Language, Gesture, and the Developing Brain

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Abstract

Do language abilities develop in isolation? Are they mediated by a unique neural substrate, a "mental organ" devoted exclusively to language? Or is language built upon more general abilities, shared with other cognitive domains and mediated by common neural systems? Here we review results suggesting that language and gesture are ‘close family’, then turn to evidence that raises questions about how real those ‘family resemblances’ are, summarizing dissociations from our developmental studies of several different child populations. We then examine both these veins of evidence in the light of some new findings from the adult neuroimaging literature and suggest a possible reinterpretation of these dissociations, as well as new directions for research with both children and adults.

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Do language abilities develop in isolation? Are they mediated by a unique neural substrate, a "mental organ" devoted exclusively to language? Or is language built upon more general abilities, shared with other cognitive domains and mediated by common neural systems? For many years, developmental scientists have addressed these questions by studying behavioral associations and dissociations between language and gesture across the period in which both systems are first acquired. Some compelling links have been observed, involving specific aspects of gesture that precede or accompany each of the major language milestones from 6 to 30 months of age. These behavioral results are compatible with an expanding adult neuroimaging literature attesting to the largely domain-general neural systems underpinning meaningful action and perception in a dynamic and informationally rich environment. However, data from a number of studies of normally and atypically developing children's gestural and language abilities present complicating, if not outright contradictory evidence relative to the domain-general account. In keeping with the "converging methods" theme of this special issue, we will compare behavioral and lesion studies of language and gesture in infants with recent neural imaging studies of language and gesture in adults, in the hope of finding a unifying explanatory framework.

We begin by reviewing results suggesting that language and gesture are 'close family': we first trace the co-emergence of milestones in gesture and language across early development, then discuss lesion and imaging studies of movement, gesture, and imitation in adults that are compatible with this lockstep developmental picture. After this, we turn to evidence that raises questions about how real those 'family resemblances' are, describing some mysterious but robust dissociations from our developmental studies of typically developing children, children with focal brain injuries, and children who are "late talkers". At first glance, these dissociations seem to preclude a transparent mapping between gestural and linguistic domains and their neural substrates. But when we enlarge our window of enquiry to include some new findings from the adult neuroimaging literature, a more interesting story presents itself, one that may offer a possible reinterpretation of these thorny developmental dissociations, and suggests new directions for research with both children and adults.

"All in the Family" Part I: Co-Development of Language and Gesture

Since the 1970s, developmental scientists have investigated links between early language development and several aspects of manual activity, with special emphasis on communicative and symbolic gesture (for reviews, see Bates & Snyder, 1987; Bates & Thal, 1991; Bates et al., 1991; Iverson & Thelen, 1999). The initial motivation for this work grew out of Piaget's ideas about the shared sensorimotor origins of linguistic and nonlinguistic symbols (Piaget, 1954, 1962, 1970; also Werner & Kaplan, 1963), although investigators were also influenced by ideas from Bruner, Vygotsky and others on the social scaffolding of meaning and communication in infancy (Bruner, 1983; Vygotsky, 1987; Wertsch, 1985).

Research in the Piagetian tradition focused on correlations between specific language milestones and specific cognitive events, including different levels of complexity in gestural communication and in symbolic (pretend) play outside of a communicative framework. Table 1 summarizes a series of early language milestones with their proposed and attested gestural correlates (with approximate ages, and supporting references). In contrast with the Piagetian tradition summarized in Table 1, work on language and gesture in the Vygotskian framework has focused more on the emergence of joint attention (how children learn to attend to objects and events that adults are watching, or indicating in some fashion — Butterworth & Cochran, 1980; Tomasello &

Akhtar, 1995). Despite differences in emphasis, results in both traditions have shown that individual differences in joint attention skills (both rate of development and frequency of use) are correlated significantly with concurrent and subsequent abilities in both gesture and language (for reviews and for further evidence, see Carpenter et al., 1998). Joint attention, symbolic play and language skills are tightly bound, in turn, to observational learning and progress in the immediate and/or deferred imitation of novel actions and sounds (Hanna & Meltzoff, 1993; Meltzoff, 1985; Meltzoff & Moore, 1977, 1989). Taken together, these findings suggest that "language is a new machine built out of old parts" (Bates & Goodman, 1997), emerging from a nexus of skills in attention, perception, imitation and symbolic processing that transcend the boundaries of 'language proper'.

Of course correlational studies of normal children can be misleading. To determine whether the above correlations can be dissociated under pathological conditions, investigators have looked at the same phenomena in atypical populations. For example, there is currently great interest in the diagnostic value and (perhaps) causal importance of joint attention, symbolic play and imitation in autistic spectrum disorders (Charman et al., 1997). A number of investigators have proposed that the delayed and often deviant language observed in children with autism is secondary to a primary deficit within the broader (and prior) neurodevelopmental system that supports joint reference, imitation, and gesture. Results have varied depending on the population in question, but a growing body of research on early language development in typical and atypical populations supports the language-gesture links summarized in Table 1. (See Table 1 at end of text).

Babbling. Canonical babbling involves the production of repeated consonant-vowel segments like {ba}, {ata}, {di} or {yaya}. This milestone often occurs outside of a communicative framework (e.g., it may occur while the child is lying alone in her crib). It is typically achieved between 6-8 months (Lewedag, Oller, & Lynch, 1994; Steffens, Oller, Lynch, & Urbano, 1992), and delays of more than 2-3 months are associated with clinically significant delays in language, speech and/or hearing at later ages (Oller, Eilers, Neal, & Cobo-Lewis, 1998). Canonical babbling has been linked to the onset of rhythmic hand banging or clapping, in the normal case and in children with babbling delays (Ejiri & Masataka, 2001; Locke, 1994; Locke, Bekken, McMinn-Larson, & Wein, 1995; Masataka, 2001). Like canonical babbling, rhythmic hand banging occurs outside of communication, but it appears to be linked to subsequent changes in word production as well as communicative gesture. For example, Masataka (2001) examined the onset of babbling and first words in infants with Williams Syndrome in relation to hand banging and series of other motor milestones (rolling, reaching, sitting, standing, walking). Hand banging correlated significantly both with babbling onset and with the subsequent emergence of first words, but did not correlate with other motor milestones, even though all milestones were delayed compared with norms for typically developing children. Hence this particular speech-gesture link appears to be quite specific.

