MOVING FROM STROKE TO DEVELOPMENT: A DECONSTRUCTION OF SKILLED REACHING IN HUMANS

AFRA FOROUD

B.Sc., University of Lethbridge, 1998
E.M.A., Université du Quebéc à Montréal, 1998
M.Sc., University of Lethbridge, 2002

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Department of Neuroscience
Canadian Centre for Behavioural Neuroscience
University of Lethbridge
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For my parents,
Nader, who says ‘*you know Afrooz, it’s aaall in the physics*’
Your kind wisdom is always here, quietly in action, or softly spoken in words; &
Zahra, whose compassion and playfulness is woven so intricately into my heart and soul.

Your infinite friendship and wisdom is pure and strong.
The light that shines from you never fades.

For my sisters,
Nora, so honest and still.
Rebecca, so bright, so sweet.

Your voices, dances, and play are deeply moving and precious to me.
You are humble in the powerful influences you bestow.

To Jeremy, *eternities pass and still I know*.

To Serge, for recognizing a diamond in me and, for your mentorship.

To Bradley, with a love that was here for you from the beginning,
that is continually, and with unspeakable pleasure, waking from within me.
To the tickling, rough & tumble playing, the discussions.
You have a gentle spirit and a powerful presence.

I am blessed because of all of you.

ABSTRACT

MOVING FROM STROKE TO DEVELOPMENT: A DECONSTRUCTION OF SKILLED REACHING IN HUMANS

The purpose of this thesis is to describe the organization of the movements of skilled reaching. Our knowledge of reaching behaviour has been limited to an understanding of specific actions. Results from this thesis describe how reaching is the product of interactions of various parameters that assemble in an integrative way in ontogeny, yet can become dismantled on one level, or generally, throughout multiple levels of what constitutes the behaviour after stroke in adults. These findings demonstrate that skilled reaching constitutes motor parameters that may not be visible in a healthy adult, but that function through development, and by inhibitory systems in adults, to create a smooth and finely articulated action. An examination of the movement patterns of reaching within the full context of the behaviour can be applied to therapeutic strategies for motor disorders and, most importantly, deepen our understanding of the relations between reaching and cognition.

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Movement is the beginning and drive of all that is living. The first known instant of the universe began with a burst of movement – the big bang – and that initial burst has yet to be stilled as it is the current of our expanding universe. From the dancing flux of molecules of gas and particles of dust that form galaxies and stars, to the steady orbit of planets and their moons, the fluid tides and storms of earth's great oceans, powerful winds, immense seismic waves that shift and shape continental plates, gravity itself, to electrical and chemical reactions, to the emergence of a single cell and the properties within, to its division, to sexual reproduction, to that which is the process of evolution. Even our ability to sense environment, feel emotion, think and speak thoughts, create tools, ideas, art, relationships, to the decomposition that follows death, the cessation of movement, to the most elementary particle of existence - which is itself just a bundle of movement - lies the underlying ever indulging force of the freeing and binding flow of continuous movement.

Afra Foroud
September 5, 2007

PROLOGUE

The Integrative Nature of Movement and how it can Fall to Pieces

Movement is inherently integrative. More fundamental than the integration of different modules such as sensory or perceptual systems, authentic movement is an integration of specified motor components and gestalt action. On one level, an action is composed by organizing patterns of its movement components, and on another level, it is characterized by the overall architecture and flow. These two levels come together in forming movement. This integrative nature of movement can be observed in the way that it comes together during development and in the way it falls to pieces after brain damage.

CHAPTER 1

General Introduction:
On Movement and Reaching Behaviour

The hand is the instrument of intelligence.

Maria Montessori
The Absorbent Mind, 1967

General Introduction:
On Movement and Reaching Behaviour

The human hand is a sophisticated and articulate connection between the self and the environment. A person explores their world by reaching out to extrapersonal space, picking up objects, and grasping their design by exerting fine manipulations over them. The architecture and motor control of the hand enables dexterity. The physical experience of hand movements and object manipulation, including sensory and perceptual feedback, influences the acquisition of knowledge of objects and interactions between the self and the environment. The hand reaches beyond physical realms: it forged the foundation from which the human mind, socialization, and language evolved [Wilson, 1998]. With the evolution of increasingly skillful hand movements came a surge of fabricated materials such as specialized tools and decorative artwork, which paved the way for complex socialization through what is now known as the creative revolution.

The shift from limited opening and closing movements of the hand to individuated control of the digits changed the way in which humans perceived and interacted with their surroundings, and had an impact on the evolution of the mind. This progression can be seen in an infant as she develops from whole handed grasping to fine articulation of the digits. The infant's perception of objects expands exponentially as her explorations of the environment progress, and influences the development of her mind [Diamond, 1990]. As she embodies the concepts of dimension and mechanics through object manipulation, there is a surge in her cognitive ability. Indeed, action and cognition are so entwined that they evolve together in development, influencing each other in the formation of functional systems, characteristic of behaviour [Diamond, 2000; von Hofsten, 2007].

The evolution of digit individuation is parsimonious. Individuated finger movements function by both biomechanical and neural constraints that limit which fingers, and to what extent selected fingers, can move independently of others [Schieber & Santello, 2004]. Tendons from different muscles in the hand are interconnected; specific motor neurons, that originate in the cortex and descend to the spinal cord, act on sets of muscles rather than on individual muscles. That is, a single neuron in the cortex can contribute to the movement of more than one finger. Thus, firing from one neuron evokes movements in multiple muscles of the hand, and contraction of one set of muscles recruits contractions of nearby muscles.

As the use of the hand diversified from limited whole handed grasping and releasing movements, an advantage for dexterity of the digits was established and descending cortical motor neurons increased outputs in the hand to a greater variety of muscle groups. Biomechanical and neural constraints were preserved as the nervous system adapted by increasing inhibitory control of muscles, rather than by re-organization to a one-cell-to-one-muscle type of control. Even in the most skillful of hand movements, such as typing and playing the piano, individuation is made possible through inhibition of the surrounding digits [Schieber, 2004; Schieber & Santello, 2004]. Lesions to the motor cortex often lead to specific and partial paralysis of the contralateral arm and hand. In such cases, one segment of the limb loses the ability to move without the simultaneous movement of the adjacent segments: this is due to the loss of inhibitory control over muscles in the limb [Schieber, 2004].

Neural Organization of Movement

Reaching movements of the hand and arm are largely organized by supraspinal structures and their interplay with spinal circuits. The interaction of cortical and spinal motor mechanisms that are used for reaching is a product of evolution, as is the experience of an infant learning to reach, with accuracy, into extrapersonal space [Georgopoulos, 1988]. The motor system is involved in all types of movement, spans throughout structures at all levels of the brain [Georgopoulos, 1994], and has multiple forms of neural organization that involve modular contributions, neural pathways, sensory and perceptual integration, synchronous oscillations for a pulsatile control, and topographic arrangements.

Modular Contributions

Understanding of the nervous system control of movement was first developed in terms of its modular organization. The cerebral cortex and cerebellum contribute to the motor system in different ways, yet function together in organizing movement [Figure 1.1]. This partnership is demonstrated in Flourens' [1824] observation of a pigeon, which is able to maintain a normal posture and respond to stimuli – including flying when thrown - but loses its ability to self-initiate motor behaviour when both of its cerebral lobes are removed. In contrast, with the removal of the cerebellum alone, the pigeon is capable of initiating and engaging in voluntary behaviour, but will do so in an uncoordinated and imbalanced fashion, as though in a drunken state [Teitelbaum, 1967]. In the 1870s, Fritsch and Hitzig first elicited contralateral muscle twitches in rabbits and dogs by stimulating the frontal cortices and noted that, in contrast, stimulation of the parietal lobes did not evoke movement [Finger, 1994]. Ferrier [1876] provided further evidence for a cortical role in the control of movement, by

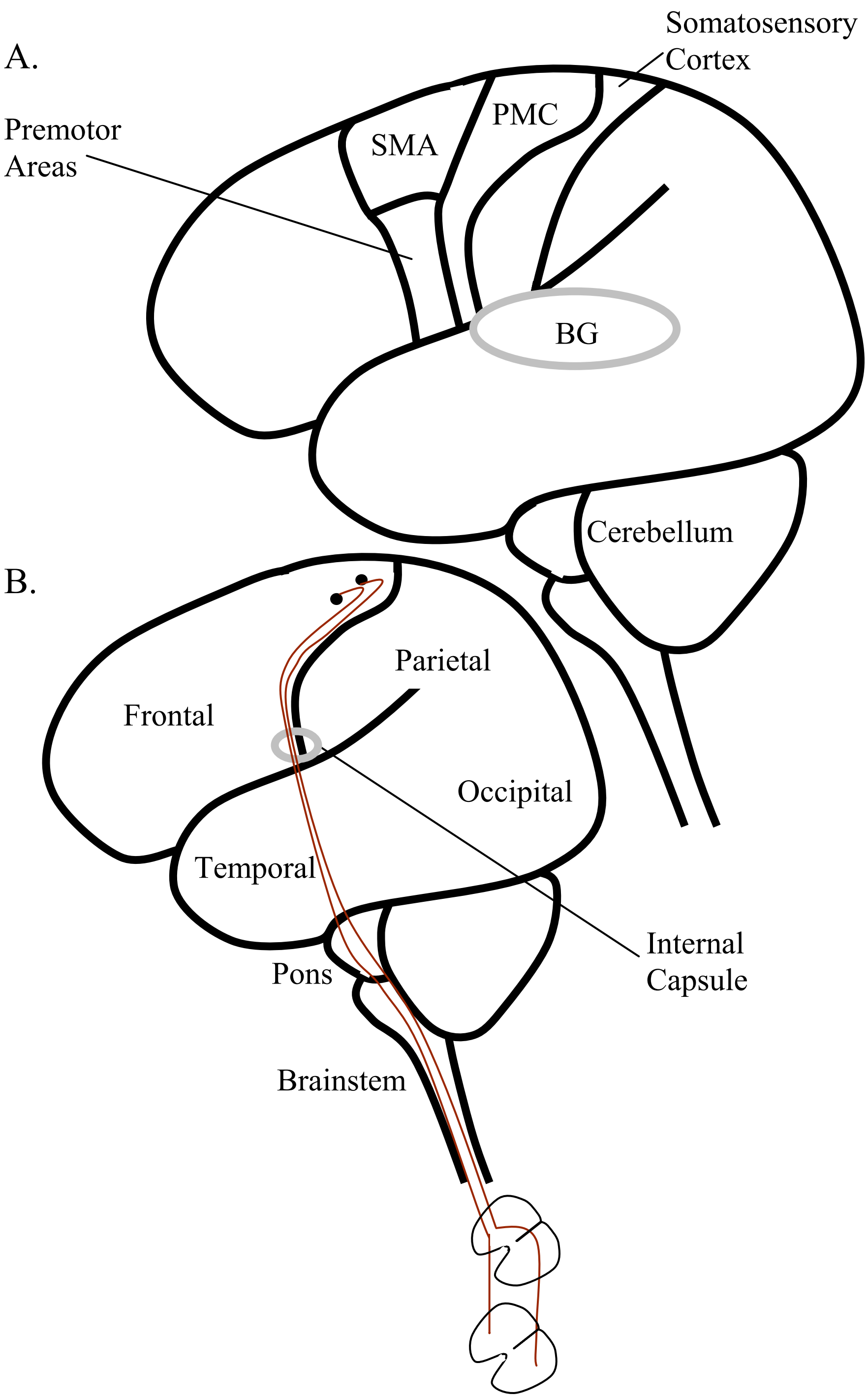

Figure 1.1 Neural Contributions for the Organization of Movement. A] Modular Contributions include: Primary Motor Cortex [PMC], Premotor Areas, Supplementary Motor Cortex [SMA], Somatosensory Cortex, Basal Ganglia [BG], and Cerebellum. B] Corticospinal Tract. Fibres [red] originate in the PMC, descend through the Internal Capsule and terminate in the spinal cord. Cortical divisions, pons, and brainstem are also labelled.

using faradic currents[1] to evoke what appeared to be voluntary movements in monkeys. Upon stimulation, it seemed as if they attempted to walk, reach for objects, and engage in scratching behaviours. He then replicated these remarkable findings in cats, guinea pigs, pigeons, fish, and frogs [Finger, 1994].

While the primary motor cortex in the frontal lobes plays the largest modular control of movement, the parietal, visual, and temporal lobes as well as the subcortical structure of the cerebellum, basal ganglia, brainstem and spinal cord, are all involved in movement organization [Georgopoulos, 1994] [Figure 1.1]. Although lesions in the primary motor cortex and other cortical areas responsible for movement do not eliminate movement [Denny-Brown & Botterell, 1947; Sherrington, 1939; Graziano & Aflalo, 2007a], they do lead to specific disruptions of movement, such as shoulder and elbow incoordination or loss of individual control of the digits. These are relatively minor impairments when compared to subcortical lesions that often result in ballistic movements,[2] loss of balance or postural control, and severe incoordination. Lesions to the neural pathways that funnel down from the motor cortex through the corona radiata and internal capsule to subcortical areas, sever the connection between the motor cortex and subcortical areas. This results in severe hemiplegia as one side of the body becomes weak, spastic, and paretic [Georgopoulos, 1994].

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[1] Earlier studies used galvanic currents, which are direct currents produced by chemical action and cannot be transmitted over large distances. Faradic [faradaic] currents are produced by induction and result in alternating currents. That alternating currents can transmit over longer currents may explain why faradic currents evoked motor behaviours rather than simple muscle twitches. It could be that by systematically stimulating and reaching further distances down into the nervous system, Ferrier was stimulating connections along the corticospinal tract [CST], rather than limiting stimulation to single cell bodies at the highest level of the CST.

[2] Ballistic movements are large involuntary excessive movements of the proximal limbs with associated changes in posture and muscle tone.

The primary motor cortices deal with the details of movements such as the regulation of contractile forces or the control of small groups of muscles in single joints. Together with premotor areas, the primary motor cortices function to facilitate and inhibit circuits, thereby allowing lower brain levels to regulate the fine details of timing during ongoing action automatically. Premotor areas receive information from posterior parietal cortex and project to the primary motor cortex and spinal cord, and are involved in the planning and coordination of complex motor sequelae.

The ventral premotor cortex contains a catalogue of complex actions for the hand. It functions to select appropriate hand actions to object shapes, which is important for grasping. In reaching behaviour, this area is active long before the grasping portion of reaching. Dorsal premotor areas are involved in directing, as well as monitoring, ongoing movements of the arm. The caudal area of the dorsal premotor cortex is specifically involved in planning and preparing movements. Major inputs to the primary motor cortex arrive from prefrontal, parietal, and temporal areas. The primary sensory cortex [anterior parietal lobe] projects directly to the primary motor cortex. Sensory contributions are important, since planning and performing voluntary movements, such as reaching, depends on physically embodying sensorimotor constructs that represent the external world, and transferring such constructs into integrative and functional motor activity.

Although the supplementary motor areas [SMA] are involved in inhibiting infantile grasping reflexes, they seem only to be active during the learning of skilled movements and decrease in activity as learning improves. Once the action becomes automatic, the SMA remains inactive during these movements. Reaching is an automatic behaviour in that the mover does not actively think about how to progress, yet, when learning a new skilled limb action, such as wood planing, the SMA would be involved in sequencing movements.

Neural Pathways for Movement

Voluntary skilled movements of the arm and hand are primarily organized through the corticospinal tract [CST]. The CST provides communication between the cerebral cortex and the spinal cord, is present in all mammalian species [Lemon & Griffiths, 2005], and controls movements in contralateral limbs, particularly the distal portions, such as the wrist and fingers [Lawrence & Kuypers, 1968a; b]. Coordination and harmony between movements of opposing limbs occur as homologous motor areas between hemispheres communicate via fibres that stream through the corpus callosum. Cortical projections from the primary motor cortex, dorsal and ventral premotor cortices, and supplementary motor cortex, form closed loops with the basal ganglia and cerebellum, as well as project to the brainstem, finally terminating in the spinal cord. Along the way, information directly descending from the CST projects to reticular and vestibular nuclei - which form their own descending motor pathways [Figure 1.1].

Closed loops between cortical motor areas, the basal ganglia, and cerebellum provide feedback during ongoing movement to cortical and brainstem motor areas, and function to regulate timing and coordinaton of ongoing movement. This forms the major subcortical inputs to cortical motor areas. These loops are separate in that they receive separate inputs from the cortices, run through separate areas of the thalamus, and project back to separate motor areas of the cortices. Basal ganglia and cerebellum are involved in making movements and posture regulation smooth. Damage to such areas results in the release of involuntary movements [e.g., Huntington's disease[3]]. The cerebellum is involved in coordination, and damage to cerebellar motor areas affects the accuracy of limb movements. CST fibres from the basal ganglia and cerebellum do not interact directly with the spinal cord, but do influence the spinal cord indirectly via the brainstem. Upon CST projections to the spinal cord, motor neurons excite and inhibit muscles through the neuromuscular junction. Ascending pathways from the spinal cord feed back proprioceptive information through the brainstem and cerebellum up to the frontal cortices.

It can be determined that the CST is not necessary for reaching movements as it remains an accessible behaviour after lesions to various levels of the tract [Lawrence & Kuypers, 1968a; b]. The oldest descending motor pathways in phylogeny originate in the brainstem and, with the exception of one, exert ipsilateral control over limbs. In their seminal work, Lawrence and Kuypers [1968a; b] first confirmed the role of the CST in limb movements upon performing bilateral decussations of the descending pyramidal of monkeys. They discovered that, in the absence of the CST, monkeys regained the general use of their limbs although deficits in speed, agility, and individuation of movement in the distal portions of their limbs [e.g., wrists and fingers] remained. Functional use of the limbs upon such lesions suggested that descending subcortical pathways contribute significantly to body and

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[3] Huntington's disease, caused by mutations in the Huntington gene, is characterized by involuntary excessive movements, hypotonia, behavioural and psychiatric abnormalities, impairments in cognitive function leading to dementia, and death after 15-20 years of onset. Cell loss in the caudate nucleus leads to under-activity of the indirect pathways of the basal ganglia and is associated with the involuntary movements expressed in the disease. These movements are classified as 1. athetosia [slow writhing movements of distal portions of the limbs]; 2. chorea [jerky and random movements of the limbs and oral-facial muscles]; 3. ballism [violent and large movements of the proximal limbs]; and 4. dystonia [simultaneous contraction of agonist and antagonist muscles] [Kandel, Schwartz & Jessell, 2000].

limb movements. Upon examining the effects of these lesions, Lawrence and Kuypers continued their experiments with systematic lesions to the lower descending motor pathways.

The vestibulospinal, reticulospinal and tectospinal are medial brainstem pathways that terminate in the ventromedial portions of spinal grey matter, thus orchestrating axial muscles for postural control and movement, although cortical areas organize postural movements that are higher in complexity. The vestibulospinal pathway is involved in vestibular control during movement, the reticulospinal pathway functions to coordinate reflexes as well as behaviours coordinated by the cranial nerves [e.g., facial expressions], and the tectospinal pathway plays a major role in the control of motor neurons in reptiles [Butler & Hodos, 1996; Iwaniuk & Whishaw, 2000].

In primates, damage to the ventromedial brainstem pathways severely impairs axial and proximal movements while relatively sparing independent distal movements [e.g., wrist and finger movement]. Ventromedial pathways control postural maintenance as well as the integration of trunk and limb movements. In contrast, whereas lesions to the lateral brainstem pathways generally spare combined body and limb movements, and whole limb movements, independent movements of the hand are severely impaired. Although hand movements are controlled in a more sophisticated manner by pathways originating in the cortex, the lateral brainstem pathways[4] have the capacity to control such movements [Lawrence & Kuypers, 1968b].

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[4] at pontine, medullary, and upper cervical levels

The rubrospinal tract [RST], descending directly from the red nucleus in the brainstem, through the medulla, and terminating in the dorsolateral portions of spinal grey matter, exerts contralateral control over limbs and is involved in goal-directed movements of the limbs. Lesions to the RST result in impairments of ipsilateral limb movements [Lawrence & Kuypers, 1968a; b].

With the exception of the vestibulospinal tract, all descending motor pathways are involved in skilled reaching in that damage to any one of them affects reaching. Medial brainstem pathways function separately in their control of movement, yet work together to produce integrated postural, limb, and hand movements. Furthermore, cells in the motor cortex project to both brainstem pathways, thus exhibiting hierarchical control over them [Lawrence & Kuypers, 1968b]. The CST forms the dominant control over reaching in humans and possibly overrides the functions of the lower originating tracts. Upon damage to the CST, the RST may provide functional compensation. Phylogenetic studies suggest that the pathways work synergistically in the control of skilled reaching [Iwaniuk & Whishaw, 2000].

