals self–other differential activity in the infant brain. However, research on adults reveals that, although common mirror systems are activated during a host of action-related functions such as action planning, action perception, and action imaging, people can of course tell the difference between their actions and the actions of others. Activity in other areas, such as the inferior parietal lobe, is differentially activated by self-versus other-action-related activity (Decety & Chaminade, 2005). Specifically, left inferior parietal activity is associated with action-related activities of the self, and right inferior parietal activity is associated with action-related activities of the other (Decety et al., 2002). Given Nadel's (2002) finding that 18-month-

olds can already at that early age engage in sustained episodes of entrained reciprocity (which necessarily demands a rudimentary self–other distinction), it seems clear the developing brain is prepared to embody a distinction between its own action-related activities and the action-related activities of others. Meltzoff and Decety (2002) offered evidence that newborn infants are already well able to make that distinction.

The neural embodiment of the self–other distinction emerges developmentally out of persistent episodes of self–other entrainment (Jordan, 2003), as well as of self-entrainment. The resulting embodiment will, therefore, also entail *self–other reciprocity*; that is, the embodiments will entail the expectation of reciprocity during interaction because the entrainment episodes themselves emerge out of reciprocal, self–other action–activation. The persistent repetition of reciprocal entrainment affords the infant the ability to embody, and thus anticipate, the dynamics of reciprocity. Thus, what started off as a *reaction* of the infants' enactive perception systems to the actions of the caregiver becomes a *goal* of the infant's actions. The infant will emit actions with the intention of having the action reciprocated. The emergence of reciprocal entrainment as a goal, as opposed to a simple reaction, is indicative of the brain's embodiment of social reciprocity.

How does this embodiment of social reciprocity apply to conversation? In conversation, people take turns. At each segment, the person who is speaking anticipates that the other will respond; this is a premise that underlies the joint activity. When the listener anticipates that it will be her or his turn to speak, the speaker detects the other's preparedness and, if necessary, constrains her or his narrative accordingly. Each presentation is continuously evaluated via the other. The anticipation of reciprocity is embedded in the current turn.

Why did we evolve to enjoy conversing? Because by conversing, we are implicitly forming alliances. Alliances are adaptive in the evolutionary sense because they facilitate the twin goals of ensuring survival and procuring reproductive opportunity. By the use of language, one orients another person to one's state of mind. If a person wants to persuade a group, the effect is much more powerful if the group is responsive (e.g., in response chanting in a church service or at a political rally). The joint activity transforms the individual conceptually into a part of a single system, by means of a one-to-many embodiment. It releases her or him from the burden of individual planning and self-control.

PRE-VERBAL ENTRAINMENT PERSISTS IN ADULT INTERACTION

As discussed earlier, 18-month-old toddlers readily engage in reciprocal, object-related entrainment with others. However, this behavior yields to language by

30 months of age (Nadel, 2002). Although at first glance the body-related entrainment of the infant appears to have been thoroughly replaced by language entrainment, data indicate that body-relative entrainment is still present in adults. For example, the aforementioned data regarding dance perception (Calvo-Merino et al., 2005) indicate that action perception activates action planning in the adult brain. Over the past decade, this finding has been validated by a host of studies (Hommel, Müsseler, Aschersleben, & Prinz, 2001), which converge on the notion that the potential for entrainment is embodied in the enactive-perceptual nature of the brain, across the whole life span. To repeat, the manner in which the brain perceives action is to represent it. Once represented, the action primes the brain to imitate the action that was perceived. The mirror neuron phenomenon is but a special case of the general design principle that all percepts potentially bias the brain to perceive accordingly, or act accordingly, as the case may be, when alternative interpretations or alternative actions are possible. This effect of the environment in shaping brain circuitry and biasing the brain's percepts, constructs, memories, and actions is an inescapable consequence of the manner in which the brain codes experience. Of course, the primed action can be inhibited in favor of an alternative act or of doing nothing at all. However, to imitate is the default option; it requires the least effort, which gives it a head start among competing responses and makes it a more probable choice than it was before the priming percept was registered.