Word comprehension. Between 8-10 months, typically developing children start to show systematic evidence of word comprehension. This milestone is correlated with the emergence of deictic gestures (e.g., giving, showing, pointing) and culturally derived gestural routines like waving bye-bye. These linked milestones are correlated in turn with a number of changes outside of communication, including first signs of tool use (Bates, Benigni, Bretherton, Shore, & McNew, 1979), categorization on the basis of different feature correlations (Younger & Cohen, 1983, 1986), and imitation of novel acts not already in the child's repertoire (Gopnik & Meltzoff, 1994). Indeed, the 9-month border appears to be a developmental watershed, characterized by changes in cognition, communication and imitation that invite speculation about underlying neural causes (Bates, Thal, & Janowsky, 1992).

Regression analyses conducted on a large sample of children screened to exclude mental retardation or other neurological disorders (Thal, Bates, Goodman, & Jahn-Samilo, 1997) showed that word comprehension and both communicative and symbolic gesture production in this early age range all contribute significant variance (at the group level) to later delays in expressive language (but see dissociations, below). Word comprehension and early gestural production are also significantly and comparably delayed in children with mental retardation (e.g., both Williams Syndrome and Down Syndrome — Singer Harris et al., 1997), and in a subset of late talkers (Thal & Tobias, 1994; Thal & Bates, 1988) and children with focal brain injury (Dall'Oglio, Bates, Volterra, & Di Capua, 1994).

Naming. At or slightly before the onset of naming around 12 months, children start to reproduce brief actions associated with specific objects (e.g., putting a phone to the ear, a cup to the lip, a brush to the hair). In hearing children, these recognitory gestures (also called "gestural names") are usually carried out with the associated object in hand (in contrast with the manual signs produced by deaf infants). As reviewed by Shore et al. (Shore, Bates, Bretherton, Beeghly, & O'Connell, 1990) and Volterra et al. (1979), several lines of evidence suggest that this really is a form of categorizing or naming: (a) recognitory gestures and vocal naming (e.g., "Doggie!) emerge around the same time; (b) gestures and naming are positively correlated across children in this period (i.e., early gesturers tend to be early namers); (c) first words and gestures are strikingly similar in content or meaning (e.g., a shared "vocabulary" about eating, drinking, greeting, bathing, dressing, household activities, vehicles, appearance and disappearance of objects); and (d) recognitory gestures, like early names, are brief and stylized in form (e.g., the child who touches cup to lip in gestural naming seems to distinguish between this act and 'real drinking'; s/he shows no surprise or disappointment if there is nothing to drink, and may even execute the gesture with miniature, nonfunctional cups or while looking at cups in a picture book). Volterra and Erting (1994) and Acredolo and Goodwyn (1990) have shown that many children also produce these gestures empty-handed, in a clear communicative framework that meets the objections of some investigators regarding the concrete or functional nature of the same gestures with a real object in hand.

It is important to note that the correlation between word production and “gestural naming” is limited to a particular period in development, between 12–18 months, on average, in typically developing children. With or without the object in hand, the phenomenon of "gestural naming" appears to be transient, dropping out for hearing children when oral language develops well enough to "take over" (although the amount and type of oral language required before these gestures drop off has not yet been determined). That is, once children have cracked the code and entered into the richly cross-referenced cue structure of a real natural language, the pace of word learning increases exponentially, and eclipses the meager system of gestural symbols. This complicates the correlational picture quite a lot: positive correlations between gestural and vocal naming are observed in the earliest stages of symbolization, but these correlations disappear across the second year of life, and sometimes turn into negative correlations at a later stage (reflecting the persistence of gestural naming in some children with language delays). Hence research on this particular language-gesture link must focus on the first stages of word production, when a positive link between word production and gestural naming would be expected.

In those studies of atypical populations that have focused on the first stages of word production, results suggest that word production does not begin until recognitory gestures have appeared — even though both events may be delayed by many months or years. This link has been reported for two forms of mental retardation, Williams Syndrome and Down Syndrome (Singer

Harris et al., 1997), and for young autistic children (Happé & Frith, 1996). It has also been observed at the group level in small longitudinal samples of children with early left- or right-hemisphere injury (Dall'Oglio et al., 1994; Marchman, Miller, & Bates, 1991) and in larger samples of brain-injured children studied with a combination of behavioral and parent report methods (Bates et al., 1997; Granberry, 1996; Monson, 1996). Finally, when investigators are able to isolate concurrent correlations between gestural naming and word naming at the appropriate stage, then the relative timing of these correlated milestones has at least some predictive value for later outcomes. That is, children who are significantly delayed in both behaviors tend to be delayed in language at later stages of development — Thal et al., 1997.

Word combinations and grammar. First word combinations typically appear between 18–20 months. This event is accompanied or slightly preceded by gesture-word combinations in vocal communication (e.g., pointing while naming — Capirci, Iverson, Pizzuto, & Volterra, 1996). These shifts toward two-unit productive combinations in communication develop in parallel with gesture-gesture combinations in symbolic play that have no obvious communicative purpose (e.g., stirring and then drinking from a cup, in a single, uninterrupted action sequence — Iverson & Goldin-Meadow, 1998; Shore, O'Connell, & Bates, 1984).

Between 24–30 months, on average, there is an explosion in grammar, with the bare telegrams of 20-month-old children giving way to more ornate sentences with inflections and free-standing function words. In typically developing children, several studies have shown that the ability to remember and imitate arbitrary sequences of manual actions (in scene construction tasks with novel objects) is correlated with the onset and growth of grammatical production from 24-30 months (Bauer & Dow et al., 1998; Bauer & Hertsgaard et al., 1998; Bauer & Thal, 1990; Bauer et al., 2000).

The gestural correlates of first word combinations and later grammar have rarely been studied in clinical populations — and the few studies that have been attempted in late talkers and children with focal brain injury have led to the curious dissociations and other anomalies that we will consider later.