Motoric organization for voluntary movement at the level of the spinal cord depends on the spinal cord’s interactions with the rest of the central nervous system as converging cortical arrangements, subcortical inputs [e.g., descending pathways originating in red nucleus], and the dynamic interrelated activity of spinal interneuronal[5] circuits within the

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[5] Interneurons are nerve cells that receive and send information to and from other nerve cells exclusively and do not directly interact with the world outside the nervous system. They interact with sensory and motor neurons primarily, and through multiple connections, spread sensory information to motor and non-motor neurons

spinal cord, function together to conduct central commands, stereotypic motor patterns, and facilitate afferent input from the moving limb [Georgopoulos, 1994].

As is the case for muscle synergies, interneuron circuitry within the spinal cord can assemble various motoneuronal pools into larger groups [Bizzi Tresch, Saltiel & d'Avella, 2000; Jankowska & Hammar, 2002]. A neuron projecting down from the cortex to the spinal cord typically excites interneurons, this results in the recruitment of muscle synergies, rather than mapping to a single muscle in the peripheral body [Graziano, 2006]. Cortical neurons involved in the control of the fingers and wrist bypass interneurons and project directly onto the motoneuron pools in the spinal cord [Bortoff & Strick, 1993; Graziano, 2006; Landgren Phillips & Porter, 1962; Lawrence, 1994; Lemon, Baker, Davis, Kirkwood, Maier & Yang, 1998].

Sensory and Perceptual Motor Integration

The visual system is involved in guiding outward limb movements [i.e., movements that carry the limb away from the body and towards extrapersonal space] [Georgopoulos, 1986; Trevarthen, 1968]. Central vision is used for accuracy in bringing the hand towards the target at the end the act [Georgopoulos, 1986; Paillard, Jordan & Brouchon, 1981], and peripheral vision is used to assess movements of the limb along the way [Georgopoulos, 1986; Held & Hein, 1963]. Sensing and perceiving the experience of moving the arm is critical for the visual guidance of reaching.

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throughout the central nervous system [Llinás, 2002]. Interneurons are fundamental to basic motor behaviours, such as reflexive movements, and are involved in most motor behaviours [Holstege, 1996].

Sensory and perceptual systems are integrated with the motor system in a variety of ways. Frontal, parietal, and subcortical areas in the monkey brain contain multimodal neurons where a single neuron codes for both visual and tactile information, or for both visual and proprioceptive information [Schendel & Robertson, 2004]. Representations of the limb in the monkey brain are encoded by vision and proprioception in a single neuron that cues limb position [Graziano, 1999] and tracks changes in limb posture. Multimodal neurons that monitor movement by sensorimotor integration may contribute to the formation of a body schema[6] that must adapt to changes in the body [Graziano, Cooke & Taylor, 2000] through movement, amputation, and tool use.

The brain responds to objects based on the way that the body interacts with them rather than for the purpose of the actual objects. The body's schema quickly reorganizes itself to incorporate commonly used tools by adapting the representation of the hand to extend to the end of the tool and the space around it [Farnè, Serino & Làdavas, 2007; Maravita & Iriki, 2004; Schendel & Roberston, 2004]. Sensory and motor systems function together to identify tools depending on their visual form, their typical motion [e.g., the rotation of a screwdriver], and the way that tools are manipulated for use [Beauchamp & Martin, 2007]. Functional neuroimaging studies have verified frontal, parietal, and temporal lobe involvement in tool representations in humans [Frey, 2007].

The visuomotor behaviour is functionally organized by two separate visual systems, each coordinated by specific neural streams originating in the primary visual cortex. These seperate *visual streams* terminate in separate areas of the cortex, each of which send

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[6] The brain's map of the body's shape and posture.

projections to the frontal cortex where information from both streams can be used in guiding eye, reaching and locomotor movements [Kolb & Whishaw, 1996; Goodale, 2001; Ungerleider & Mishkin, 1982]. First, the ventral visual stream terminates in the inferotemporal cortex and is involved in *vision for perception* - the construction of the perceptual representation of the world outside of the self - especially for objects. Lesions along the ventral stream result in the loss of perception of objects, but when a subject with such a lesion is asked to grasp an object, they do so as if their vision were intact. Second, the dorsal stream, which terminates in the posterior parietal cortex, regulates *vision for action* - actions specific to objects perceived. Lesions along the dorsal visual stream result in a state of action blindness, where the subject can see and perceive objects, but will reach for and grasp them as though blind [Goodale & Milner, 2004].

The work of Mishkin, Milner, Goodale and colleagues [1982; 2001; 2004; 2004] shows that seeing objects in our surroundings provides a subject with the ability to choose a target. However, it is the control of the prepared, initiated, and performed actions that take advantage of the visual information obtained. Perception occurs throughout the performing action, which, in itself, facilitates the need for perception of what is sensed. It is the act of moving that provides the organism with sensory information [Llinás, 2002] and it could be that the dorsal stream is involved in embodying object qualities which thus enables the self to function with the tangible aspects of the outside world.

Pulsatile Control

The specific neural organization for behaviours involving limb and hand movements is still under investigation. Outward limb movements depend on synergistic[7] movements of the shoulder and elbow joints. If the purpose of the limb movement is to grasp an object, wrist and finger movements occur concurrently in order to align and shape the hand specifically to the placement and design of the targeted object. Muscle groups are activated in a temporal sequence according to the specific trajectory, velocity, magnitude, and direction of limb movement [Georgopoulos, 1986]. Movement throughout the simple action of reaching out into space is discontinuous and acceleration is in constant flux; the action is made up of infinitesimal units of movements.

At a basic level, the control for movement is, indeed, discontinuous. Motor tasks occur in a series of infinitesimal units continually tied together by muscle twitches [Llinás, 2002]. One theory for how movements achieve high levels of smoothness is that the change in velocity between the series of most minute muscle twitches possible, occurring over time, must be at a minimum [Berthoz, 2000; Viviani & Flash, 1995] [Figure 1.2]. Studies on the dynamics of reaching suggest that the smallest units of movement lie in the spatial and temporal aspects of movement [Berthoz, 2000; Flash & Handzel, 2007]. Even in voluntary movement, the basic elements of movement are spatially and temporally organized in stereotyped ways. This is why as the proximity between the hand and the reaching target

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[7] Synergistic movements are when a group of muscles move together in a functional way upon stimulation of a single motor neuron. For example, the stretch reflex is synergistic, in that the flexor muscle is activated in order to withdraw the limb [away from danger] and the extensor muscle is actively inhibited in order to allow for the limb flexion. At the same time, the extensor muscle in the opposite limb is activated in order to provide support for the movement. In voluntary movement, such as skilled reaching, muscles in the elbow and shoulder joints move synergistically in order to extend and pronate the arm toward the target.

decreases, so does the velocity of the limb. If this does not happen, movements will be performed in a clumsy manner. That movement is organized in small units over time enables the ability to modify and reorganize movement continuously during action.

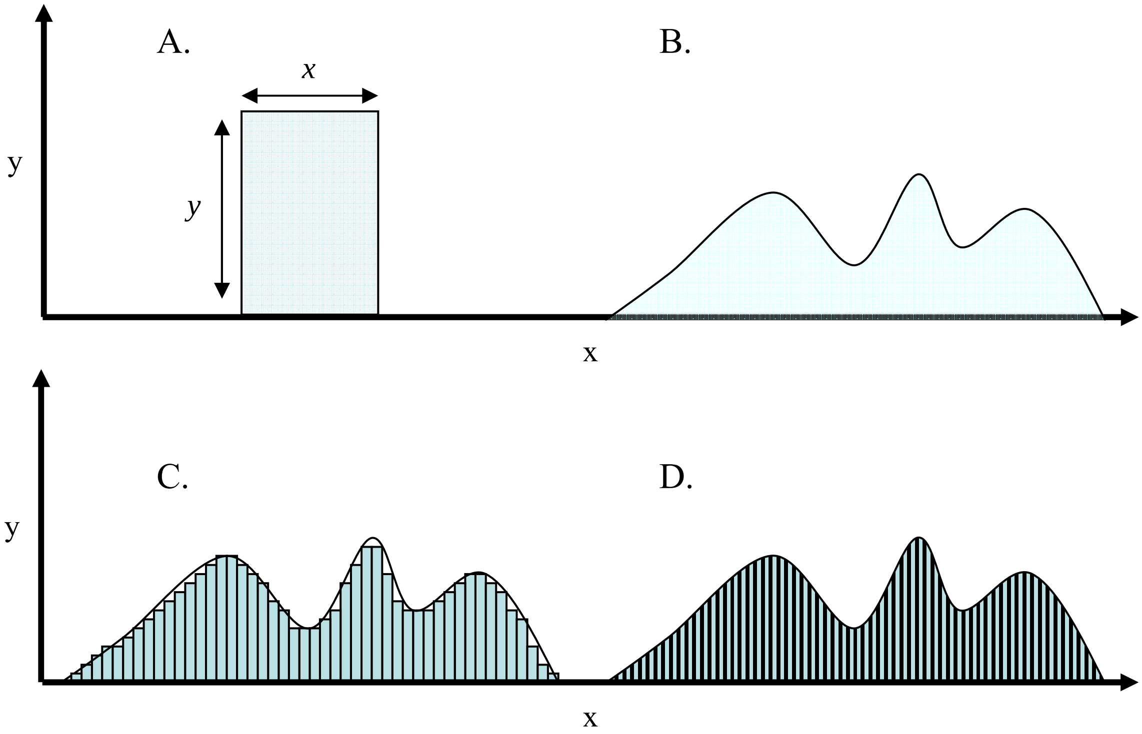

Figure 1.2 An Illustration of Infinitesimal Units. A] *x* is multiplied by *y* in order to calculate the area of the rectangle drawn in A. B] If the same formula is used to calculate the shape drawn in B, the result will be greater than the actual area. C] The sum of the areas of a series of small rectangles that fit within the shape drawn in B can be calculated in order to get a more accurate value. D] Calculating the smallest rectangles possible – the infinitesimal units – will increase the accuracy of the value. The control for movement is such that motor tasks occur in a series of infinitesimal units that are continually tied together. The change in velocity between the series of infinitesimal units occurring over time must be at a minimum in order to achieve smooth movement.

Continuous access to altering the timing between contractions of muscles is involved in adjusting the trajectory of the limb. Making movements that involve aiming toward a target, or simply a predetermined area in space, can be broken down into two main components. First, the shoulder and elbow act together to bring the distal extremity [the hand] close to the target. Second, fine wrist and finger movements articulate the hand to the exact final position [Georgopoulos, 1986]. Fine adjustments along the way are made possible through proprioceptive feedback into the CST. There is some evidence that, once the hand has reached a target,[8] the limb is used to stabilize the posture while the hand performs the intended actions [Graziano 2006]. It is likely that the postural maintenance of the limb during hand actions depends on feedback during action.

By simply observing movements, Bernstein [1967] concluded that it was necessary for the motor system to engage in 'mutual synchronization' through 'rhythmic oscillations.' More than forty years later, his theory gained physiological support. Neurons involved in movement are not limited to one section of the brain; they exist at all levels of the nervous system as well as in multiple locations within a level. Thus, neurons necessary for a specific movement, including inhibitory components, can be geographically separated. What connects them, prior to initiating a movement act, is a process of synchronization in their oscillations [Llinás, 2002]. For example, the oscillatory signals from olivocerebellar[9] areas modulate the generation of movement by the motor cortex [Lang, Llinás & Sugihara, 2006; Lang, Sugihara & Llinás, 2006]. It has been suggested that prior to the functioning command system for movement, a controller system organizes the necessary information for creating movement [Green, 1972; Llinás, 2002]. The controller system functions by synchronizing oscillatory behaviour of the neurons necessary to perform a specific movement. It is through a *pulsatile*

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[8] Targets are not limited to objects; they can be an area in space.

[9] Olivocerebellar fibres originate in the inferior olivary nucleus in the medulla oblongata and spread throughout contralateral cerebellar hemispheres.

control that the generation of a break in inertia can occur – this is the initiation of movement, the force exerted to awaken muscles from stillness [Goodman & Kelso, 1983; Llinás, 2002].

The pulsatile, discontinuous control of movement puts into action and ties together the infinitesimal muscular twitches of contractions and relaxations, and regulates the ability to prepare, to initiate, and to inhibit muscular actions, in order to perform movements in a smooth, flexible, and efficient manner. Pulsatile control of infinitesimal units of movement, or 'movemes' [Flash & Hochner, 2005], forms the control of movement, however, the way in which movement arranges itself into a motor behaviour is not organized by muscles twitches. Rather, it is organized in terms of actions, a phenomenon that can be studied by mapping movement in the brain.

The Brain Mapping Movement

When cells involved in similar functions are clustered together, they are arranged topographically. Topographical organization is one way of maximizing efficiency as cells that require regular communication are near each other and can form more synaptic connections than cells that are farther away. Somatotopic organization is a reflection on how the brain maps the body and movement [Graziano & Aflalo, 2007a; b].

The first mapping studies began with Fritsch and Hitzig [1870], who by eliciting twitching movements in an anaesthesized dog, found a region in the frontal lobe where single neurons mapped out a representation of the muscles in the dog's body. Soon after, Ferrier [1876] found a map representative of muscles in the monkey brain. Mapping of muscles in the cortical brain might suggest that movement is controlled in a marionette-like style, where single neurons become activated and descend down via CST fibres to elicit a contraction of a specific muscle. This type of organization is problematic; if the brain were to organize motor functions in terms of muscles, the organism would be limited in its motoric capabilities [Jackson, 1889]. Jackson hypothesized, '*…the CNS knows nothing of muscles it only knows movement.*' He suggested the motor system requires thousands of different combinations of interactions between the cells that control the fifty muscles in the palm and fingers of the hand.

In motor behaviours, it is rarely necessary to contract one individual muscle, however, it is continuously necessary to coordinate several muscle combinations to contract for a specific behaviour [Graziano, 2006]. There are a limited number of muscles in the body, yet the multiple combinations of how the muscles work together yield greater functions than what might be predicted from simply counting the number of muscles. Indeed, the functions of the motor system are diverse and flexible. Thus, neurons are broadly tuned to a variety of combinations of parameters that are specific to the species' behavioural repertoire. Such neuronal tuning may be trained through the experiences and ethological needs of an animal [Graziano, 2006].

Relatively recently, Graziano [2006] applied a new approach to mapping studies by using electrical pulses in the awake rhesus macaque brain that matched the time it takes for the monkey to perform an action during natural behaviour [e.g., reaching to grasp]. Rather than eliciting muscle twitches, whole actions involving complex coordination between the joints similar to actions that are performed naturally by the monkey [e.g., reaching, grasping, defensive movements] were evoked. Furthermore, different subregions within a region, such as the motor cortex, elicited different types of movements. For example, cells in one area of the motor cortex evoked movements that involve various forms of hand to mouth actions, whereas, another group of cells in another area evoked a variety of defensive movements.

Boundaries within the somatotopic map in the primary motor cortex are better defined as gradients as they are overlapping; cells for one function are often found intermingling in regions specified for another function [Graziano, 2006] and the map itself changes both over time with experience [Sanes & Donaghue, 2000] and at once, due to feedback from the moving limb [Graziano, 2006; Kakei, Hoffman & Strick, 1999; Lemon, Johansson & Westling, 1995; Sanes, Wang & Donaghue, 1992].

The nature of such organization suggests that the cortex organizes movement in a way that focuses on coordinating sets of muscles and joints as opposed to selecting for movement components and body parts that somehow must come together at subcortical levels [Graziano, 2006]. Even boundaries between the primary motor cortex and premotor areas are blurred and several of these areas send parallel projections to the spinal cord. Further, the control of movement at the level of the spinal cord is not limited to a marionette-like style, as described above - the organization of the spinal cord is more complex than simply mapping muscles [Graziano, 2006].

In a way, there is a freedom in the organization of movement where the specific underlying mechanisms for movement, such as neurons mapping to muscles, are in constant flux. This freedom of continual change in itself provides a multitude of choices, thus enabling flexibility and adaptability in the organism. In the big picture, this freedom of the motor system may be part of the driving forces of evolution. At the very least, in the small picture, it brings diversity in function and expression of the motor system, facilitates motor learning, and enables fine adjustments of movement in action.

Although the organization of movement involves mapping muscles of the body [flexible though it is], the ability to organize muscles into a sequence resulting in relevant actions lies in the ability to create, hold, and adapt abstract sets of rules [Graziano, 2006]. Neurons in the primary motor cortex are tuned to high order movement parameters such as movement sequencing. The idea that movement is organized in terms of various parameters that can go with the flow of constant change, rather than by rules for *pulling strings*[10] is supported by the fact that the same cells that are somatotopically organized also organize themselves in at least two different ways: 1. spatial organization, and 2. ethological relevance [Graziano, 2006]. One area of the brain is mapped in several ways and the unearthing of different maps requires different methodological paradigms; different lenses reveal different characteristics. As will be discussed later, the same is true when describing movements. Different systems of analysis, or even different types of hand written movement notations, reveal different characteristics of movement and lead to understanding various levels of the behavioural organization of movement. It may be that this pattern extends beyond the study

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[10] As would be the case if movement were to be controlled in a marionette-like style.

of movement and that movement itself is an intricate, multilayered phenomenon with fluctuating and constantly adapting mechanisms and parameters.

Spatial Organization

Mountcastle and colleagues [1975] showed that in the monkey brain, cells in the posterior parietal cortex become active when the arm reaches towards extrapersonal space. He classifed these cells as 'reaching neurons.' Cells in nearby areas were then discovered to respond to both stationary and moving stimuli. This finding led to work by Georgopoulos for discerning the role of certain neurons in spatial movements. The main finding was that neurons are tuned to specific directions and that a population of neurons work together to code for direction in limb movements [Georgopoulos, 1986]. He [1996] concluded that 'direction tuning is the result of orderly and delicate interplay of excitatory and inhibitory effects' and is a small piece of the puzzle on the making of limb movements. Georgopoulos showed that cells with similar preferred directions work together via excitatory connections, whereas cells with contradictory preferred directions become activated through inhibitory connections.

Stimulation of cells in the motor cortex often results in arm movements toward some sort of final posture independent of the limb position prior to stimulation. Many behaviours in primates [including humans], involve making movements with the limb that advances the arm to a final posture so as to enable the hand to perform an action such as touching, scratching, picking, or grasping [Graziano, 2006]. For example, the majority of a monkey's time during natural behaviour involves stabilizing the arm in a posture that enables skillful hand actions [Graziano, 2006; Graziano, Cooke, Taylor & Moore, 2004].

In his studies, Georgopoulous [1986] found that when the initial position of the hand was in a location central to the body, stimulation to cortical cells moved the hand to peripheral locations and that each neuron was broadly tuned toward a specific direction. By manipulating the starting position, or the posture of the arm in the same starting position, the direction a neuron was tuned towards changed [Caminiti, Johnson & Urbano, 1990; Scott & Kalaska, 1995; 1997; Sergio & Kalaska, 2003]. It is likely that variables including joint angle and posture of the arm contribute to preferred directional tuning of the cells [Graziano, 2006]. Speed, force, and muscle activity have also been found to contribute to directional tuning [Holdefer & Miller, 2002; 1999; Kakei, Hoffman & Strick, 1999; Li, Padoa-Schippa & Bizzi, 2001; Reine, Moran & Schwartz, 2001]. Graziano [2006] hypothesizes that similar to directional tuning, neurons in the motor cortex are tuned to a variety of combinations of parameters that are specifically useful to the animal. In this view, neurons tune to motor patterns based on experience and the behavioural needs of the animal.

Ethological Relevance

Specific regions in the motor cortex categorize movement into different ethological behaviours. These include: 1. central space/manipulations, 2. reaching movements, 3. defensive movements, 4. hand to mouth movements, 5. climbing and leaping movements, and 6. other outward arm movements with no specific function [see Table 1.1 for definitions] [Graziano, 2006]. The motor cortex is divided into subregions each one coding for a different category of movement. In this type of ethological relevant organizational mapping, individual neurons in the motor cortex are involved in orchestrating multiple, rather than specific, movements due to their capacity to tune broadly to multiple joint/muscle actions rather than one-cell-to-one-muscle organization. Further, cortical mapping of body musculature is continuously changing in response to feedback during action. This suggests that the ethological organization of movement is significantly influenced by experience and that relevant experience can modify topographical organization [Graziano, 2006].