Perceiving enactively does not compel the observer to imitate. Whether perceived action leads to cycles of entrainment between adults depends on whether participants inhibit the motor plan that it is enacted by as they perceive the other's actions. Echopraxia and echolalia constitute extreme examples of uninhibited entrainment. However, adults do not have to be brain damaged to entrain. At a more social level, Goodman, Isenhower, Marsh, Schmidt, and Richardson (2005) reported that if two participants sit next to each other in separate rocking chairs and look at each other while rocking back and forth, the rocking of the two will eventually become synchronous. If the two look away from each other, however, their rocking will fall out of synchrony. In addition, the unintended synchrony persists even when weight is added to one of the chairs to alter the force needed to sustain synchrony. Coupled by eye contact, the dyad unwittingly slips into entrainment. Interactional synchrony has also been reported at the level for pattern of brain activation. Five participants watched a movie. Neuroimaging revealed a "striking level of voxel-by-voxel synchronization between individuals, both in primary sensory and association cortex" (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004, p. 1634).

Although continuous, uninhibited entrainment is possible, most adult entrainment is subtle and how overt it is varies on a continuum that is defined by the inhibitory abilities of the involved persons, as well as by the social constraints of the immediate context. Evidence regarding the prevalence of subtle entrainment

derives from a host of research domains. In social psychology, researchers refer to subtle entrainment in terms of a "perception–action link" (Bargh, Chen, & Burrows, 1996), the idea being that action perception primes action production. This approach to entrainment is based on "dual-process" models of cognition (Shiffrin & Schneider, 1977) that make strong distinctions between automatic, unconscious processes and controlled, conscious processes. According to dual-process theorists, most of our daily behaviors are driven by automatic processes that are activated by environmental stimuli, such as the actions of others. Wegner (2002) presented evidence that our sense of conscious will is actually an illusion that is, our sense that our thoughts cause our actions is actually incorrect. He softened the impact of this counterintuitive claim by granting conscious will the ability to inhibit actions. However, this escape clause is subject to the same criticism. The brain begins to program inhibition and, only then, perceives subjectively that it has done so. The upshot is that the distinction between automatic and controlled processes is only confused by equating them with unconscious and conscious processes. Controlled processes typically become conscious, but are not initiated by the "will." Like automatic processes, they are initiated by the brain, and it is the brain, not conscious "willing," that has "free will" (Kinsbourne, 1996). It remains the case that during social interaction, motor plans that are activated via observations of others are, for the most part, inhibited and do not become conscious.

The Chameleon Effect (Bargh, 1999) is an empirically observed case in point of the dual-process approach to entrainment. It refers to the unconscious tendency to mimic the postures, facial gestures, and behaviors of those with whom one interacts. Interestingly enough, a pleasant feeling accompanies the automatic mimicry, and this makes the interaction proceed smoothly and fosters good feeling between the participants. Those who are dispositionally more empathic demonstrate chameleon-like mimicry more than others.

Social cognitive neuroscientists tend to emphasize the "mind-reading" potential that entrainment affords. The enactive nature of perception grants participants a degree of access to one another's emotions, movement intentions, and subjective mental states. This is because the unintended movements of the other activate the motor plan for the same actions in the observer. People unconsciously imitate one another's facial expressions, gestures, postures, body sways, tones of voice, and speech accents (reviewed by Wilson & Knoblich, 2005). Postural congruence in individual psychotherapy fosters the belief in the client that the therapist is empathic. The client's postures also influence the therapist (Maurer & Tindall, 1983). Intimations of approach, such as making eye contact, smiling, leaning forward, and head nodding, have a similar positive effect on the dyad. Gallese (2003) referred to this tendency to represent and imitate intentions as *simulation*. This term should not be regarded as designating a specifically evolved adaptation to mind read or the like, but rather as a consequence of a general design

characteristic of the brain. The "mirroring" is a spin-off from the mundane facts that observers perceive by representing, and that when we represent we do so in part by encoding a potential response. The other's encoded intention will reflect what is perceptible. A confident approach will make engagement more likely. The other side of the coin is that, should the initiator expect to be rejected, that expectation becomes self-fulfilling. Primed by the embodiment of withdrawal, the other will be more likely to reject him or her.