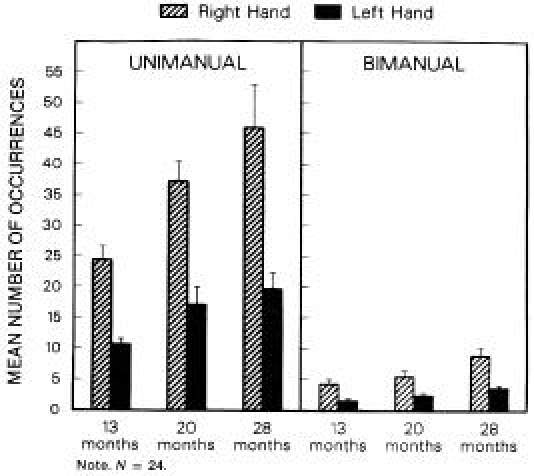

Figure 1. Mean number of unimanual and bimanual gestures with the right and left hand, from 13 to 28 months in a sample of normally developing children.

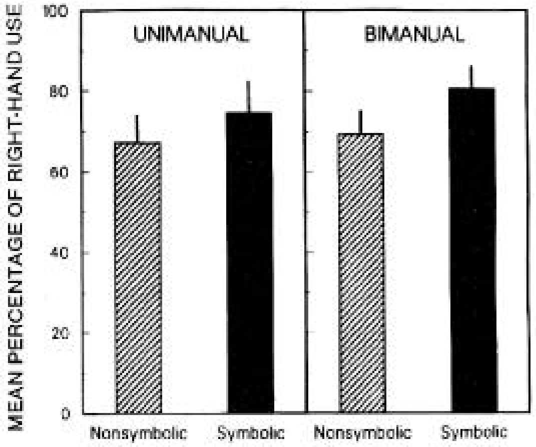

Figure 2. Mean percentage of unimanual and bimanual gestures with right-hand use; symbolic gestures for both are performed more often with the right hand.

Further evidence for language-gesture links in early development come from the study of handedness, across the milestones summarized above. Contrary to Lenneberg's early claim (Lenneberg, 1967) that lateralization for language and handedness emerge after language is acquired, a host of studies have shown strong evidence for a right-hand bias from the beginning of life (Liederman, 1983; Liederman & Kinsbourne, 1980). More important for our purposes here, right-hand bias is greater for gestures with communicative and/or symbolic content than for non-communicative/symbolic gestures, with or without an associated object in hand. For example, Bates et al. (1986) coded deictic gestures, symbolic gestures and nonsymbolic hand movements at 13, 20 and 28 months of age, in imitation and free play. There was a main effect of right-hand bias at all ages, in unimanual actions and in bimanual activities in which one hand is dominant (see Figure 1). This right-hand bias was significantly greater for pointing gestures (~80% right-handed, collapsed over age), and it was also significantly greater for symbolic than nonsymbolic actions with the hands (Figure 2). In other words, the linked lateralization of language and gesture is most obvious when we are talking about meaningful and familiar gestures. As we shall see, this distinction is also important for the adult neural imaging literature.

"All in the Family" Part II: Shared Neural Substrates for Language & Gesture in Adults

Compatible with these correlational studies of children, investigations of acquired aphasia and various forms of apraxia suggest a tight coupling between sensorimotor and language skills in the adult brain. Like adult aphasia, motor and tactile apraxias occur predominantly as a consequence of left-hemisphere damage. For instance, damage to left, but not right, parietal regions in adults causes increased errors and deviance in terms of the timing, sequencing, and spatial demands of a sequential arm movement task (Weiss et al., 2001). Haaland, Harrington and Knight (2000) report that motor-sequencing deficits occur predominantly with left-hemisphere lesions, both frontal and parietal. Goldenberg and colleagues (Goldenberg, 2001) have also shown that imitation of hand gestures is compromised by left-hemisphere damage. Interestingly, Halsband and colleagues (Halsband et al., 2001) found that left parietal, but not left prefrontal, damage caused a serious impairment in gesture imitation, but not in gesture comprehension (but see imaging results by Iacobini and colleagues, below).[1]

The link between aphasia and apraxia is especially strong for symbolic and communicative gesture (especially ideomotor apraxia, a disorder restricted to meaningful gestures). These gestural deficits are highly correlated with naming deficits in both aphasia and Alzheimer's disease (Bates, Bretherton, Shore, & McNew, 1983; Duffy & Duffy, 1981, 1989; Duffy, Duffy, & Pearson, 1975; Kempler, Andersen, & Henderson, 1995; Mateer & Kimura, 1977); Wang and Goodglass (1992) showed that both comprehension and production of meaningful gestural pantomines was significantly correlated with auditory language comprehension. Furthermore, Kertesz (1979, 1982) showed that severity of both expressive and receptive language symptoms correlated with extent of apraxic deficits at extremely high rates (r = ~.80).[2] Although dissociations between aphasia and apraxia have been reported for individual cases (Feyereisen, 1987), the dissociations run reliably in only one direction: language deficits with gestural sparing. Evidence for a double dissociation (gestural deficits with language sparing) is rare and hotly contested (McNeill, 1985, 1987).

Additional, and possibly more compelling evidence for a language-gesture link comes from "on-line" studies of the hand movements that parallel speech production in normal adults. McNeill, Goldin-Meadow and colleagues (Goldin-Meadow, 1998; Goldin-Meadow, Butcher, Mylander, & Dodge, 1994; Goldin-Meadow, Mylander, & Butcher, 1995; Goldin-Meadow, Wein, & Chang, 1992; McNeill, 1998; McNeill, Cassell, & McCullough, 1994) have demonstrated striking parallels between language and gesture in timing and form during various narrative tasks (e.g., upward movement of the hands while describing a cartoon character climbing a pipe, with such close timing that parallel planning and execution of the gesture and the verb seem likely), and in problem-solving situations (where a match or mismatch between language and hand actions predicts success or failure on tasks —Perry, Church, & Goldin-Meadow, 1992). In the same vein, Gentilucci and Gangitano (1998) — see also Glenberg (1997) — argued that, if semantic features of words are truly encoded in sensorimotor form, then physical actions or sensations relevant to those features should directly influence the "online" processing of the words or phrases. Their own experimental results and those of other investigators bear this prediction out. For example, Klatzky, Pellegrino, McCloskey and Doherty (1989) showed that subjects performing a sensibility judgement task could produce responses more quickly if they assume a posture congruent with the word or phrase's meaning (e.g., the word "dart" would be named faster if a subject were pinching his/her index finger and thumb together than if he or she were making a fist – see also McCloskey, Klatzky, & Pellegrino, 1992). In the same vein, word-gesture Stroop effects have also been observed, e.g., deformations in the velocity or trajectory of reaching movements when the target object is inscribed with an adjective, adverb or noun that is incompatible with the action (e.g., reaching up for an object that is labelled "down" (Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000). At the very least, such findings suggest that gesture is a "second window" onto speech planning at a preverbal semantic-conceptual level.