Like all other forms of motor mapping in the cortex, the boundaries within this map are fuzzy and intermingled. Insight can be gleaned from the way that the maps are intermingled. Although there is individual variation, especially since organization is experience dependent, the only ethologically relevant motor behaviour of the limb that did not have its own specific subregion was that of general outward limb movements. Cells coding for these behaviours are scattered and surround reaching and central space/manipulation subregions. Perhaps, general outward limb movements are more closely relevant to reaching and central space/manipulation movements than defensive, leaping and climbing, and inward hand to mouth movements.

The organization of the motor cortex is built around the multimodal capabilities of the neurons within, where one neuron can be involved in many different types of movement and organizational parameters for movement [Graziano & Aflalo, 2007a; b]. This type of construct adds dimension to the cortex and is parsimonious in that the same cells are used for multiple purposes, rather than growing new cells for each emerging movement. Investigating a particular behaviour in comparative studies [in animal behaviour], how it assembles during development, and disassembles with brain damage, can lead to identifying how parameters for the given behaviour are established.

Table 1.1 Ethological Categories of Movement. A summary, derived from Graziano [2006] *Annu. Rev. Neurosci., 29:105-134*, of the proposed ethological categories of movement mapped in the motor cortex of rhesus macaques.

Ethological Categories of Movement	Description
Central Space/Manipulation	Moving the hand to approximately 10 cm away from the chest while shaping the fingers in a specific way, such as, making a precision grip, power grip, or spreading the fingers as the hand supinates.
Reaching Movements	Movements for reaching out by extending the limb and wrist while opening the hand as would be done in preparation for grasping.
Defensive Movements	Defensive reactions as though in anticipation of impact or toward unexpected tactile stimulus. For example, blinking, squinting, facial grimace, shrugging the shoulder, turning the head, limb making a blocking movement, and defensive eye-movements.
Hand to Mouth Movements	Moving the limb to bring the hand to mouth with the following actions performed simultaneously: making a pincer grasp, supinating the limb, flexing the wrist, carrying the hand directly to the mouth, and opening the mouth.
Climbing and Leaping Movements	Bilateral arm and leg movements similar to climbing and leaping movements.
Other Outward arm Movements	Movements of the limb that bring the hand to a point in extrapersonal space with not concurrent hand shaping.

Behavioural Organization of Movement

The behavioural organization of movement can be categorized in terms of reflexive, rhythmic, and volitional levels, postural control, inhibitory functions, and dynamic behaviour-brain interplay. Reflexes are the involuntary synergistic contraction and relaxation of muscle actions occurring at the level of the spinal cord and evoked by the peripheral nervous system. Reflexes function to either increase contact [approach] or decrease contact [withdrawal] with evoking stimuli. Some movements begin as reflexive, like swallowing in infants, and gradually transform to rhythmic movements. Rhythmic movements are repetitive movements such as chewing, scratching, and even locomotion in quadrapeds that are regulated by the spinal cord and basal ganglia. Centrally located neuronal circuits are capable of producing rhythmic movements spontaneously but are usually triggered by peripheral stimuli. Locomotion, swimming, and flying, are rhythmic movements controlled by the spinal cord, but are regulated by higher levels in the brain in terms of intensity and modifications deemed necessary along the way [e.g., a bump in the path].

Sherrington [1906] concluded that simple reflexes are the basic unit of movement and that it is their combinations that make complex movement sequences. He introduced the motor unit, the basic unit of motor function consisting of a motor neuron and a group of muscle fibres. He was the first to document the important role of sensory information in regulating movements - though movements can occur without sensory input. He described the fundamental role of the nervous system to be integrative in that upon certain stimuli, the nervous system combines various incoming information and selects the most appropriate response to put into action. Together with Pavlov [1927], Sherrington [1906] discovered *habituation*, the temporary decrease in reflexive response after repeated stimuli.[11]

There are a variety of types of reflexes [Table 1.2]. Some are present before and shortly after birth [e.g., grasp] and fade away as other [postural] reflexes and voluntary movements [e.g., reaching] develop. Magnus [1926] realized an important role for posture in movement, and together with Sherrington, discovered a series of postural reflexes in the decerebrate cat.[12] Magnus continued these investigations at higher levels in the brain and noted a hierarchy in postural reflexes that range from simple adjustments of the head and neck, to complex righting movements involving the whole body. For the ability to move the limbs, to make simple gestures with the arms, or to shift weight between the legs, the posture must maintain balance, anticipate movements, and be flexible enough to make sudden necessary compensations or adjustments.[13]

Postural reflexes alone do not account for postural control during voluntary movements. Postural adjustments must be preceded by anticipatory responses that are

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[11] From Kandel et al., 2000.

[12] A brainstem, surgically transected at midbrain level, disconnects communication between the higher levels of brain and the spinal cord.

[13] Allow yourself a moment simply to observe your current posture. Without changing anything, try to notice the flow of your breath, the relaxed versus tense areas of your body, from the head and neck, down through the shoulder girdle, the full length of your arms, your torso, into the pelvic girdle and down the legs right to the toes. Now, imagine, for a moment, that you are thirsty and will put this thesis down, stand up from your place and walk over to the kitchen to get a glass of water. Take note to what has happened in your posture. Continue to observe [*try* not to influence] your posture, and if you will, take this activity a step further and actually put the thesis down, stand up, and start walking. You may have noticed that prior to each type of movement - planning, putting the book down, changing levels to stand up, and walking - your body made subtle postural adjustments. Without these adjustments, you would not have been able to perform any of those acts. If you wish, you may repeat this activity from the beginning, but this time, try to inhibit any preparatory shift in your posture. It will be an awkward and unsuccessful experience.

flexible in order to compensate for unexpected disturbances and must be adaptive, for example, as when learning a new movement. When a person reaches for and lifts a glass of water, the body makes many compensatory adjustments, including inhibitory ones, in order to enable an extension of the arm without falling over. Once the glass is lifted, the body makes another series of movements to compensate for the glass in hand, and to prepare itself for bringing the glass towards the midline and up to the mouth. Of course, one does not think about these things, the behaviour is simply performed while thinking about anything else. Suppose the glass is heavier than anticipated, postural and limb movements must compensate accordingly and in synchrony. If someone nearby calls out, the head may turn in preparation to respond, again, adjustments in ongoing postural and limb movements must be made quickly. Throughout all of these examples, the behaviour is performed without a conscious thought about each movement. Postural control is thus integrated within the many levels of movement organization in the nervous system including associations with cognitive functions. Among his many insightful contributions to physiological psychology, Bernstein [1967] defined posture as the ‘readiness to move.’

Table 1.2 Types of Reflexes

Types of Reflexes	
Primitive or Infantile Reflexes	Present in newborn infants and become inhibited with age.
Postural Reflexes	Function to maintain the orientation of the body in space relative to gravity.
Visceral [Autonomic] Reflexes	Involved in regulating involuntary visceral functions of the body [e.g., heart rate or digestion].
Somatic Reflexes	Involved in the contraction of the skeletal muscles in response to stimuli [e.g., stretch reflex].

This preparedness offers you the choice to reorganize your movements in case of unforeseen events; however, many of the muscles are inhibited so that you do not have to move your entire body to pick up one small item. If it happens that you have to make adjustments, not only is the posture ready to do so, but the need to inhibit some ongoing movements allows for the initiation of other prepared movements. The construct for the action must be reorganized. Inhibition, and the abnormal loss of inhibition, was first described by Jackson [1889]. Higher levels of the brain exude control over lower levels of the brain which they are built upon; loss of higher centres can result in the disinhibition of lower centres. Jackson termed this type of disinhibition *released phenomena*. For example, damage to the frontal lobe elicits infantile approach reflexes[14] and damage posterior to the somatosensory cortex in the parietal lobe results in withdrawal reflexes[15] [Denny-Brown, 1958; Denny-Brown & Chamber, 1958; Teitelbaum, 1967]. Further, it has been shown that fetal and infantile reflexes *reappear* in adults with dementia [Paulson & Gottlieb, 1968]. Inhibition is at the core of movement execution and adaptability. The major motor outputs from the cerebellum, which is involved in balance and motor coordination, are inhibitory [Melillo & Leisman, 2004]. The majority of the body's muscles are engaged and prepared to act when the hand and arm alone reaches out to pick up a glass of water.

In addition to preparing the mover with the ability to modify continuously and reorganize movement during action, inhibition permits the adult self to explore the surrounding environment to the extent of their own will [Diamond, 1990]. Diamond has

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[14] Lightly pressing on the cheek of a frontal lobe patient with no noticeable symptoms elicits the rooting and sucking reflex- two infantile *approach* reflexes. These reflexes are inhibited during development.

[15] Lightly pressing on the cheek of a parietal lobe patient results in the infantile *withdrawal* reflex of mouth closure and turning the head away from the stimulus. This reflex is inhibited during development.

shown that as infants become more dexterous in their voluntary movements, persistent infantile reflexes interfere with their ability to grasp, or even reach toward, an object of interest successfully. For example, at five months of age, the child will grasp the edge of an object while en route to reaching for a target above or behind the edge of the first object. Failure to grasp the target is due to a lack of inhibitory control over the grasping reflex. Once the grasping reflex has waned, other infantile reflexes continue to interfere. By six-and-half to seven months of age, infants who are presented with a toy inside a transparent box reach directly for the toy, even if the hand comes into contact with the side of the box. If there happens to be an opening on that particular side of the box, the infant will successfully grasp and retrieve the toy. If the opening is on another side of the box, the infant continues, unsuccessfully, to reach directly for the toy. The line of sight towards the toy provides a reaction to reach directly along the line of sight. Again, lack of inhibition interferes with successful free exploration. If the box is opaque - the line of sight lost - the infant will reach in through the opening on the side [Diamond, 1990].

By studying natural movement, Bernstein inferred general rules of cerebral function that have, thus far, stood the test of time [Bernstein, 1967; Berthoz, 2000]. He introduced a model for movement function and the nervous system - the action-perception cycle - with a *comparator* as its basic element. The comparator detects errors between the performed movement and the predicted movement, recognizes that the movement has been performed, thus setting up the system for the next movement, and initiates adaptations in the movement sequence - even if that means reorganizing the prepared plan. All of the functions of the comparator act in milliseconds. Berthoz [2000] writes ‘I think that the highest cognitive functions are the result of an evolutionary thrust toward developing this ability to reorganize action according to unforeseen events' and states what is required for this ability. The organism must hold a memory of the past, be able to make predictions[16] and thus internally simulate the future, as well as embody the first two capabilities quickly as they must integrate within an action-perception cycle that lasts a fraction of a second. The ability to modify continuously and even reorganize movement during action requires that movement itself must be organized in a way that permits sudden changes to occur smoothly.

The Role of Movement in Social and Cognitive Systems

Parallels between movement and social-cognitive behaviours have been made throughout the many years of investigation on brain and behaviour. The earliest known written record of movement is from an Assyrian tablet in 600 BC on the report of a 'noxious pustule in the ear of grain'[17] causing *dancing manias*[18] where groups of people simultaneously broke out in convulsions [Finger, 1994]. Although the symptoms of dancing manias are motoric, this disease was considered a sign of insanity since it interfered with daily functions and etiquette. In his writings, the philosopher Plato [348 BC] discussed movement, noting that a person is not educated if he does not know how to dance. He argued that the experience of dance was important for development and maintenance of moral virtues in the self and the society and that a person learns through experiential actions of the

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[16] The idea of a *comparator* has been used in a variety of studies including ones done on attention, emotion, and memory. Gray's [1985] theory on hippocampal function draws upon elements from all the theories that incorporate a *comparator* in their models of behaviour-brain interaction. He concludes that the primary function of the comparator is to *generate predictions* and that the organism must have a knowledge of its own spatial-temporal location within the construct of its motor plan.

[17] [Goodman & Gilman, 1970]. The 'noxious pustule' is a fungus [*Claviceps purpurea*] in rye causing ergot poisoning of which one of the symptoms is convulsions.

[18] Also known as *chorea Sancti Viti* or Saint Vitus' dance [Finger, 1994].

body. Montessori [1964] created a teaching methodology based on a similar principle, that learning is facilitated through physical experience. In contrast, Descartes [1664] described animals as mindless machines that are a construct of pre-organized movements designed to engage into action upon appropriate stimuli. Descartes did not realize the dynamic interaction between movement, emotion, and cognitive reasoning [Damasio, 1994]. Even changes in dynamic posture [posture during action] can change the way a person thinks and feels. This is not necessarily due to psychological effects [e.g., self-esteem and mood], but rather, appears to be physiological [Tinbergen, 1973]. The nature of movement is integrative and has an impact on all systems of an organism.

The Impact of Movement

The impact of movement provides the nervous system with information from the world outside the self and is pivotal to the development of the mind. Rhythmic movements generated and/or regulated intrinsically is functional to a certain point. The interaction woven between information moving into the nervous system, as a result of moving, and the responses to the incoming information, are regulated higher in the nervous system: this contributes to evolving voluntary movement and cognition. The comparisons between internal representations and the embodiment of the external world, through motor, sensory, and perceptual information, feed back into the system, create opportunity for making predictions, plan future movements, and prepare for unexpected events that bestows cognition. Opportunity to make decisions – *turn left, right, stop or go straight?* – would not arise without the capability of holding an image of the self within the context of the world around the self.[19] Beritoff [1965] showed that the vestibular sense – the internal sense of movement capturing inertia[20] [Berthoz, 2000] – is central to an animal's capability of spatially orienting towards objects. He also showed that this capability is really an ability to locate objects in relation to the self and other objects in the environment.

The control of voluntary skilled movements is based on variables that have yet to happen [von Hofsten, 2007]. This process of prediction contributes to the cognitive means to design tools, track and scavenge, hunt, and even communicate with another. In the nervous system, three fundamental steps must occur for an organism to be capable of making predictions. First, the organism must have an internalized sensorimotor image of the external world. Second, by making rapid comparisons between the internal representation and the context of the external world [supplied by incoming sensory information], premotor solutions, or responses, are created. Third, the externalization of the premotor solution - its execution - generates in the nervous system an internal framework of what is about to happen [Llinás, 2002]. The act of executing the movements of the premotor solution provides an opportunity for the upgrading of the internal sensorimotor image of the world that sets the organism up for predicting what is about to happen.

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[19] Voluntarily navigating through the world, regardless of the way an organism's body morphology solves for this problem, is crucial for the evolution of abstract thought – it plays an important role in developing sense of self and the other factors contributing to the origins of mindness. Navigational capabilities originate in the movement, not the mind. Darwin [1887] suggested that *dead reckoning*, the ability to return home by the most direct path without external cues and regardless of the path taken away from home, is made possible by the 'sense of muscular movement'. More recently, in his laboratory, Whishaw has shown that it is the rat's 'self movement' during exploratory behaviour that supplies it with the tools to 'plot a return' to home base [Wallace, Hamilton & Whishaw, 2006].

[20] Flourens [1824] showed that the semicircular canals and otoliths function for balance. Almost 100 years later, [1910] the physicists Mach and Helmholtz discovered that the semicircular canals and otoliths are receptors for gravito-inertial forces [in Berthoz, 2000].

The ability to make predictions in order to execute an action perhaps prepares the organism to recognize and make predictions about the actions of others. This ability has both proximal and ultimate consequences for the evolution of humans. The ability to observe and interpret each other's movements enables cooperation and competition [Tomasello & Carpenter, 2007]. For example, it can facilitate hunting, gathering, and social interactions that eventually lead to migrating, building, and establishing societies. The ability for the nervous system to recognize and make predictions about the actions of others was discovered during studies on reaching and grasping movements and has led to theories on the evolution of emotion [Niedenthal, 2007], empathy [Gallese, 2003; 2007a; b; Singer, 2007], autobiographical memory [Dijkstra & Misirliso, 2006], and language [Clark, 2006; Fogassi & Ferrari, 2007].

The Mirror Neuron System and Embodiment

The discovery of mirror neurons in the motor cortex sixteen years ago [di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992] showed that the same neuron involved in committing skilled actions of the hand and mouth [e.g., grasping and eating] is also involved in recognizing others perform the same actions [Iacoboni & Mazziotta, 2007]. Mirror neurons are typically associated with goal-oriented hand movements [di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese & Fogassi, 1996] as well as ingestive and communicative movements of the mouth [Ferrari, Gallese, Rizzolatti & Fogassi, 2003]. The mirror neuron system involves somatotopically organized motor neural circuits [Buccino, Binkofski, Fink, Fadiga, Fogassi, Gallese, Seitz, Zilles, Rizzolatti & Freund, 2001] that occur in a variety of neural systems [Gallese, 2003], including systems for memory and learning [Ferrari, Rozzi & Fogassi, 2005], emotion, social cognition, and thought [Dapretto, Davies, Pfeifer, Scott, Sigman, Bookheimer & Iacoboni, 2004; Fonagy & Target, 2007; Gallese, Keysers & Rizzolatti, 2006; Gallese, 2006; Garbarini & Adenzato, 2004; Pfeifer, Iacoboni, Mazziotta & Dapretto, 2008], and language [Clark, 2006; Fogassi & Ferrari, 2007]. The discovery of mirror neurons led to theories on the role of skilled movements, particularly reaching and grasping movements of the arm and hand, and on the evolution of social-cognitive systems. Hence, the focus of the many electrophysiological, electroencephalogram, and neuroimaging studies have investigated the role of mirror neurons during reaching and related actions, including facial expressions, in humans and non-human primates.

Two classes of mirror neurons are known to make up the mirror neuron system. Strictly congruent mirror neurons fire upon the observation of the exact action of execution, and broadly congruent mirror neurons fire during the observation of related actions or similar actions with the same goal [Gallese et al., 1996; Rizzolatti & Craighero 2004]. Broadly congruent mirror neurons encompass two thirds of all mirror neurons, suggesting that mirror neurons are not limited to pure recognition and imitation, but are also involved in action interpretation, prediction, and learning which could facilitate the emergence of social interactions [Iacoboni & Mazziotta, 2007; Newman-Norlund, van Schie, van Zuijlen & Bekkering, 2007]. Mirror neurons can distinguish between a specific action and a pantomime of the same action [e.g., grasping a target versus making the grasping movements in the absence of a target] [Umiltà, Kohler, Gallese, Fogassi, Fadiga, Keysers & Rizzolatti, 2001]. Similarly, mirror neurons can distinguish between intention movements - for example, between grasping a target to displace it versus grasping a target to eat it [Fogassi, Ferrari, Gesierich, Rozzi, Chersi & Rizzolatti, 2005]. In the absence of a visual stimulus, mirror neurons fire at the sound of actions [e.g., cracking a peanut shell or opening a carbonated drink] [Kohler, Keysers, Umiltà, Fogassi, Gallese & Rizzolatti, 2002; Keysers, Kohler, Umiltà, Nanetti, Fogassi & Gallese, 2003]. Mirror neurons have learning properties, for example, in monkeys who have never seen tool use, mirror neurons for the hand do not fire when observing the experimenter manipulate tools. Upon repeated exposure to such observations, the same mirror neurons that did not fire previously begin to fire upon observation [Ferrari et al., 2005]. This suggests a motor capacity to recognize and imitate new movements.

Although the majority of studies on mirror neurons have been conducted in the monkey, imaging studies have verified the existence and functions of mirror neurons in humans. Positron emission tomography [PET] [Grafton, Arbib, Fadiga & Rizzolatti, 1996; Rizzolatti, Fadiga, Matelli, Bettinardi, Paulesu, Perani & Fazio, 1996] and functional magnetic resonance imaging [fMRI] [Iacoboni, Woods, Brass, Bekkering, Mazziotta & Rizzolatti, 1999; Koski, Wohlschläger, Bekkering, Woods, Dubeau, Mazziotta & Iacoboni, 2002] studies confirmed mirror neurons in inferior frontal and parietal cortices, and the dorsolateral prefrontal cortex [Buccino, Vogt, Ritzl, Fink, Zilles, Freund & Rizzolatti, 2004]. fMRI studies have confirmed mirror neurons exist in children as well [Wapner & Cirillo, 1968]. Transcranial magnetic stimulation [TMS] studies have shown that subjects show increased excitability in motor areas when observing grasping actions in others [Fadiga, Fogassi, Pavesi & Rizzolatti, 1995], as well as deficits in imitation upon repeated TMS applications to Broca's area[21] [Heiser, Iacoboni, Maeda, Marcus & Mazziotta, 2003]. Studies have shown that observing others' actions forms sensorimotor images in premotor areas. For example, if the actions are object related, mirror neurons in the parietal lobe, which is involved in knowledge of articulating the body to the shapes of the objects' interaction, are activated. Furthermore, observing emotions in others stimulate similar emotional responses in the self.