Entrainment is not confined to neutral movements but extends to feelings. The sensory-motor systems are coordinated with affective neural systems. Viewing someone else's emotionally laden body movements primes similar emotional states in the observer by mirroring (Singer, 2006). This effect is "emotional contagion" (Hatfield, Cacioppo, & Rapson, 1994). Grammer et al. (2004) demonstrated that mood is reliably perceivable in posture (see also La France, 1985). Participants answered questionnaires about the mood they perceived in the postures of three-dimensional computer images. The images had been reconstructed by regressing the body angles in the images with the self-reported moods of the persons in the images. The perceived moods were reliably consistent with the reported moods. Mood can also be reflected in pupil size. Harrison, Singer, Rotshtein, Dolan, and Critchley (2006) reported that observed pupil size was mirrored by the observer's own pupil size. This finding indicates that mirroring extends to the autonomic nervous system.

Wicker et al. (2003) reported emotional entrainment as inferred from the pattern of brain activation. Observing someone looking disgusted generates neural activation in the observer's anterior insula. The insula is specialized to represent disgust and would be activated while a person feels disgusted. Lamm, Batson, and Decety (2007) reported similar emotional mirroring. However, they also found right inferior parietal activation during observation of another in pain, but left inferior parietal activation when imagining oneself to be sharing the pain. Overlap in activation in these two conditions is restricted to centers related to the *motivational-affective* nature of pain (i.e., the anterior insula, the anterior cingulate cortex, and the amygdala). It does not extend to the areas of the brain that represent the *sensory-discriminative* properties of pain. Thereby, one remains able to distinguish one's own pain from that of another. One feels the distress that pain occasions the other by emotional contagion, but not the other's perceived sensory quality of the pain that one is not oneself directly experiencing (Singer et al., 2004).

Blakemore and Frith (2005) claimed that perceiving an action that is incompatible with the action one is planning interferes with one's ability to produce the planned action. Thus, just as entrainment renders one's emotions potentially contagious, it also renders one's movements "contagious" (as is the well-known case with laughter and yawning). Entrainment also seems to be at work in "mentalizing," perceiving others' mental states (Gallagher & Frith, 2003).

Thinking about one's own thoughts (introspecting) or about the thoughts of another both reliably activate the same medial prefrontal (paracingulate) cortical territory (Mitchell, Banaji, & Macrae, 2005). Moreover, when one mentalizes about what an opponent in a game is thinking, the medial prefrontal cortex activates only if one believes that the opponent is a person. It does not activate if one believes that the opponent is a computer (Gallagher, Jack, Roepstorff, & Frith, 2002). This distinction is due to a belief about whether the opponent is a thinking entity. It occurred, although the opponent actually produced a random sequence of responses in both the person and the computer condition.

One can unconsciously learn much that is relevant to cost–benefit considerations from and about another's behavioral, emotional, and mental states simply via subtle entrainment (Krebs & Dawkins, 1984). Indeed, Grammer and Oberzaucher (2006) cautioned that the unconscious, automatic nature of entrainment leaves one vulnerable; unconscious shifts in gaze, gesture, and posture reveal one's emotional and intentional states. Grammer and Oberzaucher argued that the vulnerability that results from persistent, unconscious entrainment leads to the evolution of social manipulation, social deception, and social probing. Kinsbourne (2004) commented on the social consequences of such multidimensional, automatic entrainment:

> People approach one another, withdraw from one another, reciprocally engage and disengage. Or, hesitating to commit themselves, they indicate their intention or inclination with corresponding gestures or signs, either deliberately or unintentionally. They emit fragments, rudiments and simplifications of the overt patterns of the movement they are contemplating as stand-ins for the activity in question. These fragmentary movements and shifts in posture have semiotic value, as do corresponding inscriptions and other recordings. Since the neurological organization of motor control is a universal found in people everywhere, it is to be expected that beyond culture-specific minor details, similar meanings will be non-verbally represented by similar movement patterns, even in cultures that have never been in contact. Such functional convergence from disparate origins would make it unnecessary to invoke spread by information transmission. Rather, the nervous system constrains the motor expression of the major categories of meaning, regardless of epoch and culture. (p. 150)