As might be predicted from these findings for normal and brain-injured adults, both intracortical recording/stimulation and neuroimaging studies (in both human and nonhuman primates) have shown that motor representations of oral and manual movements (over many levels of complexity and abstraction) are either adjacent or partially overlapping in many frontal and parietal regions, including (but not exclusive to) the primary motor (F1/M1/Brodmann's Area 4), ventral premotor (PMv/F4 and F5), intraparietal sulcus (AIP/VIP) and inferior parietal (PF/Brodmann's Area 7) areas (Cavada, 2001; Matelli & Luppino, 2001; Rizzolatti et al., 1988).[3]

The ventral premotor area, termed F5 in the monkey literature, is of central importance for our purposes here, for several reasons. First, the hand/arm and mouth representations in this area appear to overlap substantially when mapped by intracortical stimulation and recording (Gentilucci et al., 1988). Second, there is growing consensus that the general anatomical human homologue of this region is Brodmann's Areas 44 and 45, cytoarchitectonic regions often referred to as Broca's area, a region implicated in the planning and articulation of speech and in language processing in general (for discussion, see Rizzolatti & Arbib, 1998, as well as Dick et al., 2001). Finally, F5 is neural home to the first-discovered "mirror neurons." It had been known for some time prior to the discovery of mirror neurons that individual neurons in primate prefrontal cortex will fire when an animal is planning a hand gesture of a particular type (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). It was within this framework that Rizzolatti, Gallese and colleagues first noted a compelling phenomenon: the same neurons that fire when the animal is planning a specific arm movement or gesture also fire when the animal observes someone else producing that movement (typically in mirror-image orientation).

Rizzolatti, Gallese, and colleagues suggest that the mirror neuron system (which now has also been found in area AIP — Rizzolatti, Fogassi, & Gallese, 2001) allows the observer to understand others' actions through a transformation of visual input onto a particular 'motor schema' (like "hand picking an apple"). In other words, the observer may be able to understand what an actor is doing by using her or his experience of moving and interacting with the world.[4] These results have inspired some broad speculations about the role of the mirror neuron system (both frontal and parietal components) in the evolution of imitation, observational learning and social coordination in humans. On these arguments, the mirror neuron system permits the overt or covert "simulation" of behaviors by conspecifics, leading to a deeper understanding of intentionality and emotion in other individuals (Gallese, 1999, 2000a,b, 2001a,b; Meltzoff, 1990; Meltzoff & Gopnik, 1994; Meltzoff, Gopnik, & Repacholi, 1999).

There is compelling evidence from functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (rTMS) studies that regions homologous to macaque F5 and AIP also play similar roles in adult humans. [These methods are both described in a parallel special issue of Developmental Science on imaging methods (Casey, Davidson & Rosen, 2002; Moll, Heinrich & Rothenberger, 2002)].. Most importantly for our purposes here, the mirror neuron system overlaps to a remarkable degree with anterior and posterior regions that are in areas consistently implicated in language production and comprehension. Studies from several different labs (including Buccino et al., 2001, and Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998) have shown that observation and/or imitation of hand and finger gestures, grasping movements, and pantomime evoke activation in both 'Broca's' and inferior parietal areas. Perhaps most convincingly, Iacoboni and colleagues (personal communication) have stimulated with rTMS the left and right pars opercularis of the inferior frontal gyrus (with the occipital lobe as control stimulation site) when subjects were imitating actions of pressing in sequence two keys of a keyboard. As a control task, subjects were doing the same motor act, but here the keys to be pressed were cued spatially, rather than by action observation. Iacoboni et al. found that stimulation of either left or right frontal pars opercularis (but not the occipital site) caused a significant worsening of performance in the imitation condition, with absolutely no effect on the spatially cued condition. These data tally with a meta-analysis of fMRI data on hand action observation (with 62 subjects) by the same group (Iacoboni, personal communication); here they find three bilateral peaks of activation in inferior frontal cortex, in Brodmann's areas 6, 44, and at the border between Brodmann's areas 45 and 47. In the large subgroup of subjects (n=39) who also performed a hand action imitation task like that reported in Iacobini et al. (1999), an activation peak was again found in Brodmann's area 44.

Putting together the results for children and adults, the picture that emerges is one in which perception, imitation and spontaneous production of language are superimposed on a broadly distributed set of neural systems that are shared with the perception, imitation and spontaneous production of manual gestures. But before we can embrace this unifying view, we turn to some dissociations in the developmental literature that are (at first sight) difficult to square with the adult literature. As we shall see, some of these peculiarities may find a partial resolution in recent neuroimaging studies.

Dissociations of Language and Gesture in Children

As investigators pursued the correlated milestones in Table 1 in more detail, in typical and atypical populations, some puzzling and unexpected dissociations have emerged between language and gesture, and between perception and action within language itself. There are a number of possible "fault lines" that we might have expected. For example, we might have found that some children show language well in advance of gesture, or vice-versa. Alternatively, if the system cleaves along perceptual-motor lines, we might have expected to find dissociations between comprehension of language on the one hand (i.e., perception), and both gesture and word production on the other (i.e., action). Instead, the critical variable in determining how things "come apart" in language and gestural development seems to be the presence and amount of contextual support that is available for processing within and across modalities. As we shall see later, this same variable has proven to be important in neural imaging studies of language and gesture in adults. We will illustrate these points below by starting with factor analytic studies of word comprehension, word production and gesture in normally developing children, followed by studies of the same three modalities in late talkers and in children with focal brain injury. This will lead into the next section, where we review analogous results in adult imaging studies.[5]

In the language domain, word comprehension and word production correlate highly at the group level. However, marked dissociations have been observed in individual children (e.g., apparently normal infants who produce no speech at all despite receptive vocabularies of >200 items (Fenson, Dale, Reznick, & Bates, 1994). Studies employing various measures of word comprehension, word production and gesture production in typically developing children have used factor analysis to reduce a larger list of correlated variables to their underlying components, exploring associations and dissociations among these variables between 12–16 months (Bates et al., 1988; Shore et al., 1990. Using parental report and/or laboratory observations (in various combinations from one study to another), these investigations confirmed the existence of at least two orthogonal factors: a <u>comprehension factor</u> and a <u>production factor</u>. This result has been replicated in several separate studies of typically developing children, late talkers (Thal & Bates, 1988; Thal & Tobias, 1992) and in children with focal brain injury (Bates et al., 1997; Granberry, 1996; Monson, 1996). These reliable findings are not surprising to child language researchers, since the existence of a comprehension-production split within language has been known for some time. However, this may appear (at first glance, but see below) to contradict the strong perception/action correlations that have appeared in recent neural imaging studies (Grèzes, Costes, & Decety, 1999; Grèzes & Decety, 2001; Rizzolatti et al., 2001).