Neuropsychological evidence supports the role of the mirror neuron system in social cognition. The idea is that people understand others by unconsciously simulating their actions, emotions and even thoughts [Gallese, 2007a; b; Goldman, 2006]. fMRI studies have shown that the inferior frontal mirror neuron area distinguishes between grasping actions within different contexts, this suggests that human mirror neurons can recognize intentions [Iacoboni, Molnar-Szakacs, Gallese, Buccino, Mazziotta & Rizzolatti, 2005]. fMRI studies have also shown that mirror neurons interact with the limbic system [the emotion network of the brain], the anterior insula and amygdala in particular, suggesting their involvement in empathy. The ability to recognize and feel others' emotional states [Carr, Iacoboni, Dubeau, Mazziotta & Lenzi, 2003] is critical for social behaviour.

The traditional view of cognition is that the mind is a product of mental symbols and associated rules of manipulations, and that the role of the body is limited to executing cognitive commands. The question is how the mental symbols and rules that make up the mind emerge. The embodied view of cognition proposes that mental abstractions have an

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[21] specifically to the pars opercularis

evolutionary and functional basis in the body's experiences.[22] The dynamic relationship of an organism's interactions with the world provides the foundation for the ability to understand *other* – other organisms, with their own intentions, existing outside of the self [Gallese, 2003, 2007a; b]. Understanding of other individuals is based on the ability to form a sense of self, have a variety of motor, sensory and emotional states in common with others, and that the same neural structures that are involved in common motor, sensory, and emotional states exist between organisms and are involved in the observation of such states [Gallese, 2007a]. Therefore, upon observing another, be it an action or a complex social situation, the observer forms a sensorimotor internal representation within itself where bodily states associated with the observed actions, sensations, and emotions are evoked. The observer experiences what the observed experience on a multimodal level [Gallese, 2007a]. Embodiment is not limited to observations and interactions with others. For example, spatial awareness is also body based. Neurophysiological evidence suggests that the coding of space is an extension of awareness of the body. That is, the way that space is perceived is carved out from the body's interactions with its environment [Fogassi, Gallese, Fadiga, Lupinno, Matelli & Rizzolatti, 1997; Graziano, Hu & Gross, 1997].

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[22] Studies on the development of play fighting in rats suggest that the experience of placing oneself in vulnerable positions during play fighting in the juvenile phase, when cortical areas involved in social behaviours are developing, modulates the development of social and cognitive functions [Foroud & Pellis, 2002; 2003; Foroud, Whishaw & Pellis, 2004; Pellis, Pellis & Foroud, 2005]. During play fighting, rats tumble about each other in fluid sequences punctuated by pinning [Panksepp, 1981]. By analyzing the movements of the rats during play fighting, it has been shown that the truly pinned rat has rotated completely to a supine position [Pellis & Pellis, 1987]. The pinning rat either holds its partner down with its forelimbs while anchoring its hind limbs to the ground, or places itself completely on top of the pinned rat. Juveniles - at the height of their frequency of play fighting behaviour - engage in the latter form of pinning more than infant or adult rats [Foroud & Pellis, 2002; 2003]. By placing their bodies completely on top of their wiggling, pinned partner, juvenile rats create an unstable situation where it becomes difficult to predict what is about to happen and how they must prepare for such. They also increase the range of their physical experiences of vestibular, tactile, and proprioceptive senses in a dynamic and unpredictable social context. Taken together, the experience of play fighting contributes to, and may even be critical for, the development of socio-cognitive systems [Foroud, 2002; Pellis et al., 2005].

Nonetheless, the question on how movements are assembled for particular actions or behaviours remains. Reaching behaviour involves the integration of sensory and motor systems that prepare and organize the direction and amplitude of movements for grasping and manipulating specific targets, including the anticipation of, and compensation for, various loads [Georgopoulos, 1994]. The planning and execution of movement are processed via different pathways[23] [Georgopoulos, 1994]. Regardless, information for specific components of reaching from various cortical and subcortical areas converge in the motor cortex and descend to the spinal cord [Georgopoulos, 1994].

Movement cannot be purely localized in the nervous system. Even as aspects of movement have localized to specific areas, their boundaries are blurred, continually reorganizing, and functionally multifaceted. Localization of function in the nervous system, in a pure sense, is rare for complex behaviours [e.g., emotion and cognition], or even for [deceptively] simple systems [e.g., vision] – though of course, aspects of function and behaviour must have localization properties. Much like movement, the nervous system is integrative and dynamic in the ebb and flow of its internal and external interactive functions that lends itself to its flexibility and creativity.

Movement is the integration of multiple sensory, perceptive, and neuro-musculo-skeletal arrangements that weave emotional, cognitive, and social systems. To move is to function, express, create, evoke, recuperate, exist. Every act from the diverse and creative repertoire within the motor system is articulated by the biomechanical and neural organizations specific to the behaviour in procession [Graziano, 2006]. Traditional views of

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[23] Premotor areas are involved in planning movements, motor areas in their execution.

the motor system have resulted in a search for ultimate parameters that guide all motor behaviours. Recent studies have led to the theory of optimal central strategy, where for each motor act, the nervous system draws upon a specific set of parameters best suited for the behaviour in action [Graziano, 2006; Scott, 2004; Todorov & Jordan, 2002]. The present thesis provides a significant contribution to the understanding of the guiding principles of reaching behaviour, by comparing how it disassembles after various lesions in the adult with how it develops in early infancy.

The Thesis

One problem in the study of movement for scientific exploration of the organization of neural structures, in the evolution of language, emotion, and cognition, and for clinical research, is that the motor tasks are either manipulated to be unnatural, or the intended behaviour[s] are taken out of context. Movement is diverse in that there are a variety of types of actions and combinations of actions, some of which are invariable, and others variable, between species. Certain actions are species typical as they function within morphological constraints and often become optimally organized in a fashion that is tailored to the behavioural context. Even within the organization of the motor cortex, connections from a neuron to a muscle are feedback dependent rather than fixed, and descending pathways are strengthened, or weakened, by the condition of the limb [Graziano, 2006]. The context of the behaviour plays a significant role in modulating the parameters that organize the movement. Therefore, it is important to consider the behavioural context in the study of movement.

Much can be gained from examining, in isolation, specific aspects within an action, such as the synergistic movements between the shoulder and elbow joints [Bobath, 1990; Levin, 1996a; Twitchell, 1957]. However, a great deal of information is lost when the behavioural context, for example, synergistic movements between the shoulder and elbow joints during crawling versus reaching to eat, is ignored. Evolutionary, biological, and functional understandings of these movements are lost. This loss is detrimental to our understanding of the way living organisms evolve, grow, change and adapt - in effect, the way that our world exists through time.

This thesis focuses on a natural motor behaviour performed and taken for granted by people in every culture, but used a multitude of times daily. Skilled reaching, that is, reaching for the purpose of eating, has been, and still is, studied extensively by a variety of methods [e.g., kinematic and electrophysiological studies]. The present thesis examines skilled reaching through observation, and provides descriptions on the behavioural parameters. This thesis will demonstrate the importance of looking at movement within the context of the behaviour, that the value of observation remains relevant in today's technologically advanced world, and that fascinating riches are quietly passing us by as each infant develops. There is much to be gained by the observation of movement during development and this can contribute to our understanding of how movement falls apart due to injury and disease.

Skilled Reaching

Definition and Function

Skilled movements begin as consciously derived actions that are under cognitive control and become automatic with experience and practice [Halsband & Freund, 1993;

Leiguardia & Marsden, 2000]. Skilled reaching becomes automatic early in development and in terms of the hierarchical classification of movement, skilled reaching belongs to a group of voluntary movements that is at one of the highest levels. Skilled body-limb coordination in dance, sport and playing a musical instrument would be the highest, when, no matter how automatic a movement becomes, the performer can always improve upon it by actually thinking and consciously tweaking the movement prior to and at initiation, at execution and until completion – including follow through.

Skilled reaching is a natural behaviour of reaching for, grasping, withdrawing, and manipulating a target for some purpose. The purpose, and sometimes the original position of the target, determines variations of the behaviour. Generally, skilled reaching is used for the purpose of moving objects during grooming, eating, cooking, cleaning, handiwork, paperwork, and so on. Consider to yourself, how many times a day you perform skilled reaching. It would number in the thousands. Skilled reaching and variations of the behaviour are also used in social situations, not just in retrieving an object that is offered [e.g., a glass of wine], but also, for example, when reaching out to embrace a friend or stroking a child's hair. Skilled reaching for the purpose of eating is a task that is commonly studied in neuroscience [Whishaw, Suchowersky, Davis, Sarna, Metz & Pellis, 2002].

Movements of Reaching

In order to perform skilled reaching to eat, the subject must orient itself towards the target. The rat will orient through the olfactory system by sniffing, the human through vision. Next, the body must orient towards the target in order to set itself up to make the following movements as efficient as possible. The reaching limb will then perform a series of synergistic movements, including preparation for grasping and shaping the hand to match the object, as it advances towards the target. At the same time, the torso engages in a lateral postural adjustment that supports the movements of the limb. Nearing the target, the limbs' movements are organized in such a way so that the hand is perfectly aligned and shaped for grasping. Upon grasping, the limb performs a series of synergistic movements for withdrawing the target toward the mouth. During this time, the torso makes a lateral postural adjustment that extends to head movements that aid in aligning the head and mouth to the approaching target. Before reaching the target, the mouth begins to open, and upon reaching, the target is placed into the mouth as the subject releases it from the grasp. The subject immediately begins rhythmic chewing movements as the limb and torso move to a neutral or preparatory [for the next action] position [Whishaw et al., 2002].

Evolution of Reaching

Phylogenic studies suggest that skilled limb movements emerged early in tetrapod evolution [Iwaniuk & Whishaw, 2000]. The origins of skilled reaching are thought to have emerged from phylogenic ancestors who were moderately predatory – especially for small vertebrate prey where rapid manipulation is necessary - who incorporated, though not primarily, arboreal lifestyles, with broad feeding niches, and who may have even used their forelimbs for locomotion and habitat invasion into novel niches [Iwaniuk & Whishaw, 2000]. The motoric events in the evolution of skilled reaching are thought to be as follows. First, there are 'scooping' movements, where the animal extends the digits and uses the back of its hand to push food into its mouth. Second, 'wiping' movements emerge, where the palms are used to push prey towards the midline. Third, grasping movements emerge, where the digits are used to grasp and bring the prey toward the mouth. Fourth, grasping with rotation appears, where the wrist rotates upon grasping, thus increasing the ease in bringing the prey towards the mouth [Gray, O'Reilly & Nishikawa, 1997; Iwaniuk & Whishaw, 2000]. Grasping and grasping with rotation movements have continued to evolve as diversity of levels of dexterity between species are evident, the highest of which is displayed in humans.

One theory on the origin of skilled limb movements is that they originally emerged to counterbalance axial movements and eventually to aid in navigation. Iwaniuk and Whishaw [2000] suggest that limb movements progressed on a continuum: from locomotion to the specialization of skilled scooping and wiping movements of the forelimbs, and that feeding drove the extension of such movements. It is possible that the emergence of limb movements occurred in order to stabilize axial movements for terrestrial locomotion. Georgopoulos [1988] proposes that forelimb placement movements evolved from the movements used to place the limb accurately during locomotion. It may be that movements for skilled reaching began with the mouth, transitioned to the limb as the forelimbs began to aid in bringing food/prey towards the mouth, and then generalized to non-eating related skilled limb actions. The developmental study in the present thesis suggests that skilled reaching may have begun with the mouth as this type of movement occurs in infantile development prior to acquisition of the skill by the arm and hand.

Neural and Behavioural Organization of Reaching

Organizational control over movement is not limited to coding of the relevant information by neurons. Specific regions in the motor cortex categorize movement into different ethological behaviours such as reaching movements, hand to mouth interactions, and defensive movements. Single neurons broadly tune to multiple joint/muscle actions and can orchestrate multiple movements. The motor nervous system is in constant flux as it continually responds to feedback during action [Graziano, 2006]. In the adult human nervous system, skilled reaching – as with all voluntary movement - is primarily organized through the CST. The neural control for reaching is not limited to agonist and antagonist muscular recruitment - it is complex and adaptive as it can function within and during a variety of other motor and non-motor behaviours. For reaching [and other limb and hand actions] to occur, a population of muscles must be recruited. However, when attempting to understand the neural organization of reaching, one must keep in mind that it is not about which cells and pathways organize reaching compared to other limb movements - it is about identifying the rules that organize for this specific behaviour. Further, how do the rules shift with variances in achieving the behaviour, for example, when one reaches to grasp a moving stimulus, or a target that is around the corner, or when walking at the same time?

Development of Reaching

Most of what is known on the development of skilled reaching is limited to after the child is capable of performing the complete task. The problem, which is addressed in this thesis, is that little is known on the ontogenetic steps that lead to the acquisition of the task. Earliest studies on reaching began with the grasping reflex by Twitchell [1969; 1970], who then followed the ontogeny of reaching and attempted to uncover how grasping transitions from being reflexive to voluntary. Inhibition over infantile reflexes throughout development is necessary for the transition to voluntary movement and postural reflexes. The development of inhibitory control is likely modulated by developing supplementary motor areas and dorsolateral prefrontal cortices. Inhibitory control over reaching is just as important as the ability to acquire new behaviours and creates the opportunity in the developing infant to test their knowledge of abstract concepts [e.g., hidden objects], thus increasing the depth of their explorations in the environment [Diamond, 1990].

That cognition and action are so entwined, that they evolve together in development, influencing each other in the formation of functional systems required for behaviours [Diamond, 2000; von Hofsten, 2007] holds true for skilled reaching. The fine voluntary control of the arm and hand provides a highly articulate way for the self to interact with the environment. Newborn infants are capable of guiding their arm through space towards objects of interest [von Hofsten, 1982], for example, to keep their hands inside a beam of light projected above them [van der Meer, 1997]. The ability to guide the limbs, though in a rough manner, is likely an intrinsic skill present at birth that requires further development throughout infancy. Through a series of experiments, Galloway and colleagues [2006; 2007; 2007; 2008] have shown that very young infants make changes during spontaneous limb movements upon the presence of a toy. Such changes, evident in the complexity of hand kinematics [i.e., speed] and shouler-elbow coordination, likely play a vital role in the development of skilled reaching.

In terms of skilled reaching, visually orienting towards the target is present within a few weeks after birth [Rosander & von Hofsten, 2002]. By approximately four months of age, infants are capable of orienting and shaping the hand simultaneously with the target [Lockman, Ashmead & Bushnell, 1984; von Hofsten, 2007], as well as anticipating the need for grasping and supinating, prior to contact with the target [von Hofsten & Rőnnqvist, 1988]. It is not until between the ages of nine and thirteen months that infants become capable of adjusting the aperture of the hand to match the size of the target [von Hofsten, 2007].

Thelen and Spencer [1998] posit three movement stages of development necessary for the emergence of voluntary reaching. The infant must become capable of stabilizing the head and activating posture stabilization during precocial limb movements. Then, the infant can begin to select appropriate muscle patterns in order to achieve the reaching goal. Finally, reaching must continue to progress through a continuous interaction between the nervous system, the body, and the environment.

How Reaching can Fall to Pieces

Studies on experimental lesions in animals and neurological diseases in animal models and in human patients are often used in the neurosciences to piece together normal functions of the nervous system. The many intricate ways in how the behaviour - skilled reaching in this case - can fall to pieces depends on various dysfunctions and losses within the nervous system. Two examples follow. First, lesions to the dorsal visual stream leaves the mover in a state of action blindness, where they can see and perceive objects, but will reach and grasp them as though they are blind [Goodale & Milner, 2004]. Second, although people with Parkinson's disease, a disorder of the basal ganglia,[24] display certain deficits in the details of reaching and grasping [e.g., limited rotatory limb movements], the way that movements are organized for reaching reconfigure to become proximally, rather than distally, driven [Whishaw et al., 2002].

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[24] The symptoms of Parkinson's disease, primarily defined by tremors and slowness of movement, are caused by the progressive depletion of dopaminergic cells in the substantia nigra [Kandel et al., 2000].

The effects of stroke on reaching are diverse in severity and type of motor changes. This is due to location and size of lesion[s], and probably to some extent, experience prior to affliction. Upper limb function is often studied in stroke subjects either for the purpose of rehabilitation or for gaining further understanding in the neural control of limb movements in humans. Most lesions affecting movement occur contralaterally and result in paresis, general lack of coordination, loss of synergistic joint movements, and loss of the independent digit control. The exact nature of each of these symptoms [e.g., loss of shoulder versus elbow synergistic movements] depends on the changes in the neural organization for voluntary movements. The problem is that most studies on stroke subjects define the experimental group by gross motor symptoms. Defining criteria may depend on the display of hemiparesis, or whether lesions are cortical versus subcortical. Naturally, a great deal of information is lost this way – a problem that is addressed in this thesis.

Methods of Movement Observation

Two forms of hand written movement notation were used throughout this thesis, Eshkol-Wachman Movement Notation [EWMN] and Laban Movement Analysis [LMA]. Although there is overlap in what the notation systems describe, each one offers a unique lens. In each form of movement analysis, different characteristics of movement are emphasized. Therefore, using a combination of notation systems increases the level of analysis. Both systems can either provide a *shorthand* form of notation that captures essential aspects of the performed movement, or a highly detailed notation with which a reader can fully re-enact the sequence without ever having seen it performed.

Eshkol-Wachman Movement Notation [EWMN]

EWMN is a form of movement analysis developed by choreographer Noa Eshkol and architect Abraham Wachman [1958]. EWMN describes the spatial-temporal components of movement made by the body. The body is defined as a system of articulated axes [i.e., body and limb segments]. A limb segment is any part of the body that either lies between two joints or has a joint and a free extremity. These are imagined as straight lines [axes], of constant length, which move with one end fixed to the centre of a sphere [Figure 1.3]. Based on this system, there are three types of movement - planar, rotatory, and conical – all of which are described by magnitude of size, spatial orientation, and direction [Figure 1.4]. EWMN provides quantitative measures of the angles, as well as the temporal relationship, between limb segments. Changes in relationships between body segments within the context of other still and moving body parts, and to the stationary or changing environment - including ever-changing relationships with other movers, are described [Eshkol & Wachman, 1958].

By expressing the relations and changes of relations between limb segments in different coordinates, EWMN may describe invariances in the motor behaviour in relation to some or all of the following: 1. the subject's longitudinal axis, 2. gravity, or 3. the next proximal or distal segment. For further descriptions of EWMN, see Eshkol & Wachman, 1958; Golani, 1976;[25] Pellis, 1981;[26] 1982; 1983; Teitelbaum, Benton, Shah, Prince, Kelly & Teitelbaum, 2004; Teitelbaum, Teitelbaum, Fryman & Maurer, 2002; Teitelbaum, Benton, Shah, Prince, Kelly & Teitelbaum, 2004; Whishaw, Dringenberg & Pellis, 1992; Whishaw &

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[25] Seminal paper introducing EWMN to ethology [see http://biology.mcgill.ca/perspage/ew_page.htm].

[26] First use of EWMN in non-mammalian species [see http://biology.mcgill.ca/perspage/ew_page.htm].

Pellis, 1990; and Whishaw et al., 2002. EWMN has been used in scientific research for the study of human movement [Teitelbaum, Teitelbaum, Nye, Fryman & Maurer, 1998; Teitelbaum et al., 2002; 2004; Whishaw et al., 2002] and non-human animal behavior [Golani, Bronchti, Moualem & Teitelbaum, 1981; Fentress, 1973; Golani & Fentress, 1985; Pellis, 1981; 1982; 1983; 1989; Whishaw, Pellis & Gorny, 1992a; Whishaw, Pellis, Gorny & Pellis, 1991]. Through the use of EWMN, human patients have been described as using more proximal, rather than distal, muscle groups to move limb segments in Parkinson's disease [Whishaw et al., 2002] and in children with autism [Teitelbaum et al., 2002] and Asperger's syndrome [Teitelbaum et al., 2004]. Furthermore, the use of EWMN in the study of animal behaviour has revealed behavioural patterns that have slipped through the cracks of traditional measures [e.g., Eilam & Golani, 1988; 1989; Pellis & Officer, 1987; Pellis & Pellis, 1987; Pasztor, Smith, MacDonald, Michener & Pellis, 2001; Whishaw & Pellis, 1990].

Although EWMN provides a description for the structural components of movement, there are other aspects of movement that must be considered. For example, two people can grab someone by the shoulders by using the same timing, arrangement of body limbs, and biomechanics; but one can do it aggressively, and the other can do it romantically, what is the difference? Laban Movement Analysis [LMA] describes both structural and expressional components of human movement [Laban, 1960; Hutchinson, 1977], with a focal observation on the process of the movement, which provides the observer with the tools to distinguish the difference.