MULTI-SCALE ENTRAINMENT AND COOPERATIVE ACTION

Collectively, the research of social psychologists, social-cognitive neuroscientists, and ecological ethologists clearly demonstrates the presence of automatic, multi-scale entrainment in adult interaction; and, although the emphasis on vulnerability might lead to a pessimistic take on the role of entrainment, such

entrainment might also underlie our potential for cooperative interaction, for it entails potential benefits as well as costs (Krebs & Dawkins, 1984). For example, Singer and Fehr (2005) claimed that, although entrainment ultimately allows one to predict another's pending behavior and, thus, obtain information that can be used for making self-interested choices, *entrained empathy* allows one vicariously to experience another's emotions. Therefore, entrainment is likely to render the observer's thoughts more *other-regarding*. Evidence for this comes from a study by Warneken, Hare, Melis, Hanus, and Tomasello (2007) in which they found that 18-month-olds will spontaneously assist an adult stranger accomplish an unfinished goal, such as reaching for an object, regardless of whether the infant is rewarded for doing so. Apparently, emotion-laden entrainment is present quite early in life and is capable of compelling one toward altruistic acts. Might this affect-laden tendancy toward entrainment also underlie our ability to engage in cooperative imitation and cooperative coordination of our actions?

Cooperative Imitation and Skill Learning

Entrainment supports cooperative interaction by providing a medium for observational skill learning (i.e., imitation). Byrne (2002) distinguished four types of imitation: stimulus enhancement, response facilitation, emulation, and true imitation. The two, more automatic forms (i.e., stimulus enhancement and response facilitation) refer to responding to a stimulus another is responding to, and responding to a stimulus after observing another being rewarded for doing so, respectively. Rizzolatti et al. (2002) referred to these types of imitation as constituting *low-level resonance* because the organism does something it sees another organism do, but the observed event is not a goal as much as it is a *releasing signal* for a fairly fixed behavior pattern, such as a bird flapping its wings in response to the wing flapping of another bird.

Low-level resonance facilitates the spread of motor contagion, but it does not facilitate behavioral learning via observation. High-level forms of resonance (i.e., emulation and true imitation), on the other hand, do facilitate behavioral learning. Emulation refers to imitation of the goal only, whereas true imitation refers to imitation both of the goal and of the actions used to attain it. The distinction between the two is supported by developmental studies. Although younger children easily imitate the goals of an actor, they tend to use the most efficient means (i.e., actions) to do so. Only later in life do they come to imitate both the goal and the action (Bekkering, Wohlschläger, & Gattis, 2000).

In human interactions, true imitation is just as ubiquitous as emulation. Horner and Whiten (2005) investigated the conditions under which 3-year-old humans and chimpanzees would switch between true imitation and emulation. Participants observed an actor in the act of retrieving a reward from a puzzle

box that was either transparent or opaque, so that they could see, or not see, respectively, the causal relations between the actor's actions and the effects they had on the box. Some of the actions were relevant to retrieving the reward, whereas some were not. In the transparent-box condition, chimpanzees switched to emulation, ignoring actions that were goal-irrelevant, whereas 3-year-old humans generated high amounts of true imitation, regardless of the relevance of the imitated action to the goal. The authors expressed their surprise at the 3-year-olds' "over-imitation" of irrelevant actions.

In a follow-up study, McGuigan, Whiten, Flynn, and Horner (2007) repeated the task with 3-year-olds and 5-year-olds, and added a condition in which the participants observed a videotape of the actor (vs. observation of a live actor). Again, to their surprise, 5-year-olds imitated both relevant and irrelevant actions equally in transparent–opaque-box conditions and live–video conditions. This led the authors to refer to the 5-year-olds as "super-imitators." Three-year-olds, on the other hand, imitated relevant and irrelevant actions in the live condition, as they had done in the previous study, but rarely imitated irrelevant actions in the video condition (i.e., they switched to emulation). It appears that the physical presence of the agent tended to elicit exact imitation by 3-year-olds by means of some social factor unrelated to the details of the task.

The results of these studies were surprising because researchers assumed that effectively switching from true imitation to emulation constituted a developmental increase in imitative sophistication, and they expected more developed participants (i.e., 3-year-olds vs. chimpanzees and 5-year-olds vs. 3-year-olds) to be more selective in their allocation of imitative assets. To the contrary, further studies have revealed that this developmental increase in inefficient true imitation even continues into adulthood (Custance, Prato Previde, Spiezio, Rigamonti, & Poli, 2006). Because it is not logically optimal in use of resources, the literal imitation is more likely to be an instance of entrainment than of rational choice of the means to proceed.