Do infants show a dissociation between comprehension and production within gesture that is comparable to the comprehension/production dissociation for words? As it turns out, this depends entirely on how gesture is assessed. Specifically, most of the relevant studies of gesture in infancy employ elicited imitation ("Do what I do"), which involves a combination of comprehension and production that is hard to disentangle. We are aware of only one published study of gestural comprehension *per se* in infancy, without an elicitation component. Shore et al. (1990) showed normal 28-month-olds a series of familiar gestures, modeled without the object in hand (e.g., pantomime of drinking), and asked them to choose the associated object from a 3-object array (e.g., cup, shoe and brush). Even though these gestures had been in the infants' expressive repertoires for at least a year, many of the children performed at chance and none were at ceiling. Even though children were not asked to imitate the gestural models (that is, elicited imitation was not the point of this procedure), half of the infants did spontaneously imitate the adult gestural model while it was presented; the other half produced no imitations at all. Post hoc analyses uncovered a surprising but statistically reliable U-shaped relationship between imitation and comprehension of gesture: no imitations were observed in low or high comprehenders; all of the children who engaged in "on-line" imitation of the model fell within the middle range on the comprehension task. This result supports a long-standing contention by Kagan (1981) and others regarding the nature and purpose of imitation in infancy: children tend to imitate in the service of learning, reproducing those actions and sounds that lie just outside their current level of understanding. Hence the relationship between gestural imitation and gestural comprehension is quite complex, and seems to depend on the child's current level of development within each modality.

What becomes of gesture-language correlations (see Table 1) when language comprehension and expression become dissociated? We might have expected gestural production (elicited or spontaneous) to pattern with levels of expressive language. Instead, several studies (including the factor analyses mentioned above) suggest that language <u>comprehension</u> "wins custody" of most gestural correlates (Bretherton & Bates, 1984; Bretherton et al., 1981; Bretherton, O'Connell, Shore, & Bates, 1984; Laudanna, Caselli, & Volterra, 1983). Indeed, the language-comprehension/gesture-production factor is predictive of the eventual prognosis (on the group level) of ‘late talkers’, defined as apparently normal infants between 18–24 months who are in the bottom 10th percentile for expressive language. Late talkers who are spared in both word comprehension and gesture production (both assessed under naturalistic conditions) tend to be "late bloomers", moving into the normal range in the next 12–24 months. By contrast, late talkers who are also delayed in word comprehension/gesture production tend to remain delayed, and some eventually qualify for a clinical diagnosis of language impairment (Thal & Tobias, 1992).

To confuse things even further, the nature and direction of these gesture/language correlations vary depending upon how both word comprehension and gestural production are measured (Bretherton & Bates, 1984; Bretherton et al., 1981; Bretherton et al., 1984; Shore et al., 1990). <u>Specifically, the link between word comprehension and gesture production is most apparent when both of these skills are assessed in a strongly supporting context.</u> This would include observations of both comprehension and gesture in naturalistic situations, or through parent report (which is also based on observations in context). Under these conditions, both word comprehension and gesture production can dissociate from word production. In contrast, <u>when word comprehension and/or gesture production are assessed under experimental conditions, with little or no contextual support, then both of these modalities are once again strongly correlated with progress in expressive language.</u>

With regard to the relationship between word comprehension and word production, several studies have shown that the "vocabulary burst" (a non-linear acceleration in the growth of expressive language between 16–20 months) is accompanied by a synchronous "comprehension burst", evidenced in context-impoverished preferential looking and picture-pointing tasks, and in event-related brain potentials to digitized auditory words (Goodman, 2001; Mills, Coffey-Corina, & Neville, 1997; Reznick & Goldfield, 1992; Zangl, Klarman, Thal, & Bates, 2001; see Taylor & Baldeweg, 2002, for a description of event-related brain potentials in a parallel special issue of <u>Developmental Science</u> on imaging methods). In other words, comprehension and production of language do “travel together” in the early stages of development, but this link is most evident when comprehension is assessed with minimal contextual support.

With regard to the relationship between gesture production and word production, several studies have asked children to imitate a gesture that they have never seen before (Bates, Thal, Whitesell, Fenson, & Oakes, 1989), and/or to reproduce familiar gestures without contextual support — e.g., a drinking gesture modeled empty-handed or with the wrong object — Bretherton & Bates, 1984; Bretherton et al., 1981; Bretherton et al., 1984. In these studies, significant positive correlations between numbers of gestures correctly produced and independent measures of language production are now observed. Hence word production and gesture production also “travel together” in the early stages of development, but this relationship (like the relationship between expressive and receptive language) is evident when gesture is assessed with minimal contextual support.

This complex nest of results is summarized in Table 2: "Strand I" refers to those measures that <u>do correlate significantly with word production</u>. These include word comprehension and gestural production measured in a laboratory setting with little or no contextual support. "Strand II" refers to those measures that <u>do not correlate significantly with word production</u>. These include word comprehension and gestural production assessed through parent report or observations in naturalistic settings, with ample contextual support. The critical insight here is that these apparent dissociations are driven not by domain (language vs. non-language) nor by the contrast between comprehension and production (perception vs. action), but rather by the presence or absence of supporting context. As we shall see later, the same variables have proven to be very important in adult imaging studies. (See Table 2 at end of document)

Studies of language and gesture in children with perinatal focal brain injury suggest that the two strands are also associated with differences in side and site of lesion, albeit not in the direction predicted by the adult literature (Bates et al., 1997; Granberry, 1996; Monson, 1996). Briefly, frontal injuries were associated with expressive language delays, but this effect was symmetric: left or right frontal damage were associated with delays in both vocabulary and grammar. However, an asymmetrical effect was observed for injuries involving the temporal lobe. Specifically, children with LH injuries (involving left temporal regions) displayed more severe delays in language production (vocabulary and grammar) with sparing of both word comprehension and gesture production (both assessed in context-rich environments). Indeed, some of the LH children overused gesture compared with normal controls, as if they were using this modality to compensate for their delays in expressive language. This is precisely the opposite of what we might expect based both on language-gesture correlations in brain-injured adults and on activation profiles observed in adult neuroimaging studies, both in terms of left-right lateralization and intrahemispheric locus.