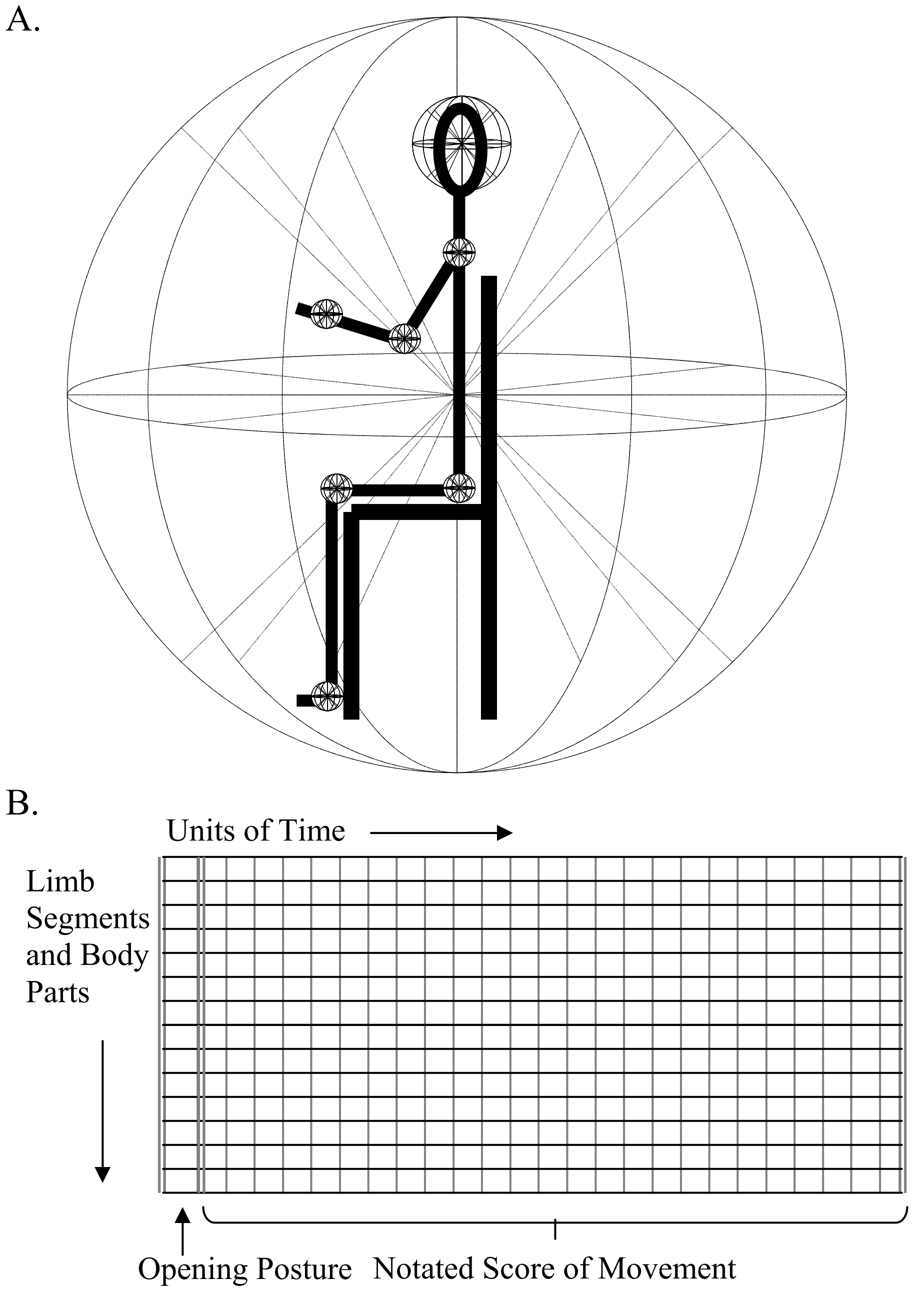

Figure 1.3 Eshkol-Wachman Movement Notation. A] The Sphere as the System of Reference. Vertical and horizontal coordinates on the sphere are used to define location. The sphere defines the space around the subject and defines the topographical locations on the surface of the body and body parts. Each limb segment moves with one end fixed to the centre of a sphere. B] Manuscript Page used for Notation Scores. In the notation, the body is represented on a horizontally ruled page. Each horizontal space represents a part of the body. Vertical lines divide the manuscript page into columns that denote units of time [or video frames].

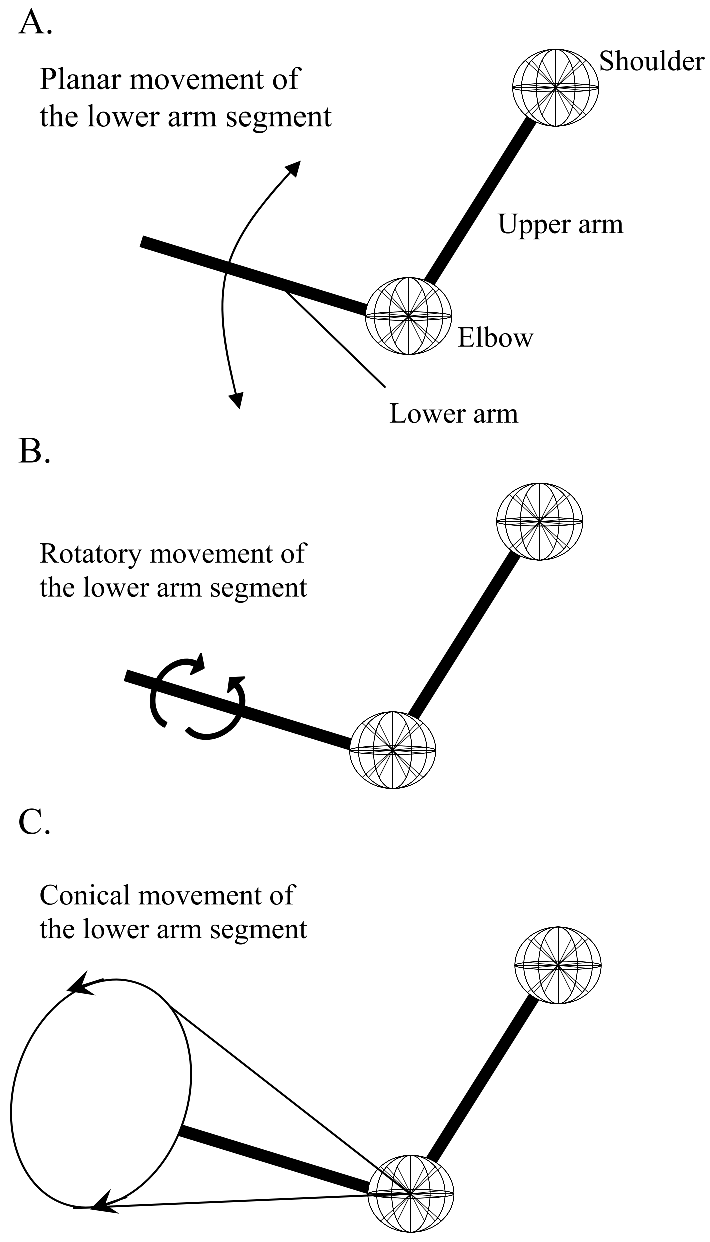

Figure 1.4 Types of Movement Defined by EWMN. A] Planar Movements are when ‘the angle between the axis of movement and the axis of the limb is 90 degrees. The path of movement of the limb’s axis then has the form of a plane surface.’ B] Rotatory Movements are when ‘the angle of movement is 0 degrees. The axis of the limb coincides with the axis of movement…. When the angle between the axes is zero [i.e. they coincide], no surface is created by movement of the axis of limb, which simply rotates about itself.’ and C] Conical Movements are movements ‘in which the angle of movement is greater than zero and less than 90 degrees, so that the resulting path has a conical shape.’ [Eshkol & Wachman, 1958].

Laban Movement Analysis [LMA]

LMA is a language that provides a system of observation and notation for human movement that focuses on *how,* rather than *what*, movements are performed. Rudolf Laban [1879-1958] integrated concepts from biology, physics, the spatial concepts of architecture, dance and other expressive arts to develop theories on the structure of the human form, the qualities the body accesses to perform the movement, and human movement itself. A long time colleague, Irmgard Bartenieff, described Laban as someone who:

> '…observed movement process in all aspects of life: from the martial arts to spatial patterns in Sufi rug weaving, factory work tasks, rhythmic patterns in folk dances, crafts, and the behaviour of emotionally disturbed people. It was the process itself that compelled his attention, not just the end points or goals of the action, and he, with his colleagues, refined movement observations into an exquisitely precise method of experience, seeing, and recording them so that body movement functional and expressive implications became increasingly apparent.' [Bartenieff & Lewis, 1980].

Laban worked with dancers to explore his understanding of human movement and developed *movement scales* and exercises. People called on Laban and his expertise to designate factory workers to stations that would suit their individual body structures and *movement signatures* so that they would be able to work more efficiently and with less injury. Today, LMA is used primarily for recording the great classical ballets and other historically valuable choreographies. Modern choreographers still draw upon Laban's theories to create their own dances and train their performers. There are many offshoots of LMA that are primarily used in the arts, humanities, and various forms of physical therapies.

Fagen, an ethologist known for his studies on play behaviour in animals developed an interest in the use of LMA to classify animal movements. He tested for and found a high inter-observer reliability of Effort analysis, one of the major four components of LMA [Fagen, Conitz & Kunibe, 1997].[27] Since then, I have used LMA in studies of play fighting in rats [Foroud & Pellis, 2003;[28] Foroud, Whishaw & Pellis, 2004], mounting behaviour in Japanese macaques [Vasey, Foroud, Duckworth & Kovacovsky, 2006], and even skilled reaching in rats [Whishaw, Gorny, Foroud & Kleim, 2003; Alveradashvili, Foroud, Lim & Whishaw, 2008], vervet monkeys [Foroud, unpublished work[29]] and humans [Foroud & Whishaw, 2006]. The details of LMA are explained in Chapter 2.

The Bartenieff Fundamentals

After many years of collaboration with Laban, Bartenieff [1890-1981] left Europe to work with polio patients in New York, where she established the Laban/Bartenieff Institute of Movement Studies [LIMS].[30] She found that recovery of movement was greater after having had patients move their own bodies, even if the movement was so minute that it remained invisible to the observing eye, than when nurses therapeutically moved the patient's immobile limbs for them. Through this work, Bartenieff established a set of movement exercises for the recovery and development of movement called the Bartenieff Fundamentals [BF]. Her theories are applied to the study of movement in anthropology and child development. The BFs are used by dancers for self-development, postural and

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[27] The first publication in ethology describing LMA.

[28] The first use of LMA for describing behaviour in the behavioural neurosciences.

[29] In collaboration with Aurelio Campos at the Departamento de Fisiologia, Faculdad de Medicina, Universidad Nacional Autonoma de México, J. Fernandez lab.

[30] Established in 1978, the Laban/Bartenieff Institute of Movement Studies [LIMS] is the centre for movement studies dedicated to the exploration and study of movement through the foundational work and teachings of Rudolf Laban and Irmgard Bartenieff. See www.limsonline.org for more information.

alignment training during action and recovery after injury, as it is a method that integrates isolated body movements with whole body movement [e.g., isolated movements of the pelvis during walking, turning, jumping etc.]. Today, Bartenieff is considered a pioneer in physiotherapy and dance/movement therapy [DMT].[31] Principles from her work were drawn upon in observations made throughout the present thesis, as well as in the creation of a movement therapy program for one stroke subject [a pilot study described in Chapter 7].

Thesis Part I: Reaching after Stroke

For decades now, stroke has consistently been a leading cause of motor deficits in adults [Jang, 2007]. The majority of the deficits occur in the upper extremities where they are usually both more severe and disabling than deficits in the lower extremities [Cirstea & Levin, 2000; Levin, 1996a]. As suggested above, the comparative study of skilled movement on various lesion sites in human subjects can offer a wealth of information for the neural organization of skilled reaching. Common effects of stroke on the motor system include high/low muscle tone [spasticity], hemiplegia/paresis [weakness/paralysis on one side of the body], neglect, and ataxia [uncoordinated movement] [Bourbonnais & Vanden Noven, 1989]. The long-term effects of stroke vary, depending on the lesion location and size as well as the patient's previous life experience.

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[31] Born out of dance, occupational and physical therapy, and clinical and research psychology, the basic principle of Dance/Movement Therapy [DMT] is that the unity of body and mind is embodied through movement. The DMT idea is that through movement, one can express, learn, communicate, and release emotions, thoughts, and ideas. Our bodies carry our mental, emotional and physical injuries and it is through the body that an individual can heal in all aspects of the self. The American Dance Therapy Association defines DMT as: '*the psychotherapeutic use of movement as a process which furthers the emotional, cognitive, social and physical integration of the individual.*' www.adta.org

The purpose of the first section of this thesis is to explain the use of stroke as a comparative model to assess changes in skilled reaching upon varying lesions in humans. The thesis begins with two case studies that provide detailed descriptions of movements in two stroke subjects, one with mild, and one with severe motor symptoms. Information gathered from these initial notations were then compiled into a rating scale for skilled reaching in stroke subjects [Chapter 2]. The scale is applied to a group of stroke subjects with varying lesions and motor symptoms [Chapter 3]. Finally, a comparative analysis between individual stroke subjects is made [Chapter 4].

Thesis Part II: Early Ontogeny of Reaching

The purpose of the second section of this thesis is to gleam an understanding of how reaching develops. In order to find out how something works, or how it can fall to pieces, we need to understand how it develops in the first place. This principle of investigation has been studied in several behaviours including righting [Pellis, 1996], exploration [Golani, Bronchti, Moualem & Teitelbaum, 1981], and feeding [Teitelbaum, Cheng & Rozin, 1969a; b; Teitelbaum, 1971].

Infants are born with the grasping reflex where the entire hand closes upon stimulus. In terms of hand movements and finger individuation, Schieber and Santello [2004] have shown that grasping movements are foundational whereupon individual movements between the fingers become superimposed. Martin and colleagues [1982] suggest that infants are born with clear somatotopic organization as they have shown that the boundaries in somatotopic organization become blurred with experience. By approximately two to three months, infants are capable of voluntary grasping. By ten to twelve months, the ability to articulate thumb opposition and finger individuation emerge. Increasing coordination between the fingers and the temporal patterns between hand shaping and limb reaching takes approximately the first decade to achieve [Schieber & Santello, 2004].

Most studies of reaching in infants begin when the child is capable of performing the task [approximately sixteen weeks of age]. The present developmental study examines infants as early as four weeks and follows their progression until the infant is capable of completing the task - skilled reaching - so much so, that their interest in the act of reaching [which appeared at first to intrigue them in itself] seems to be faded. By this stage, it has become part of their daily activities - taken for granted as in adulthood. Infants were videotaped upon presentation of a motivational stimulus [one of the toys they often look at or chew on]. Videotaping began as early as four weeks, when reaching is not functional, or obvious, and continued weekly for the following five months, then monthly, until nine months of age [Chapter 5].

Thesis Part III: Ontogenetic Movement Patterns for Reaching after Stroke

One way of better understanding how movement falls apart in adulthood due to injury or disease is to compare recovery with development. This work has been done at the cellular level. Though cortical plasticity is at its peak during development, it also occurs normally during adulthood and is briefly heightened after cortical injury [Cramer & Chopp, 2000]. Cellular reorganization is known to occur during recovery of function after stroke [Butefisch, 2004; Caramia, Palmieri, Giacomini, Iani, Dally & Silvestrini, 2000; Castro, 1990; Hlustik, Solodkin, Guillapalli, Noll & Small, 2001; Kleim, Barbay, Cooper, Hogg, Riedel, Remple & Nudo, 2002; Morecraft, Herrick, Stilwell-Morecraft, Louie, Schroede, Ottenbacken & Schoolfield, 2002; Muller, Watson, Muzik & Chugani, 1998; Nudo & Milliken 1996; Rauschecker, 2002]. After his own stroke, Brodal [1973] wrote '…intact fibers take over for damaged ones.' Today, evidence supports Brodal's hypothesis. For example, cortical areas normally representing the face are involved during finger movements made by a person recovering from stroke [Weiller, Ramsay, Wise, Friston & Frackowiak, 1993]. Furthermore, as recovery in the affected hand improves in stroke patients, mild deficits in the unaffected hand emerge [Cramer, Nelles, Benson, Kaplan, Parker, Kwong, Kennedy, Finklestein & Rosen, 1997].

The cellular changes occurring during recovery are similar to those of development. After a stroke, there is an increase in developmental proteins that are linked with plasticity in glial structure, neuronal growth, angiogenesis, and cellular differentiation. There is also an increase in synapse number followed by a period of pruning, a series of events seen during development [Cramer & Chopp, 2000]. A similar pattern of recovery recapitulating ontogeny has been observed in certain behaviours such as locomotion in monkeys [Hines, 1942], feeding and drinking in rats [Teitelbaum et al., 1969a; b; Teitelbaum, 1971], limb placement in cats [Teitelbaum, 1980], and postural reflexes [Teitelbaum, Wolgin, DeRyck & Marin, 1976] and righting movements in mammals [Pellis, 1996]. With respect to reaching, the only example to date is in the acceleration of movement. In the healthy adult, the acceleration of movement is discontinuous, however, in infants, it develops gradually, with a series of smaller movements that make up a bigger one. Larger amplitudes in movement are achieved with age and movement acceleration becomes discontinuous [von Hofsten, 1979]. This progression gradually disassembles in Parkinson's patients as the disease progresses [Georgopoulos, 1986]. The question is how does the developmental pattern of skilled reaching appear in adults after brain damage that has caused impairments in reaching? Though cellular changes occur in similar ways after injury as they do in development, the context in which the changes are made differs greatly. A fully developed adult brain with a lesion[s] is completely different to an infant brain that has yet to manifest. The experiences, in the adult, prior to a lesion, are incomparable to those of a newborn infant and developing child. With stroke, the adult loses function as correlated neural connections that have previously been established change. In development, the infant is in the process of gaining function as neural connections are continually interacting with the accumulation of day-to-day experiences. Do you remember what it is like to see, touch, smell, and taste a rose, not to mention its thorns, for the first time? Imagine that is what your world is like all day, every day. It is no trivial matter to lose previously acquired abilities and to develop from what has remained. The purpose of the third section of this thesis is to compare the new measures for the behaviour skilled reaching that have been derived from the developmental study in Part II, to the stroke subjects initially assessed in the Part I of the thesis [Chapter 6]. Perhaps, in the future, this new information can be used to maximize functional cortical plasticity during rehabilitation after stroke.

Through the course of investigations on skilled reaching in stroke subjects, infants, and back to stroke subjects, a series of behavioural parameters for the organization of the behaviour have been identified. The first step, however, involved using LMA to define the movements for skilled reaching after stroke. Skilled reaching can be characterized by natural divisions - or phases - in movement, where each phase can be divided into finer and finer motor characteristics. Parameters for the organization of skilled reaching identified in the following study involve the inhibition of non-kinematic aspects of movement, such as intensity and shape, and are described for the first time in the following chapter.[32]

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[32] Each chapter in this thesis is written in a format that allows for reading independent of the rest of the thesis.

PART I

REACHING AFTER STROKE

I see no irreconcilable conflict between artist and researcher at this level of study. Whether it is a ritual dance, an intricate skill, an expressive gesture, movement may be perceived and systematically described in its own terms. Accurate perception and description of movement is the common ground… whether it becomes the inspiration for choreography or teaching, or the data for research.

Irmgard Bartenieff
www.adta.org

CHAPTER 2

Changes in the Kinematic Structure and Non-Kinematic Features of Movements during Skilled Reaching after Stroke:

A Laban Movement Analysis in Two Case Studies.[33]

ABSTRACT

The purpose of this study was to adapt a universal language for human movement, Laban Movement Analysis [LMA], to capture the kinematic and non-kinematic aspects of movement in a skilled reaching to eat task by subjects whose movements had been affected by stroke. Two control subjects, one stroke subject with internal capsule damage, and one subject with right posterior parietal stroke were video recorded while performing the reaching task. The movements of limb advancement, grasping the food, and limb withdrawal to place the food in the mouth, were notated using LMA. A scale, the Expressive Reaching Scale [ERS], was derived from the notation. All subjects completed the task; however, the stroke subjects displayed abnormalities in both the kinematic and non-kinematic aspects of movements during reaching with either limb. The most extensive impairments were in the contralateral-to-stroke limb and were most severe in the subject with internal capsule damage. The ERS rating scale may be a useful diagnosis and assessment tool.