The selective advantage of entrainment-based super-imitation is evidenced by the human propensity for tool making. Toth, Schick, Savage-Rumbaugh, Sevcik, and Rumbaugh (1993) observed a bonobo ape in the act of tool making (i.e., stone knapping). However, instead of truly imitating, by striking a stone supported in one hand with a stone held in the other, the ape simply threw the source rock at the hard ground and picked out a flake from the debris. Byrne (2005) proposed that the ape engaged in emulation (vs. true imitation) because stone knapping requires coordination of distinct roles for each hand. Specifically, the striking hand must generate a powerful, accurate blow to a rock firmly held in the other, supporting, hand. To be sure, great apes are able to generate sequences of hierarchically organized actions, and they possess both limb power and delicate precision abilities. The missing skill, therefore, at least regarding highly skilled tool making, seems to be an inability to truly imitate

two, highly specific, action-effect contingencies simultaneously (i.e., supporting a rock in one hand against a blow delivered by rock held in the other hand).

Cooperative Action Coordination

Although true imitation and the entrainment underlying it are ubiquitous in human interaction, certain forms of cooperative action require that participants produce different, although complementary, actions if the group is to achieve a common goal. Cooperatively carrying a dresser up a flight of stairs, canoeing down a river, and playing a game of soccer are but a few examples. In each case, the actions generated by each participant are different. Yet, each must plan his or her own actions in anticipation of the actions of the other. For example, in the case of carrying a dresser up a flight of stairs, one participant walks up the stairs backward and pulls, whereas the other walks forward up the stairs and pushes. For the dresser to get up the stairs, the pushing and pulling must be coordinated and, therefore, be executed with the expectation of cooperation. Only then will each participant be in a position to move the dresser with maximum force.

Although the need to generate different actions might seem to discount entrainment as an underlying mechanism for cooperative action coordination, the mechanisms underlying cooperative turn taking and the ability to generate predictions about the pending actions of another actually seem to emerge developmentally out of entrainment. As was stated earlier, during entrainment with caregivers, over time infants come to embody the reciprocity (i.e., turn taking) that emerges naturally out of the enactive properties of perception. Again, this manifests itself as turn taking in the object-oriented entrainment of 18- to 30-month-olds (Nadel, 2002), and as spoken-language entrainment after 30 months. This multi-scale expectation of reciprocity reveals an ability to generate expectations about the actions of others that emerges, developmentally, out of reciprocity-generating dynamics of entrainment.

In adult interaction, tracking the pending actions of others is just as automatic and prevalent as subtle entrainment and true imitation, and it is mediated by the mirroring systems that underlie the enactive nature of perception. Sebanz, Knoblich, and Prinz (2003) engaged participants in a two-choice reaction-time task in which on every trial an image of a hand pointed outward toward the participants. The task required participants to respond as quickly as possible to the color of a ring on the index finger of the pointing hand (e.g., if the ring was red, they were to press the right button; but if it was green, they were to press the left button). Participants did the task either alone or in pairs. In the latter condition, each participant was responsible for only one of the two possible responses, withholding the other. Results revealed that in the alone condition, reaction times were significantly slower if the button press indicated by the ring (e.g., the green ring indicated a left button press) was

incompatible with the pointing direction of the finger (i.e., the finger pointed to the right button). In other words, the pointing finger automatically primed one response (i.e., the right button), whereas the color of the ring primed a different response (i.e., the left button). The same response conflict occurred in the pairs condition—that is, reaction times were significantly slower if the finger pointed to one participant's button, but the ring indicated a response by the other participant. This is interesting because one might assume participants should have been able to simply ignore the other participant's task and treat their task as a simple go/no-go task (e.g., simply press their button when their triggering stimulus appeared). Sebanz et al. (2003) interpreted the fact that the incompatible response indicated by the pointing finger generated a response conflict, although the incompatible response belonged to the other participant, to indicate that participants were automatically tracking the other's response options.