Finally, in another striking contrast with the adult literature, RH-injured children in the Bates et al. study were mildly delayed in both word comprehension and word production, and severely delayed in gesture. Of the 10 RH cases in this substudy, 9 had documented parietal involvement (for the 10th case, radiological data were insufficient to define the lobes involved).

Putting these findings together, Bates et al. cite research with adults (e.g., Martinez et al., 1997; Stiles-Davis, Kritchevsky, & Bellugi, 1988) suggesting that the right hemisphere is specialized at integration of information across modalities and across levels of analysis. In contrast, posterior regions of the left hemisphere are specialized for the extraction of fine-grained auditory and/or visual details. In this framework, children with RH lesions may be more impaired in early comprehension and gesture because integration of information in context is especially important when children are at the entry level and "cracking the code". By contrast, children with LH lesions (especially left temporal) may be more impaired in expressive language because the translation of auditory input into motor analogues requires more detailed perceptual information than the same children require when they are figuring out what a word or gesture means in context. In other words, injuries to the left hemisphere (especially left temporal sites) may delay those aspects of language and gesture that require fine-grained analysis, independent of context; injuries to the right hemisphere (especially right parietal sites) may delay those aspects of language and gesture that require integration of information, including the supporting context.

These lesion findings for infants are complex, and the interpretation proposed by Bates et al. involves (as they note) considerable speculation. Their results do not map easily onto lesion findings for adults, although they do reflect the comprehension/gesture vs. production profiles observed repeatedly in typically developing infants and in late talkers (Table 2). Specifically, the Strand I pattern contains those capacities that are impaired in children with LH damage (especially those with injuries involving the temporal lobe). The Strand II pattern contains those capacities that are impaired in children with RH damage (especially right parietal cortex). Let us now return to the adult imaging literature, to see if we can find evidence that will help to resolve these apparent contradictions.

Towards a Possible Reunification

Much of the data we have discussed demonstrate that perception and production of gesture and language travel at the same time (over development) and in the same places (in the brain) – as shown in Table 1. However, these fellow travelers sometimes stage a dramatic breakup, as seen in studies of normal children, late talkers and children with focal brain injury (Table 2). Furthermore, the neural homes of language comprehension and production and gesture production in children are different from where they seem to reside in adults. Is there anything that we can learn from the adult neural imaging literature that will help us to untangle these thorny but persistent results? In this final section, we will demonstrate that the strong links between language and gesture in adult neural imaging studies that we reviewed earlier are also dependent on issues such as level of contextual support (e.g., presence/absence of the associated object) and the familiarity of the gesture that is modeled for the adult observer. In other words, the same parameters that appear to govern the relationship between language and gesture in normal and abnormal development are also affecting the patterns of brain activity observed in language and gesture, in comprehension and production, in neural imaging studies of normal adults. After we address similarities between the child and adult literatures with regard to contextual support, we will end with a discussion of the issue of left-right asymmetries in cerebral mediation of gesture, in both these literatures.

On the role of contextual support.

In their review, Grèzes & Decety (2001) qualify the perception-action linkage in adults along some parameters that may prove useful to our quest:

> "The intention to act may be necessary in establishing a functional and an anatomical link between perception and action. However, there are good arguments in favor of a gradient of activation, at least in the precentral cortex, from observation, to simulation, and eventually execution."

They go on to consider some of the regions of activation that distinguish among these stages. We suggest that children in the early stages of language learning may require a different weighting of observation, simulation and execution, resulting in a differential recruitment of the regions required for each one.

First, consider the contribution of context to the patterns summarized in Table 2: word comprehension and gesture dissociate from expressive language when they are assessed in a richly supportive context; this dissociation disappears when either skill is assessed without contextual support (e.g., gestures elicited empty-handed or with novel or inappropriate objects; word comprehension assessed in response to a disembodied voice with no context other than a multiple-choice array of potential object referents). The central role of context has some important parallels in the adult neural imaging literature. Specifically, interesting differences in patterns of activation emerge when gestures are modeled with or without the appropriate object in hand. When hand or mouth gestures are modeled <u>with</u> the object in hand (e.g., eating an apple or picking up a ball), bilateral frontal (premotor and 'Broca's area') and parietal (inferior parietal lobule, intraparietal sulcus, presumed AIP, and superior parietal lobule) regions are activated. When the gesture is performed <u>without</u> the object (e.g., a mouth chewing, or reaching towards a nonexistent object), the same frontal regions are engaged, but all parietal activity drops below threshold (Buccino et al., 2001). Buccino et al. broadly suggest that the various premotor activations are caused by 'internal replication' of the action being observed, whereas the parietal activations are related to haptic, visual, and motor analysis of objects within one or more spatial frames (see also Milner & Goodale, 1995). Thus, presence of strong visual cues recruits additional brain systems (parietal networks) that are 'not interested' when those visual cues are absent – and when those visual cues are absent, the frontal systems are left to deal with the gestural model on their own.

How do these adult findings fit with the developmental story? We suggest two possibilities (and these are not mutually exclusive): (1) developmental changes in the need for contextual support as a result of learning and experience, and

(2) maturational changes in the strength and efficiency of frontal vs. parietal brain regions. Both of these hypotheses are based on the idea that parietal cortex supports the assimilation of speech and gesture models to an ongoing context, while frontal cortex supports both the recognition and the execution of well-formed and familiar motor plans.

1) Experience-based changes in the need for contextual support. In the first 30 months of life, infants are building up rich internal representations to mediate perception and action, but many years will pass before their sensorimotor schemata are as rich and resilient as those that adults can access and deploy in milliseconds.

2) Maturational dissociations between frontal and parietal networks. Expressive language delays with sparing of comprehension and gesture may reflect deficits or maturational delays in the frontal 'internally generated action' network. Expressive language delays accompanied by deficits in comprehension and gesture may also (or instead) involve deficits or maturational delays in parietal networks that coordinate recognition of objects and our relationship to them in intra- and peripersonal space.