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[33] This chapter is modified from Foroud A, & Whishaw IQ. [2006]. *Journal of Neuroscience Methods, 158:137-149.*

INTRODUCTION

Classification and diagnosis of motor disorders are based on experimental and clinical observations. For example, depending on the type of lesion, stroke can impair movements of the upper limb in reaching and grasping. The change in limb function can be measured in many ways, including end point measures such as success [Farr & Whishaw, 2002], computerized kinematic analyses [Cirstea, Mitnitski, Feldman & Levin, 2003; Platz, Bock & Prass, 2001; Trombly, 1992], through measures of muscle activity and synergy [Lang & Schieber, 2004; Micera, Carpaneto, Posteraro, Cenciotti, Popovic & Dario, 2005; Trombly, 1993], applied grip forces [Aruin, 2005; Boissy, Bourbonnais, Carlotti, Gravel & Arsenault, 1999], and standardized rating scales [Levin, Desrosiers, Beauchemis, Bergeron & Rochette, 2004]. The use of biomechanical analyses provides rigorous quantification of movement variables, such as muscle flexion and extension, limb pronation or supination, and coordination, and is a useful tool for clinicians and therapists to diagnose and design therapies for the changes in kinematic motor function after stroke. Nevertheless, there are non-kinematic changes in the movements of patients after stroke such as fatigue, increases in effort required to produce movement, and intrusive movements such as tremors, tics, and gestures that are more difficult to document [Jackson, 1932; Jeanerrod, 1988; Klein, 2005]. An observer may recognize these non-kinematic changes in movement but may find them difficult to quantify.

One method of enhancing the classification of the symptoms of stroke is to use a formal *language* for movement description that captures both the kinematic features of movement as well as the non-kinematic features. Laban Movement Analysis [LMA], derived from the study of dance, is a formal and universal language for human movement [Bartenieff & Lewis, 1980; Dell, 1966; Hutchinson, 1977; Laban, 1960] that has been applied to experimental research [Foroud & Pellis, 2003; Whishaw, Gorny, Foroud & Kleim, 2003; Foroud, Whishaw & Pellis, 2004; Vasey, Foroud, Duckworth & Kovacovsky, 2006]. LMA provides an analysis of both the kinematic and non-kinematic features of movement by categorizing movement descriptions into four components: Body, Effort, Shape, and Space. A full LMA analysis describes how the observed motor action uses the four components of movement, and how each component of movement is related to one another [Bartenieff & Lewis, 1980; Hutchinson, 1977; Foroud & Pellis, 2003; Foroud et al., 2004; Laban, 1960; Vasey et al., 2006; Whishaw et al., 2003]. The kinematic structure of movement is described through Body and Space, which provides a rich description of how the many spatial-temporal body and limb relationships change in relation to one another and to the environment. The emphasis of the Body and Space description is on *how* the changes occur, rather than *what* the changes are - as is the case with traditional kinematic measures. Non-kinematic features of movements are the seemingly qualitative aspects of movement that can be reliably categorized through observation by the study of LMA - Effort and Shape [Bartenieff, 1973; Bartenieff & Davis, 1973; Bartenieff, 1974; Fagen, Conitz & Kunibe, 1997]. Effort and Shape capture the exertion of movement by providing a way of describing changes in the intensity, shape, force, flow and rhythm of movement. These changes are more expressive than changes in the spatial-temporal body relations, described by Body and Space, and can be influenced by many factors including the temperament of the mover, the situation he/she is in, and the environment [Bartenieff & Lewis, 1980]. There are many anecdotal accounts of various non-kinematic changes in the movements of human stroke patients [Trombly, 1992] that remain unclassified and might pass relatively unnoticed in biomechanical analyses. LMA thus potentially provides a useful addition to conventional biomechanical descriptions of movement disorders as it can be used to classify the non-kinematic aspects of movement. At present, there have been no previous attempts to use formal languages to describe upper limb dysfunction in human stroke patients and no previous attempts to describe any neurological disorders using LMA.

The purpose of this study was to use LMA to analyze movements of two stroke subjects during a reaching for food task [Whishaw, Suchowersky, Davis, Sarna, Metz & Pellis, 2002]. The goal in this study is to provide a detailed enough description of skilled reaching after stroke that captures both kinematic and non-kinematic aspects of movement that can later be quantified into a standardized rating scale for use by those unfamiliar with the details of LMA. The comparison of two stroke cases, one mild and one severe, allows detailed movement analysis, which when completed, can be generalized into a standardized rating scale. The derivative rating scale can be used in studies of a single patient, as might occur for occupational therapy, or in conventional research experiments. The first subject in this study suffered from a stroke causing damage to the parietal cortex. This subject was compared to the second stroke subject who suffered from middle cerebral artery stroke that had damaged the internal capsule, as well as to two age-matched controls. Reaching movements were notated using LMA. From the notation, a rating scale called the Expressive Reaching Scale [ERS] was derived. This scale can be used as a diagnostic and assessment tool.

METHODS

Subjects[34]

Subjects included two stroke subjects and two control subjects. All four subjects are right-handed adult males, two of whom were recovering from right hemisphere strokes which caused motor dysfunction on the left side of their bodies. The first stroke subject had damage in the right posterior parietal lobe and the second stroke subject showed damage to the right posterior limb of the internal capsule. At the time of participation in this study, both stroke subjects were at the beginning of their occupational and physiotherapy program as outpatients at the rehabilitation clinic at the local hospital. The remaining two subjects were healthy age-matched controls for each of the stroke subjects.

Parietal Lobe Stroke Subject [PL]

PL is a 59 year-old male who suffered from a stroke causing a lack of coordination of the left arm as well as numbness and weakness in the left arm and leg. CT scans indicated damage in the right superior posterior parietal cortex. At the time of participation in this study, the subject was independent, but was using a walker as a precaution. The control for PL was a right-handed 64 year-old male.

Internal Capsule Stroke Subject [IC]

IC is a 72 year-old male recovering from a stroke that caused left-sided hemiplegia. A MRI showed damage in the posterior limb of the internal capsule. The subject uses a

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[34] All of the subjects for the stroke studies in this thesis provided informed consent to participate in the study. The study was conducted with the approval of the University of Lethbridge Human Subjects Ethics Committee, and the Chinook Health Region.

wheelchair and needs assistance with dressing and other tasks that require the use of both arms and/or legs. The control subject for subject IC was a 72 year-old right-handed male.

Reaching Task

For the reaching task [Whishaw et al., 2002], subjects were asked to reach for a piece of food and place it in their mouth to eat. This is a natural behaviour that is likely used daily by a subject and requires no special learning. The subjects were comfortably seated on a chair with a pedestal on an adjustable post positioned directly in front of them, approximately 10 cm beneath their outstretched palm. A food item was placed on the pedestal. At the beginning of the filming session, each subject was instructed to place both hands on their thighs, with their palms flat. Subsequent instruction consisted simply of telling the subject when to begin and which hand to use. When instructed to begin, a subject was expected to reach for the food item, place it in his mouth for eating, and then return his hand to his thigh. Due to anticipated patient fatigue in the stroke subjects potentially hampering the data collection, subjects were instructed to reach with one hand until two successful trials were completed, and then with the other hand for two successful trials. Subjects were given a choice of one of four food items: Smartie, raisin, gumdrop, or a shelled peanut.

Video Recording

Canon 2R40 Digital Video Camcorders [30 frames/second] were for video recording. One camera was placed in front of the subject so that a whole body view of the subject could be obtained. A second camera was placed in front of the subject and recorded the subject's hand when it grasped the food item on the pedestal. Video was uploaded onto a G4 Macintosh computer and viewed in iMovie for a frame-by-frame analysis.

Procedure

Ipsilateral- and contralateral-to-stroke limbs were compared between stroke subjects and to their matched controls. Data analysis was done using a LMA notation derivative called Motif and a movement rating scale - the Expressive Reaching Scale [ERS] - was derived from the notated scores.

Laban Movement Analysis

LMA was developed for describing the kinematic, or dynamic changes in the structure of movement [Body and Space], such as the changes in the relation of the body segments and spatial pathways or directions, as well as the non-kinematic, or expressive features of movement, such as the intensity, force, and rhythm of specific movements [Bartenieff & Lewis, 1980; Foroud & Pellis, 2003; Foroud et al., 2004; Vasey et al., 2006]. LMA emphasizes the processes underlying motor actions rather than the resultant motor action as the notation, or its shorthand derivative, Motif, records how the four movement components - Body, Effort, Shape and Space [BESS] - are integrated, or not, throughout the observed movements. LMA was used in this study in order to provide an empirically derived description of the kinematic and non-kinematic movements made by stroke subjects during skilled reaching to eat. The reliability of the non-kinematic measures in LMA has been validated in previous studies [Fagen et al., 1997; Foroud et al., 2004]. Detailed descriptions of the components of LMA are described in Bartenieff & Lewis, 1980; Dell, 1977, Hutchinson, 1977 and Maletic, 1987. The following is an abbreviated description of BESS. For clarification, the first letter in LMA terminology is always capitalized.

> **Body** is the architecture defining the alignment relationships between anatomical segments during postural control and movement. The basic components of the body architecture are divided into the Upper [head/neck, chest/upper spine, shoulders/scapulae, arms/forearms/wrists/hands/fingers] and Lower Units [lower back/abdomen, pelvis/hips/thighs/lower legs/feet/toes]. Basic components can be divided in several different ways [e.g., midline, contralateral] according to the style of movement the mover is expressing [Figure 2.1A]. Depending on the way the subject moves, the body can also be expressed by the limbs, limb segments, and/or articulations [Figure 2.1B]. Body movements can also be categorized as Postural or Gestural. Postural movements involve the simultaneous movements of several basic components of the body that result in a shift in the centre of mass. Gestures are single actions involving the torso, head, limb, limb segments, or distal articulations.
>
> **Effort** is the change in the intensity of exertion throughout movement. There are four types of Effort, called Effort Factors, *Weight, Time, Space, and Flow*. Each Effort Factor moves on a continuum moving from the powerful, resisting, fighting end of Condensing Efforts to the gentle, non-resistant, “going with the flow”, Indulging Efforts: *Strong Weight to Light Weight, Quick Time to Sustained Time, Direct Space to Indirect Space, and Bound Flow to Free Flow* [Table 2.1].

A.

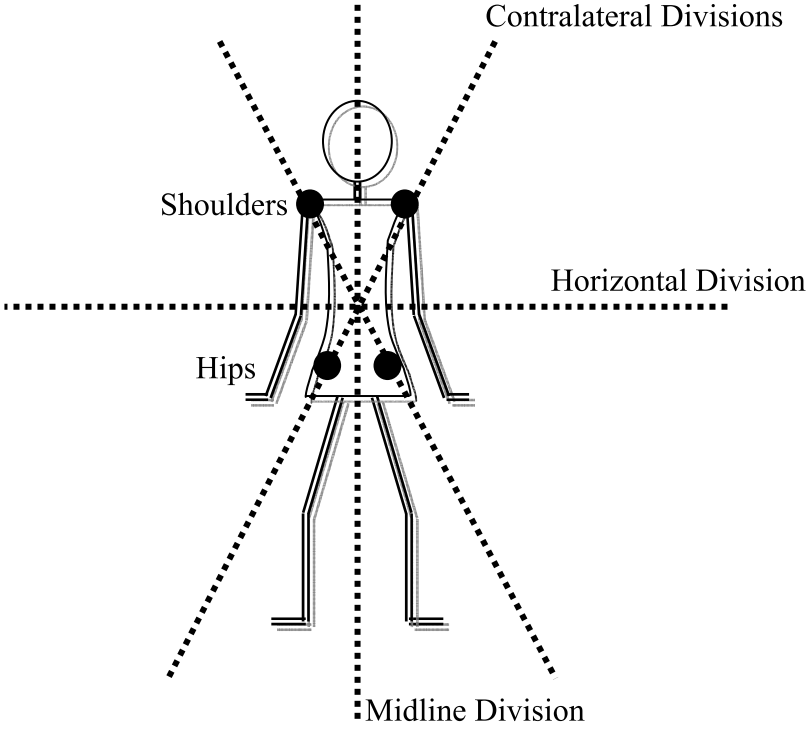


Figure 2.1 A Diagram and LMA Notation Symbol Index of the Descriptors for LMA Body. A] The basic components of the body architecture divided into Upper [head/neck, chest/upper spine, shoulders/scapulae, arms/forearms/wrists/hands/fingers] and Lower Units [lower back/abdomen, pelvis/hips/thighs/lower legs/feet/toes]. Basic components can be divided in several different ways: vertically across the midline, horizontally at the waist, and contralaterally.

B.

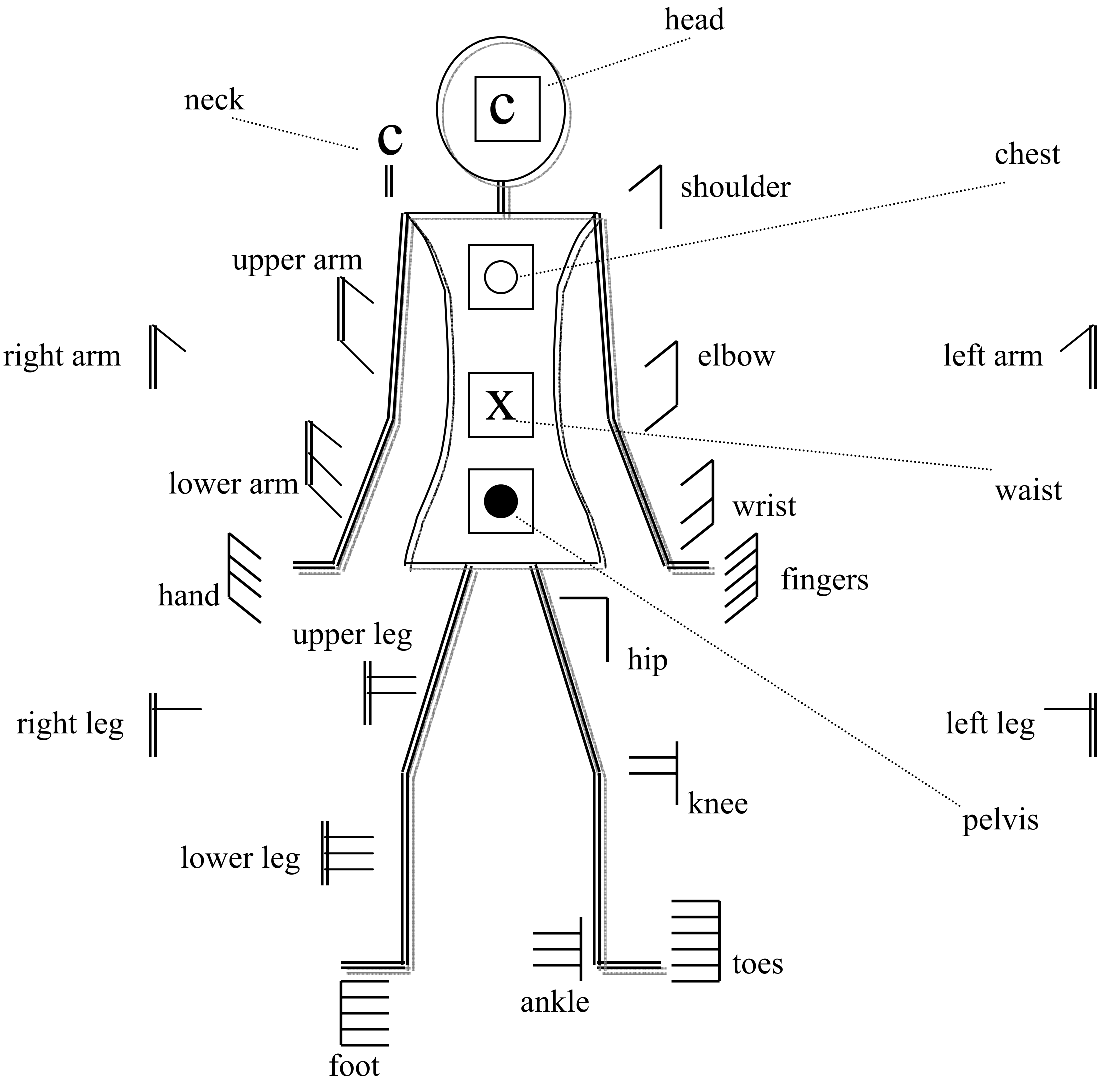


Figure 2.1 [*continued*] B] The classification of the minor components of the body architecture by limbs, limb segments, and/or articulations [e.g., head, shoulder, upper arm etc.] Adapted from Foroud and Whishaw, 2006.

Table 2.1 Effort Factors and the placement of Effort Qualities on the Indulging-Condensing Effort Continuum.

Effort Factors	Effort Qualities	
	Indulging	Condensing
Weight	Light Weight	Strong Weight
Time	Sustained Time	Quick Time
Space	Indirect Space	Direct Space
Flow	Free Flow	Bound Flow

Adapted from Foroud and Pellis, 2003.

Indulging Efforts are not limp or passive movement qualities: they are active qualities that are gentle. Limp or passive movements are not described by Effort analysis, they can be described by an LMA Body analysis as limp and passive movements are defined by the structural body movements' relationship with an external force such as gravity. Although single Efforts can be performed alone, it is very difficult to produce a single Effort. Often Efforts are performed in combinations of two, three, and less often, four. Efforts are traditionally taught by a combination of verbal descriptions and movement experience in a dance studio. Therefore, in order to deepen his/her understanding of each Effort quality, the verbal definitions of the single Efforts, described below, are accompanied with some examples with which the reader [dancer or not] is encouraged to experiment with. An exercise for each Effort quality is also provided. The following definitions and several of the examples are referenced from Bartenieff & Lewis [1980, p. 54-56].

The Weight Effort Factor is about creating impact through movement by changing the force or pressure exerted throughout a movement.

Strong Weight Effort [Condensing] is the increase of force or pressure throughout a movement. Smashing an object with a fist, playing forte on a piano, or beating a rug are some examples of Strong Weight Effort. Exercise: try moving your arm with a vigorous impactful and powerful quality as if the air is so thick you have to push through it.

Light Weight Effort [Indulging] is the release of force, or pressure, throughout a movement. Handling delicate bone china, wiping tears from a child's eyes, or touching a newborn infant's hair are some examples of Light Weight Effort. Exercise: try moving your arm with a delicate and airy quality as if it were a feather floating in the breeze.

The Time Effort Factor is the mover's exertion of velocity throughout an action. Duration of time is irrelevant to Time Effort. That is, both Quick and Sustained Time can be used to make the same gesture in a one-minute time frame; it is the mover's approach on how to use the time throughout the movement that is described by Time Effort.

Quick Time Effort [Condensing] involves acceleration throughout movement. Removing one's hand away from sudden contact with a hot stove, being startled and darting out of someone's way upon running into them from around a corner, or swatting a fly are some examples of Quick Time Effort.

Exercise: try moving your arm with a sudden urgent and hasty quality as if you are catching mosquitoes in your palm.

Sustained Time Effort [Indulging] involves deceleration throughout movement. Embracing a close friend, getting up from a warm chair by the fire, or waving goodbye to a loved one, are some examples of Sustained Time Effort. Exercise: try moving your arm with a lingering quality as if you want to savour every sensation in the action.

The Space Effort is about how the body attends to the space in which it is moving by attending to something specific or to everything at once.

Direct Space Effort [Condensing] is a pinpointed focused attention to the environment throughout a movement. Cracking an egg, plucking an eyebrow, or pointing to a specific target are some examples of Direct Space Effort. Exercise: try moving your arm with a zeroing-in quality as if you are pointing out the needle you spotted in the haystack.

Indirect Space Effort [Indulging] is the multifocused attention to the environment throughout a movement. Folding beaten egg whites, waving flies out of the way, or scanning the parking lot for your car are some examples of Indirect Space Effort. Exercise: try moving your arm with a flexible and allencompassing focus as if you wish to point to everything in the room in one gesture.

The Flow Effort is about the quality of the progressive continuity of one's movement whether it is resisting flux or abandoning oneself to go with it.

Bound Flow Effort [Condensing] is an increase of constraining and restricting tension that is exerted throughout a movement. Arm wrestling with an equal match, walking in a dark and cluttered room, or making a gesture of cautious refusal are some examples of Bound Flow. Exercise: try moving your arm in a restrained way so that you are prepared to stop moving at any moment as if you are trying to control the flow of movement by holding back.