A follow-up event-related potential study (Sebanz, Knoblich, Prinz, & Wascher 2006) revealed more fronto-cortical inhibition (i.e., a larger no-go P3) when the ring stimulus indicated the *other* was to respond. Again, this is interesting because one might assume participants should have been able to simply treat the task as a go/no-go task, and there should have been no reason to inhibit a response when the ring stimulus indicated the other should respond. The fact that they did inhibit a response the *other* was supposed to produce is consistent with the idea they were automatically tracking the action options of the other via the systems they would use to generate the same response themselves—that is, they had to inhibit a motor plan in their own brain that was initiated by an external cue for another.

Further evidence that the mirror system is involved in tracking alternative action options comes from a study in which participants observed an action (i.e., either a power grip or a precision grip) and either imitated the action in one block of trials or executed the complementary action in another block of trials (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007). Before each trial, a cue indicated whether the participant was to follow the condition instruction (i.e., imitate or generate a complementary action) or violate the instruction and generate the opposite action. Reaction times were faster in the imitative condition when the action was preceded by an image of an identical action, yet were faster in the complementary condition when the action was preceded by an image of a complementary action. This indicates that the "priming" effect of observing an action depended on the participant's goal (i.e., imitate or complement). If the goal was to generate a complementary action, participants planned in terms of the complement of the observed action. When the cue indicated they were to produce a different action than the planned complement, reaction times became slower. This is consistent with the idea that participants were able to track action options in relation to their current goal. Additional

functional MRI data located this ability to track action options in the mirror systems. Mirror systems were more active when participants generated an action that violated their goal (i.e., imitate or generate complement). In other words, the mirror systems became more active when participants had to plan an action that was different from the one they were anticipating at the moment when the stimulus was presented. The mirror circuitry was competing with the envisaged motor plan for control of behavior. Collectively, the data are consistent with the view that observers automatically track action options, and that doing so is mediated by the mirroring that is entailed in enactive perception of actions. This ability to track action options extends across both self and other. (See Jordan, this issue, for a review of how this ability to distinguish self and other plays out during real-time action coordination.)

CONCLUSION

Phylogenetic and ontogenetic time scales pre-tune the brain for sustaining interactions with others. This pre-tuning in time provides the foundation for the development of full-blown communication. At the phylogenetic scale, the developmental dynamics of the brain anticipate the presence of the other; it is experience expectant of the presence of other humans. At the ontogenetic scale, the enactive nature of perception anticipates (again, is experience expectant) that the infant will utilize the bodies of others as a surrogate means of developing its own sense of body ownership. At the scale of the immediate interaction, the enactive nature of perception allows the infant's planning states to be "downloaded via remote control" via the movements of others. In short, the movements of others put the infant's brain into anticipatory planning states. The scaffold-like nature of these interactive time scales reveals the anticipatory experience-dependent nature of the brain, as well as the pattern of regularities that is anticipated at each level of scale.

The ability to plan one's own actions in relation to the action options of another during real-time action coordination is yet another example of the bootstrapping power of entrainment and the brain's developmental ability to embody anticipation at increasingly complex scales. What starts off as spontaneous entrainment, due to the enactive nature of perception, develops into anticipated reciprocity. By 18 months, anticipated reciprocity extends across bodies to include objects (Nadel, 2002). By 30 months, it extends beyond immediate objects and into the realm of language objects (i.e., words). In the remaining articles of this special issue, researchers will be examining the various ways that entrainment plays out across many different time scales (e.g., eye movements, head movements, gestures, syntax, and semantics). All along the

way, what underlies this progressive increase in the distality of the realms in which we are able to entrain is the brain's capacity to embody anticipation and the evolutionarily important fact that doing so feels good. Michael Oakeshott (1959) stated:

> Indeed, it seems not improbable that it was the engagement in this conversation (where talk is without a conclusion) that gave us our present appearance, man being descended from a race of apes who sat in talk so long and so late that they wore out their tails. Education, properly speaking, is an initiation into the skill and partnership of this conversation in which we learn to recognize the voices, to distinguish the proper occasions of utterance, and in which we acquire the intellectual and moral habits appropriate to conversation. And it is this conversation which, in the end, gives place and character to every human activity and utterance. (pp. 196–198)

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