Both of these hypotheses assume that the modalities in question (word comprehension, gesture production, word production) typically differ in the amount and kind of contextual support that they require. Even for adults, recognition of words and production of gestures in real-world contexts both take place with a great deal of "scaffolding," based on intimate and continuous exchanges with the outside world. For language comprehension, this ongoing context includes "top-down" information from the ongoing discourse, and a continuous "bottom-up" flow of spectral and temporal cues in the auditory input. For gesture production, the available context also includes proprioceptive feedback from relatively large movements in intra- and peripersonal space. Perhaps because so much context is available to support these two skills (even for adults), they also tend to develop earlier than expressive language (whether it is signed or spoken) in young children. In contrast, less context is available for speech production. The same top-down context that helps the listener to anticipate upcoming words in comprehension often underdetermines the words that must be selected for production. Furthermore, the fine-grained movements required for speech production (and for rapid manual movements in a sign language) provide relatively little proprioceptive support compared to the relatively gross movements involved in the communicative and symbolic gestures used by hearing children and adults. These differences between modalities may be magnified in infants who are still struggling to "crack the code", trying to segment, analyze and then reproduce their auditory input in the service of speech production (or, in the case of a manual sign language, to segment, analyze and reproduce the rapid and systematic blitz of manual contrasts that distinguish true sign from the gestures of hearing people — Emmorey, 2001; Volterra & Iverson, 1995).

Based on the evidence before us for children and adults, we propose that parietal cortex is especially well suited for the mediation of extrinsically driven, object- and space-centered information. For children in the early stages of language development, e.g., children with little knowledge or experience with the world, context is especially important, and parietal regions that mediate integration over context may be called into play to a greater degree than they would be for an adult for whom the same activities would be familiar or overlearned. In contrast, ventral-temporal cortex seems to be better suited for the rapid extraction of specific environmental cues ("local processing"), and connections between these ventral-temporal regions and frontal cortex may be implicated in the rapid selection and staging of well-known motor plans. Hence there may be a developmental passage (based as much on experience as it is on maturation) from processing that is heavily based on frontal-parietal circuits, to that in which frontal-ventral circuits play a more important role.

On left-right asymmetries.

We have found some commonalities between the adult and child literatures regarding the role of context, with special reference to the relative contributions of frontal and parietal areas that comprise the “mirror neuron system”. However, we have yet not addressed the issue of hemispheric asymmetries for language and gesture, which presents us with a number of discrepancies that need to be resolved.

(1) In studies of brain-injured adults, deficits in gestural production (i.e., various forms of apraxia) are more common with left-hemisphere damage, and tend to be correlated with both the presence and severity of aphasic symptoms.

(2) Normal infants show a significant right-hand bias for manual activity, a bias that is stronger for gestures with symbolic and/or communicative content, compatible with the hypothesis that such gestures are mediated by the left hemisphere.

(3) However, imaging studies of gesture observation in normal human adults have not yielded consistent evidence for lateralization. Most studies of action-perception correlations in adults report either bilateral activation, or greater activity in the left hemisphere (Grèzes and Decety, p. 9, Table II), although a small number (see below) have elicited more activation on the right side of the brain.

(4) There is also little evidence for a left- or right-hemisphere bias in the original mirror-neuron studies with monkeys.

(5) Finally, the peculiar left-right findings that we find in brain-injured children (i.e., greater delays in gestural production in children with right-hemisphere damage) do not find a ready explanation in any of these literatures (points 1-4).

In our search for a resolution of these disparate findings, the few adult imaging studies that have demonstrated a right-hemisphere bias for gesture observation may be informative.

First, Iacoboni et al. (1999) observed greater right anterior parietal activation when adults are instructed to imitate meaningless finger movements (note also that Goldenberg (2001) finds that right parietal regions are critical for matching and imitation of finger, but not hand gestures; he also suggests that right parietal areas are necessary for ‘gesture analysis’). Decety, Grèzes, Perani and colleagues (Decety et al., 1997; Grèzes et al., 1999) report greater right-hemisphere activation during observation of meaningless gestures, compared with gestures that are meaningful and well known. Finally, Levänen, Uutela, Salenius and Hari (2001) found that adults naïve to Finnish Sign Language showed activity in several right parietal regions, whereas experienced signers did not. In other words, the right parietal areas tend to be more active when adults are struggling to understand and/or reproduce something new, and therefore need to rely on extrinsic cues (i.e., context) to guide their action and understanding. By analogy, we might expect greater reliance on the right parietal system in infancy, during the period in which new gestures are analyzed and acquired (see also the developmental study of global/ local processing of Moses, Stiles, and colleagues, discussed in this issue).[6] If this hypothesis is correct, then it could explain why infants with right-hemisphere lesions (involving right parietal cortex) are especially delayed in the development of early communicative and symbolic gestures.

Finally, we offer a speculation (albeit one that can be subjected to a rigorous empirical test) that might explain some of the shifting left-right asymmetries in functional imaging studies of gesture perception and gestural imagery in human adults. Specifically, we propose that these asymmetries in mental activity are linked to overt asymmetries in handedness (and shifts in those asymmetries) when humans imitate each other. Our hypothesis rests on a key assumption in the mirror neuron literature, namely, that gesture perception and/or gestural imagery involve a process of "covert simulation", also referred to as analysis by synthesis, or knowing-by-doing. As we noted earlier, human infants tend to do their simulating "out loud", with overt imitation of gestural models that they are just beginning to understand. Suppose that we were to ask our adult subjects to do the same. What would they do? When adults are asked to reproduce a familiar gesture (e.g., saluting or waving goodbye), the model typically produces that gesture with her dominant (right) hand and the subject responds by producing the same gesture with his own dominant (right) hand. In other words, the imitator usually inverts the incoming visual image in the service of production. In a neural imaging study, this strategy of gestural inversion would lead to greater activation in the left hemisphere. However, there are other circumstances in which the imitator responds by literally mirroring the actions produced by the model, meeting a right-handed gesture with a left-handed response. This is particularly likely to occur when we are asked to imitate complex and asymmetrical hand or body movements that have no meaning (and hence no pre-existing motor representation that we can generate for ourselves). For example, when an aerobics instructor moves his right arm to the right, we usually respond by moving our left arm to the left. A similar primitive and literal tendency to mirror the activities of others is often observed novice signers (Emmorey, 2001): instead of inverting the right-dominant signs produced by their teachers (as they would if they were generating a meaningful sign for themselves), novice signers tend mirror the input, coming up to meet it with a clumsy reproduction by their nondominant left hand. In a neural imaging study, this kind of mirroring behavior would lead to greater activation in the right hemisphere.