Free Flow Effort [Indulging] is a release of constraining tension throughout a movement. Children playfully tumbling on a trampoline, or swinging a heavy object before releasing it [e.g., javelin] are examples of Free Flow Effort. Exercise: try moving your arm in with a sense of abandonment and easy flowing ready-to-go-at-any-moment way as if you are playfully exaggerating your walk.

Shape is the exertion in the manner in which the body changes in posture to adapt to the surrounding environment throughout a movement. There are three ways in which Shape can change throughout a movement. 1] Directional Shape is the type of shape the body takes along a particular trajectory; 2] Shapeflow is how the body responds to internal and/or external perturbations. Internal perturbations include changes in breath, emotions, and thoughts. External perturbations can be changes in stimuli [e.g., light, sound etc.] and the relationship between self and the people in the environment; 3] Shaping is the qualitative changes in the shape of the body. There are six Shaping Qualities defined in LMA: *Rising, Sinking, Spreading, Enclosing, Advancing, and Retreating*. Shaping Qualities can be performed individually, or in combinations of two or three. Shaping is not equivalent to spatial orientation. For example, **Rising** is the quality of lifting regardless of direction of movement. One can sit down with a Rising Quality. The reader can do this exercise by pretending someone is gently pulling a strand of hair from the top of his/her head as he/she is in the process of moving from a standing position to sitting in a chair. **Sinking**, the opposite of Rising, is the quality of sinking, regardless of direction of movement. A person can walk up a staircase while sinking in the torso, as if someone is pulling down an imaginary string tied to the tip of the tailbone. **Spreading** is the quality of opening or expanding body volume. For example, when simultaneously yawning and stretching, the body expands in a Spreading Quality. **Enclosing**, the opposite of Spreading, is to gather inward. After yawning, the body Encloses. **Advancing** is the quality of approach or progression forward, despite direction of movement. Walking upstream in a rapid shallow creek requires the use of an Advancing quality. **Retreating**, the opposite of Advancing is to withdraw. A cautious or frightened person may step towards the source of fear with a Retreating quality.

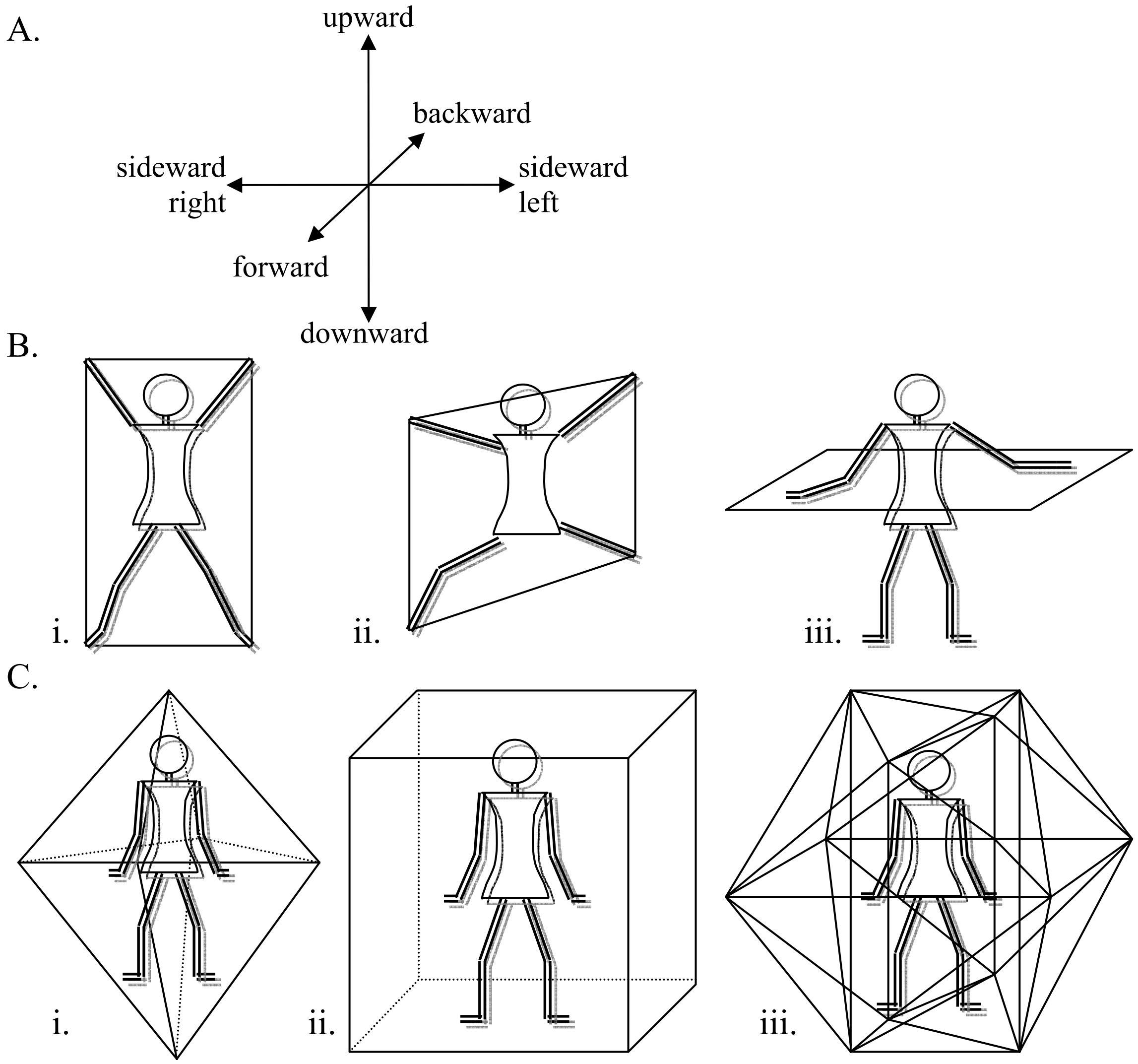


Figure 2.2 Diagrams of some of the Organizational Definitions of LMA Space. A] The Axis Scale constructed from the length, width, and depth of the body represents the six, pure, vertical, horizontal, and longitudinal directions that the body can move through Space. B] The three planes of spatial movement are derived from the axis scale in which each direction in the plane is a combination of two pure directions: i] the Vertical Plane [Upwards + Sidewards right or left, Downwards + Sidewards right or left]; ii] the Sagittal Plane [Upwards + Forwards, Upwards + Backwards, Downwards + Forwards, Downwards + Backwards]; and iii] the Horizontal Plane [Forwards + Sidewards right or left, Downwards + Backwards right or left]. C] Three examples of the geometric shapes that the body can move through Space: i] the Tetrahedron; ii] the Cube; and iii] the Icosahedron. The Tetrahedron is comprised of the three planes, whereas each of the directions in the cube and Icosahedron use a combination of three of the pure directions from the Axis Scale [e.g., the top right hand corner of the Cube is made up of the pure directions: forward + upward + sideward right]. Adapted from Foroud and Whishaw, 2006.

Space is the interaction between the body and the spatial environment. The environment is conceptualized as a geometric space constructed from the length, width, and depth of the body. These dimensions of the body represent the vertical, horizontal, and longitudinal directions the body can move through Space [2.2]. Space considers orientation [where you are in the room], movement trajectories [pathways], and spatial pulls [e.g., two simultaneous spatial pulls during one movement can be Upward and Forward].

Expressive Reaching Scale [ERS]

The ERS is a scale derived from the LMA notations of reaching made in this study [Table 2.2]. This scale is novel to other rating scales used for skilled reaching as it provides a method for quantifying the exertion of the movement by assessing the non-kinematic features of movement that have a more expressive quality than the kinematic structure of movements. The ERS evaluates four phases of the skilled reaching task: Advance, Grasp, Withdrawal, and Release. Each phase is a major motor component that should be performed in one action [gesture] and contains subcomponents resulting in an overall total of 23 subcomponents [Table 2.2]. The 23 subcomponents of the ERS are descriptions of the inappropriate movements that contribute to reaching abnormally. For each subcomponent, an individual can receive a score of 0 [movement description not observed], 0.5 [movement description partially observed], or 1 [movement description fully observed]. A maximum score of 23 points would be a poor performance.

Table 2.2 The Expressive Reaching Scale [ERS]

Expressive Reaching Scale		
Components	Subcomponents	Score
A. Advance	1. Uses more than one gesture	0, 0.5, 1
	2. Limb moved by torso	0, 0.5, 1
	3. Strong Weight Effort observed	0, 0.5, 1
	4. Indirect Space Effort used at the end of the advance	0, 0.5, 1
	5. Direct Space Effort not used at the end of the advance	0, 0.5, 1
	6. Bound Flow Effort observed	0, 0.5, 1
	7. Shaping Qualities observed	0, 0.5, 1
B. Grasp	8. Uses more than one gesture	0, 0.5, 1
	9. Limb moved by torso	0, 0.5, 1
	10. Hand appears to be stuck on the pedestal	0, 0.5, 1
	11. Use of increased use of Bound Flow Effort	0, 0.5, 1
	12. Shaping Qualities observed	0, 0.5, 1
C. Withdrawal	13. Uses more than one gesture	0, 0.5, 1
	14. Limb moved by torso	0, 0.5, 1
	15. Strong Weight Effort observed	0, 0.5, 1
	16. Indirect Space Effort used at the end of the withdrawal	0, 0.5, 1
	17. Bound Flow Effort observed	0, 0.5, 1
	18. Shaping Qualities observed	0, 0.5, 1
E. Release	19. Uses more than one gesture	0, 0.5, 1
	20. Limb moved by torso	0, 0.5, 1
	21. Strong Weight Effort observed	0, 0.5, 1
	22. Bound Flow Effort observed	0, 0.5, 1
	23. Shaping Qualities observed	0, 0.5, 1
		Total = 23

Adapted from Foroud and Whishaw, 2006.

Kinematic Components

Uses more than one Gesture: A gesture is one action made by one limb or one limb segment. A normal reach consists of four phases each to be performed by a single gesture: [A] Advance [arm], [B] Grasp [hand], [C] Withdrawal [arm], and [D] Release [arm]. Any additional gestures made by any body part during these primary gestures receives a score of 1 [Table 2.2, points 1, 8, 13, and 19].

Limb moved by body/torso: The gesture of moving the arm during reaching should be made independently of the torso. Although the torso may make supporting contralateral movements, it should not carry the arm. A score of 1 is given if the subject uses the torso to move the reaching/grasping limb during the [A] Advance, [B] Grasp, [C] Withdrawal, or [D] Release [Table 2.2, points 2, 9, 14, and 20].

Non-Kinematic Components

Hand appears to be stuck on the pedestal: After grasping the target, the hand should lift-up without resistance. Upon grasping, if the hand seems to resist lifting and appears to be too heavy to lift, or stuck on the pedestal, a score of 0.5 is given. If the hand seems to be stuck on the pedestal while the subject seems to be actively [grunting, clenching, flexing, breathing heavily, twisting the body] trying to lift or move the hand away from the pedestal, a score of 1 is given. The length of time it takes to lift the hand after grasping is irrelevant to this component of the rating scale. Instead, it is the effort exerted to lift the hand upon grasping that is to be scored [Table 2.2, point 10].

Efforts: Normal reaching requires the use of Direct Space Effort towards the end of the Advance. A person may use Light Weight or Quick Time Efforts during the Advance or Withdrawal phases to increase the smoothness of the behavior. Other than Direct Space, the following Effort Qualities can hinder the performance of the task.

Strong Weight Effort [Condensing] is the increase of pressure throughout a movement. A score of 1 is given if the subject uses Strong Weight during the [A] Advance, or [C] Withdrawal [Table 2.2, points 3, 15 and 21]. If the subject is using Strong Weight Effort, it will look like he/she is pushing or lifting something heavy.

Indirect Space Effort [Indulging] is the multifocused attention to the environment throughout a movement. A score of 1 is given if Indirect Space is observed during the [A] Advance, or [C] Withdrawal [Table 2.2, points 4 and 16]**.** If Indirect Space Effort is used, it will look as though the subject is moving his/her arm in the dark towards an object in which the approximate position in space is known.

Direct Space Effort [Condensing] is a pinpointed focused attention to the environment throughout a movement. A score of 1 is given if Direct Space is NOT used toward the end of the [A] Advance [Table 2.2, point 5]. If the subject is using Direct Space Effort, it will appear that his/her arm aims clearly towards the target throughout the movement.

Bound Flow Effort [Condensing] is an increase of constraining and restricting tension that is exerted throughout a movement. A score of 1 is given if the subject uses Bound Flow during the [A] Advance, [B] Grasp, or [C] Withdrawal [Table 2.2, points 6, 11, 17 and 22]. If Bound Flow Effort is used, it will look like the subject is resisting the movement – as though his/her body/arm is being held back.

Shaping Qualities: A score of 1 is given if the subject uses any one or combination of Shaping Quality[ies] with the torso during any phase of the reach [Table 2.2, points 7, 12, 18 and 23]. If Rising and/or Sinking Qualities are used, the subject may look like he/she is trying to lift and/or is slumping the body. If Spreading and/or Enclosing Shaping Qualities are used, the subject may look like he/she is moving in a writhing or contorted way. If Advancing and/or Retreating Qualities are used, it may look like the subject's torso is being pulled forward or backward.

RESULTS

All control and stroke subjects were able to complete the reach successfully by picking up the food item and placing it in their mouths. Furthermore, all subjects except for IC, successfully completed the task on every trial. IC also completed the task on every trial when reaching with his ipsilateral-to-stroke arm, although when reaching with his contralateral-to-stroke arm, IC failed at several attempts. The control subjects showed individual differences in some fine aspects of their movement, but the majority of the motor components of the task were similarly performed. Both PL and IC showed a variety of abnormal movements when reaching with either their ipsilateral- or contralateral-to-stroke arms. The severity of motor symptoms was greater in their contralateral arms. IC displayed the greatest severity and it took several more attempts for IC to complete two successful reaches with the contralateral-to-stroke arm. He completed the task successfully on his fourth and seventh trial. On his first trial, IC rested with his reaching arm on his lap after grasping the target and used his other hand [ipsilateral] to reposition the target in the reaching hand before bringing the target successfully to his mouth. He dropped the target upon grasping it on his second and fifth trials, and he dropped the target at his mouth on his third and sixth trial. Figure 2.3 provides an example of the Motif scores of the reaching task performance from this study.

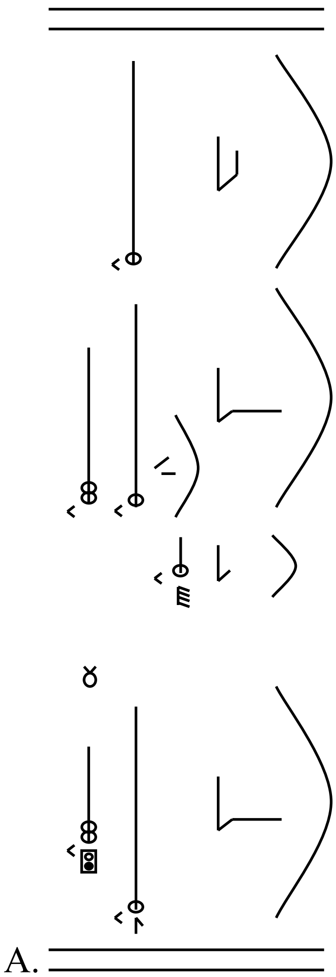


Figure 2.3 Notated Scores of Skilled Reaching in One Control Subject and Two Stroke Subjects. A] Reaching with the right arm in one control subject, B] subject PL reaching with the right arm and C] with the left arm, D]. subject IC reaching with the right arm and E] with the left arm. The notated scores are shorthand LMA notations, called Motif, that are written, and read, from the bottom up. The double horizontal lines drawn at the bottom and top of the Motif indicate the beginning and end of the behaviour. In a case where the description for the behaviour is too long for one column, single bar lines are drawn at the top of the first column and at the bottom and top of the following columns, until the final column, where a double bar line at the top indicates the end of the behaviour. Sub-columns toward the left notate the dynamic structure of movement and correspond to the sub-columns towards the right that notate the expressive features of movement. The left outermost sub-columns describe whole

body postural movements, the next sub-column describes the movements of the torso, the next sub-column describes gestural movements of the hand, then the head, then Efforts, and finally, the right outermost sub-column describes Shape [only Motif scores B, D, and E have a column for Shape]. Time duration is depicted in the sub-columns by the length of the symbols. A person without training in LMA can observe that the notated scores are different one from another. A rating scale, the ERS [Table 2.2], was created based on the differences described in these notated scores, in order to provide a method for quantifying the differences described, that can be used by someone who is not trained in, or does not read, LMA or Motif. See Appendix 1 for detailed descriptions of the Motifs.

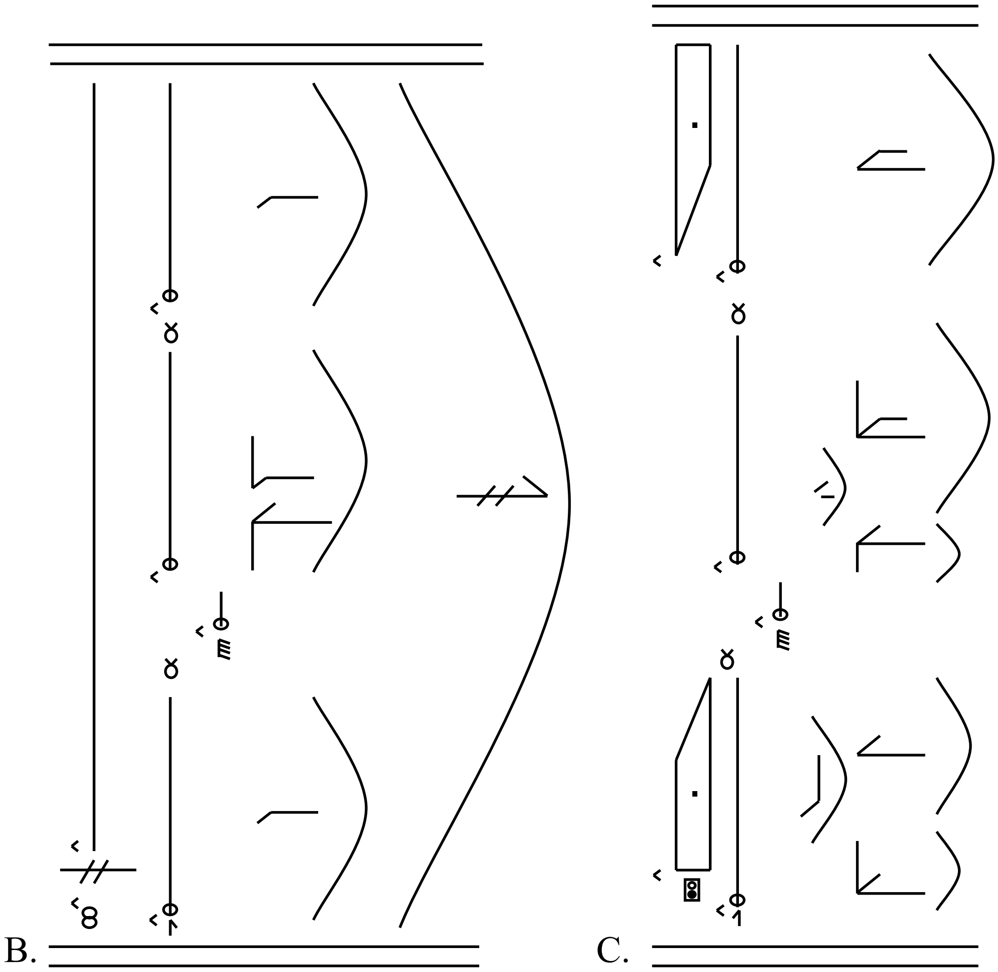


Figure 2.3 [*continued*] B] Subject PL Reaching with the Right Arm. C. Subject PL Reaching with the Left Arm.

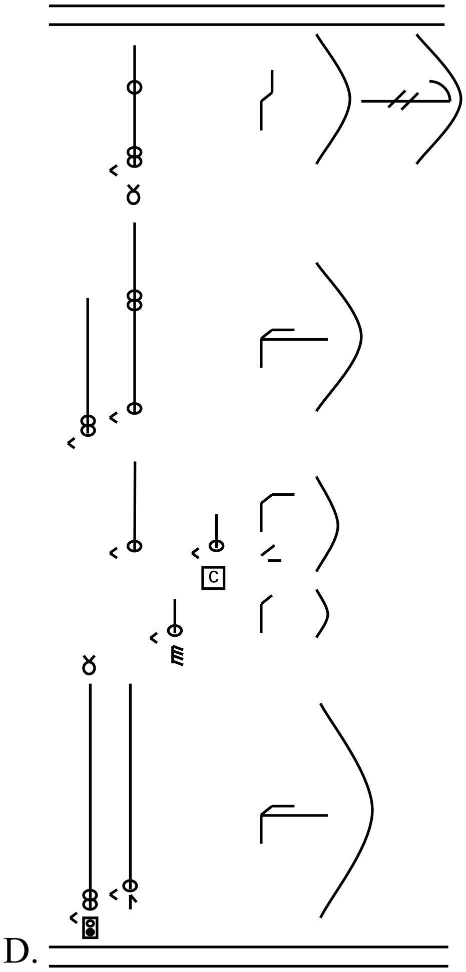


Figure 2.3 [*continued*] D] Subject IC Reaching with the Right Arm.