Based on these facts, we make the following prediction: those gestural models that have been shown to elicit inverted imitations (right-handed model, right-handed imitation) in overt tasks will show left-biased activation in imaging studies of gesture comprehension. Conversely, those gestural models that have been shown to elicit mirror imitations (right-handed model, left-handed imitation) should show right-biased activation in such imaging studies. In other words, at least some of the unexplained shifts in asymmetry that have been observed across imaging studies of gestural perception may be the result of shifting patterns of hand use that are visible in overt gestural imitation.[7]

In conclusion, the division of labor in the brain does not seem to break down neatly into language vs. non-language, nor is it neatly characterized by a split between comprehension (perception) vs. production (action). Instead, the relevant dimensions for both children and adults seem to be: (a) sensorimotor organization (which involves some somatotopic separation despite substantial overlap between language and gesture); (b) stages of observation, perception-action matching, action planning and execution that are highly task dependent and draw on different regions to different degrees; (c) variations in the age and expertise of the individual; and above all, (d) the amount of context required for successful performance at different ages and stages of development. Children are not adults, so why would we expect a perfect mapping? And yet, these general principles may apply to children as well as adults, and may be useful for our understanding of brain development and brain organization across age levels.

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Author Note

This research was supported in part by grants to Elizabeth Bates, “Cross-linguistic studies in aphasia” (NIH/NIDCD RO1-DC00216), “Origins of communication disorders” (NOH NIH NGA 5 P50DC01289-10), “Center for the study of neurological basis of language” (NOH NIH NGA 5 P50 NS22343-15) and to Frederic Dick "Language, Communication and the Brain" CRL training grant (NIH T 32 DC00041), and "Training Program in Cognitive Neuroscience" NIH/NIMH 1 T32 MH20002-02.

We are grateful for helpful comments from Cristina Caselli, Kara Federmeier, and

Virginia Volterra, and give special thanks to Vittorio Gallese, Daniela Perani, and Marco Iacoboni for their generous sharing of new data as well as invaluable explanations and clarifications.

Footnotes

[1] We should note that many regions in the parietal lobe (particularly the supramarginal and angular gyri) are implicated in language tasks (e.g., Binder et al., 1997; Perani et al., 1996; Robertson & Gernsbacher, 2001, St. George, personal communication).

[2] It is important to point out that apraxia is not a simple loss of movement — rather, it is an inability to initiate and perform more complex, voluntary motor operations and to interact appropriately with objects in the environment.

[3] Note that the mapping of these functional and anatomical divisions, particularly across primate lines, is currently a subject of some debate – see Cavada (2001) and Matelli & Luppino (2001) for discussion.

[4] This kind of action-based perception (also called "analysis by synthesis") had been proposed many years earlier for speech (the Motor Theory of Speech Perception – Liberman & Mattingly, 1985) where it was believed to be a peculiar and species-specific property of the human brain that evolved expressly for language.

[5] We hasten to note that our use of the term ‘dissociation’ in no way implies that language and gesture production and comprehension are supported by non-overlapping neural substrates and/or representations. As many have argued (including the present authors – Dick, Bates, Wulfeck, Utman, Dronkers, & Gernsbacher, 2001), the existence of behavioral dissociations (single or double) does not necessarily imply that the underlying processing representations and/or resources are neurally segregated (see Munakata, 2001, Juola & Plunkett, 1998, and van Orden, Pennington, & Stone, 2001, for further discussion).

[6] Interestingly, in a more recent PET study by Perani et al. (2001), right parietal activation was observed when subjects viewed a real hand pick up an object, whereas virtual reality simulations and monitor projections of the same action did not cause the same parietal activation. Perani et al. suggest that realistic displays elicit an internal simulation by human subjects that involves "nonretinocentric coordinates (ego-centric and allocentric), related to the spatial representations necessary for high-order motor planning" (p. 756).

[7] The reason for the disparity between the hemispheric asymmetries in some human neuroimaging studies and the lack of such asymmetries in the primate neurophysiology literature is currently unclear. Dual-methodology comparisons (e.g., Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) and closer matching of task constraints over experiments should shed light on this mystery.

Age In Months	**Language Milestones**	**Gestural Correlates**	**References**
6-8	canonical babbling	rhythmic hand movements	(Locke, 1993; Masataka, 2001)
8-10	word comprehension	deictic gestures, gestural routines, first tool use	(Bates, 1979; Bates, Benigni, Bretherton, Camaioni, & Volterra, 1977; Bates & Snyder, 1987)
11-13	word production (naming)	recognitory gestures	(Bates, 1979; Bates et al., 1977; Bates et al., 1983; Bates & Snyder, 1987; Bates & Thal, 1991; Bates et al., 1989; Caselli, 1990; Shore et al., 1990; Volterra et al., 1979)
18-20	word combinations	gesture-word & gesture-gesture combinations	(Bauer, Hertsgaard, Dropik, & Daly, 1998; Bauer & Thal, 1990; Bauer, Wenner, Dropik, & Wewerka, 2000; Capirci, Iverson, Pizzuto, & Volterra, 1996a; Iverson & Thal, 1997; Iverson, Capirici, & Caselli, 1994; Shore et al., 1984)
24-30	grammaticization	sequences of 3-5 arbitrarily ordered gestures	(Bauer et al., 1998; Bauer & Thal, 1990; Bauer et al., 2000)

Table 1: Language and gesture milestones, by age and with associated references

Aspects of language & gesture from 10-36 months	**Strand I**	**Strand II**
Word production	X	
Word comprehension with contextual support		X
Word comprehension without contextual support	X	
Spontaneous communicative & symbolic gestures in context		X
Elicited gesture (imitation) with associated objects		X
Elicited gesture (imitation) without associated objects (empty-handed, wrong object, novel object)	X	

Table 2: Two 'strands' of language and gesture in typical and atypical populations, from 10-36 months. The emergence and development of behaviors within a single strand are highly correlated; they tend to be uncorrelated with the emergence and development of behaviors in the opposite strand.