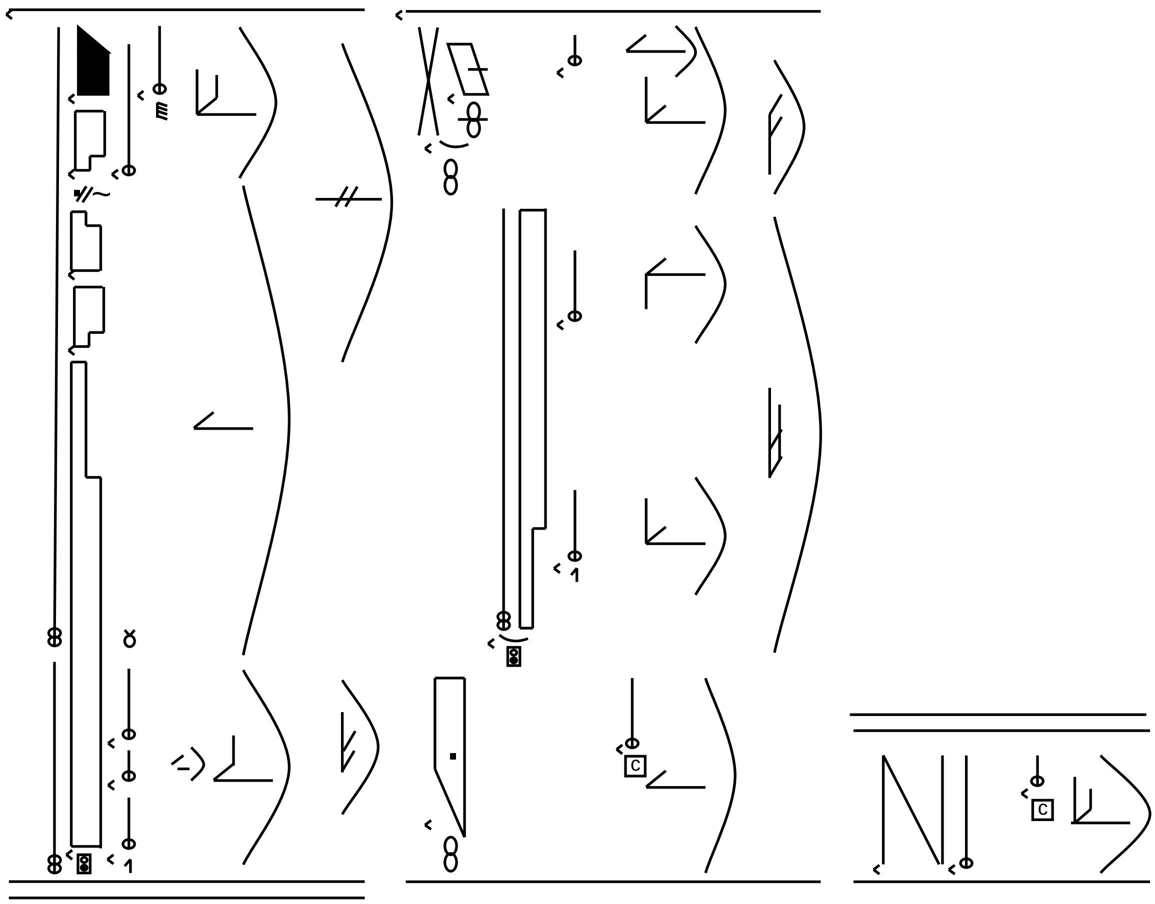
E. 

Figure 2.3 [*continued*] E] Subject IC Reaching with the Left Arm. The Motif shows that, when reaching with the left arm, IC makes more movements, involves more of his body, and uses more types of expressive movements than all other subjects.

Expressive Reaching Scale [ERS]

Three of the four subjects scored above the perfect score of 0 on the ERS. The control for PL had a mean of 1 with the right arm and a mean of 1.5 out of 23 with the left arm [Figure 2.4]. When reaching with either arm, he used some non-kinematic movements [Efforts] that are inappropriate for the reaching task during the Advance and Withdrawal portions of the reach. The control for IC scored 0 out of 23 with either arm, therefore showing no errors on the ERS [2.4].

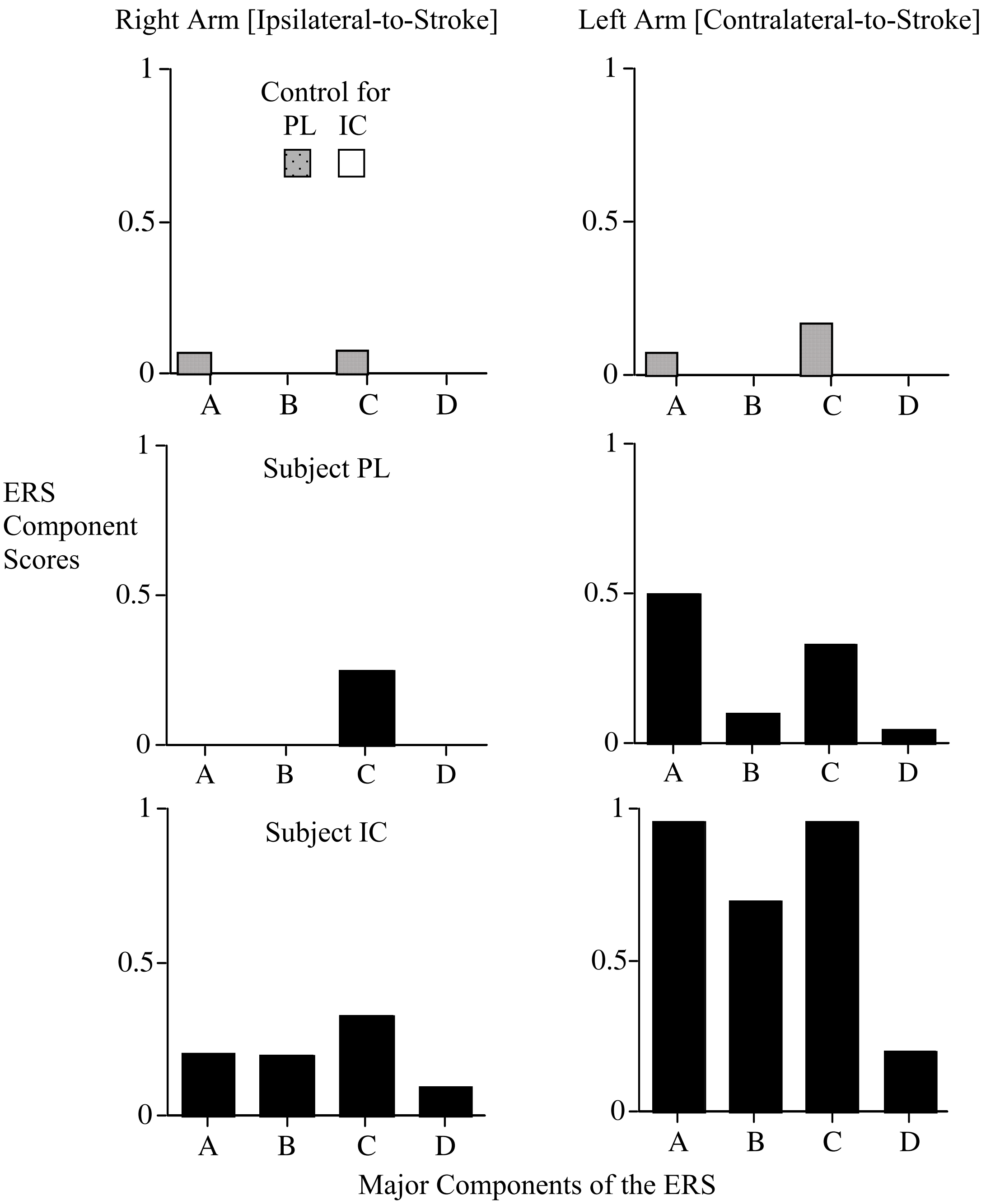


Figure 2.4 Subjects' Scores from the Four Major Components of the ERS, **A.** Advance, **B.** Grasp, **C.** Withdrawal, and **D.** Release, on the Expressive Reaching Scale [ERS]. Component scores are depicted on the y-axis in all the graphs. The graphs in the first column represent scores from the right [ipsilateral-to-stroke] limb and the graphs in the second column represent the scores from the left [ipsilateral-to-stroke] limb. Figures in the top row show results from the control subjects, the middle row, results from Subject PL, and the bottom row, results from Subject IC. Adapted from Foroud and Whishaw, 2006.

PL scored a total of 1.5, when reaching with the ipsilateral arm. When reaching with the contralateral arm, he scored a total of 6.25, showing the use of both kinematic and non-kinematic movements that are inappropriate for the reaching task during the Advance, Grasp, Withdrawal and Release components of the ERS [Figure 2.4]. IC scored a total of 5 with the ipsilateral arm showing the use of both kinematic and non-kinematic movements that are inappropriate for the reaching task in every component of the scale. When reaching with his contralateral-to-stroke arm, IC scored a total of 17 and showed greater differences in his use of inappropriate kinematic and non-kinematic movements for the reaching task during the Advance, Grasp, Withdrawal, and Release components of the scale on successful reaches [Figure 2.4]. The ERS was also used to analyze two unsuccessful reaching trials and one incomplete reaching trial by IC when reaching with his contralateral-to-stroke arm. On the two unsuccessful trials scored, IC completed every portion of the reach, but used either his right [ipsilateral-to-stroke] arm to adjust his grasp of the target, or lost the food target when it was near his mouth. The average score on the ERS on these two trials was 17.75. On the incomplete trial that was scored, IC dropped the target upon grasping it, and so, rather than completing the task, he returned his reaching arm to the starting position. Therefore, the Withdrawal component of the ERS was not applicable as IC did not perform it. On this incomplete trial, IC received a score of 10 out of 17 applicable potential points. Figure 2.5 summarizes overall scores and compares the kinematic versus non-kinematic impairments captured by the ERS. In all cases, the non-kinematic impairments are higher than the kinematic ones.

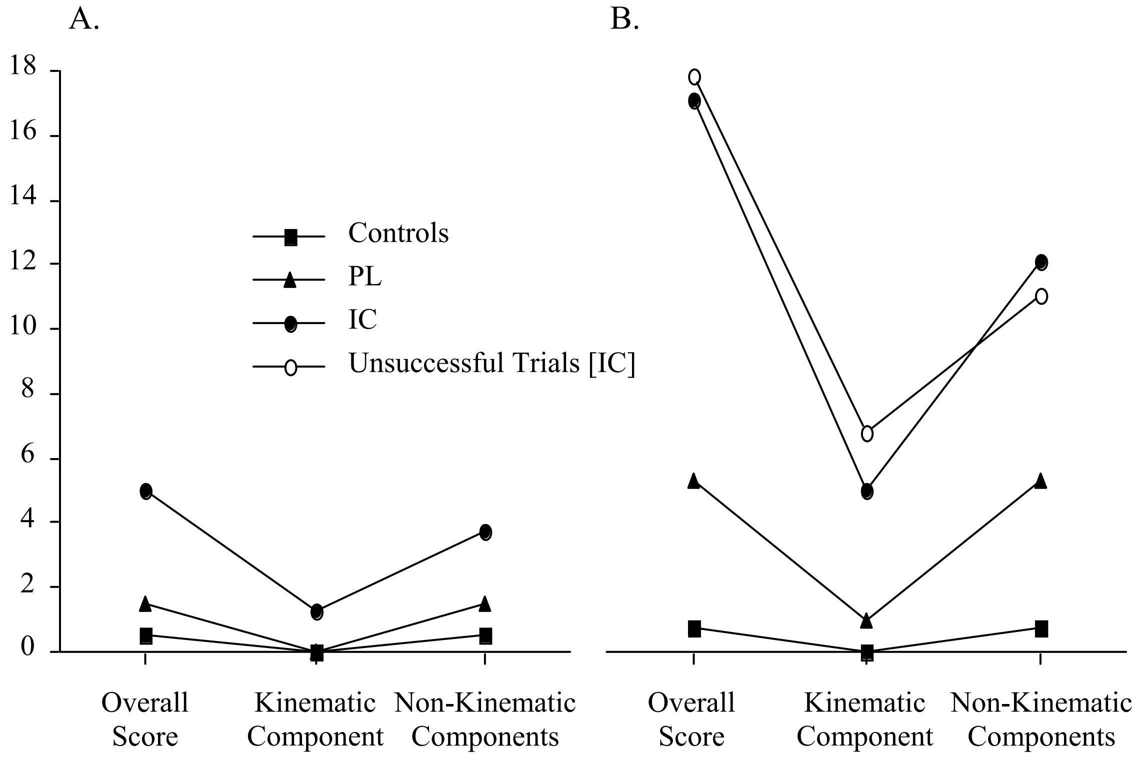


Figure 2.5 Summary of Overall, Kinematic, and Non-Kinematic Scores on the ERS. Score values are represented on the y-axis. The maximum overall score is 23, with a maximum possible score of 8 in the kinematic subcomponents, and 15 in the non-kinematic subcomponents. A] Reaching with the ipsilateral–to-stroke [right] arm B] Reaching with the contralateral-to-stroke [left] arm. Adapted from Foroud and Whishaw, 2006.

PL

When reaching with the ipsilateral arm, PL was slightly rigid [Bound Flow Effort] and used too much pressure [Strong Weight Effort] throughout the Withdrawal portion of the reach. When reaching with the contralateral arm, PL consistently demonstrated the following abnormalities as highlighted in Figure 2.6:

Kinematic Components

The reaching limb was moved by body/torso. The limb was lifted then carried forward towards the target by leaning forward with the torso during the Advance. During the Withdrawal, the torso carried the reaching limb as the torso leaned back, away from the pedestal. Once the torso was returned to the natural upright position, the reaching limb lifted the hand towards the mouth.

Non-Kinematic Components

Several inappropriate Effort Qualities were observed throughout the gestures in the reaching task. The subject gave the appearance that, rather than reaching for a small food item, he was using his arm to push a heavy object [Strong Weight Effort]. Although the trajectory of the arm was a direct route towards the target, the way the arm moved along the trajectory was multifocused, as if the subject were reaching in the dark [Indirect Space Effort]**.** Throughout the reaching task, the subject showed an increase of constraining and restrictive tension [Bound Flow] as if his muscles were too rigid or tight to perform the task smoothly.

IC

When reaching with the ipsilateral arm [right], IC had mild abnormalities in every major component of the ERS. He exerted more pressure [Strong Weight Effort] than necessary throughout the Advance and Release. He was rigid [Bound Flow Effort] during the Advance, Grasp and Withdrawal. During the Grasp, rather than lifting his hand without resistance, his hand lingered on the pedestal; and he made more than one gesture during the

Release. When reaching with the contralateral arm [left], IC had the following abnormalities as highlighted in Figure 2.6.

Kinematic Components

The subject made several gestures during each component where only one gesture was necessary for normal movement [Figure 2.6]. By raising the torso and leaning forward, the subject allowed the reaching limb to be carried towards the target on the Advance. Upon grasping the target with his fingertips, the subject's hand appeared stuck to the pedestal. During the grasping component, the subject leaned forward and twisted his torso in order to slide his hand off the pedestal. The subject actively tried to lift or move his hand away from the pedestal. At this point, he was grunting, breathing heavily, and twisting his body in an attempt to move his hand off the pedestal. It took great force for him to slide his hand off it. During the Withdrawal, IC simultaneously lifted his torso and leaned back so as to move the limb away from the pedestal. At this point, his head was carried by the movement of his torso as the distance between the hand and the mouth remained constant. Once his hand was away from the pedestal [an action that requires a simple lifting up of the hand in control subjects], IC attempted to bring the food target to his mouth. At this point, he lowered his head as his torso continued to move backward. During this time, the distance between the torso and limb became smaller, but it then remained constant as IC continued to lean backwards with his torso. The continuation of leaning backwards while maintaining a fixed distance between the hand and the mouth prevented IC from successfully bringing the food item to his mouth. He then twisted his torso in an attempt to bring his mouth closer to his hand. Finally, after swaying slightly from side–to-side, the subject managed to bring his mouth to his hand and eat the food target.

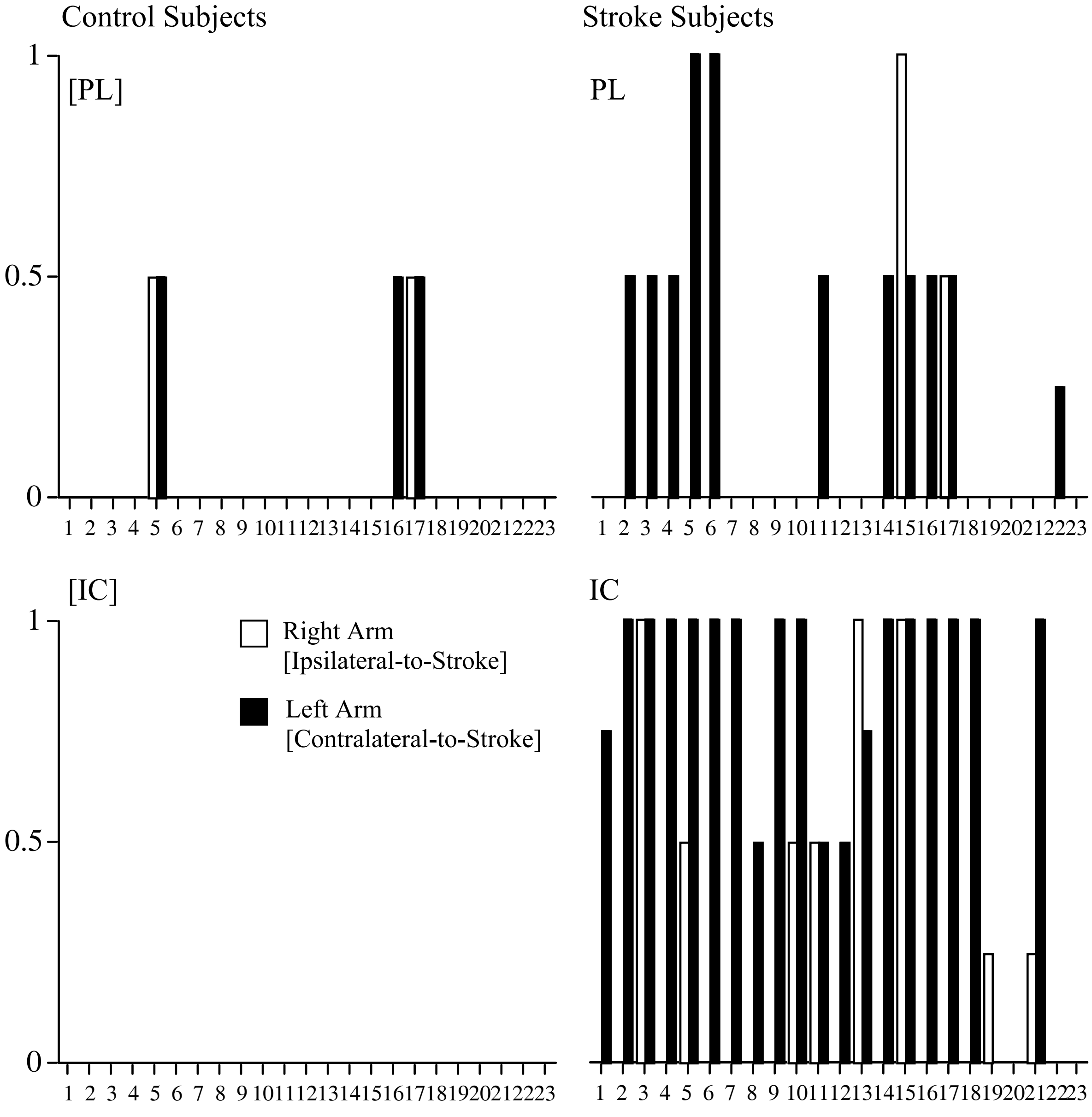


Figure 2.6 Subjects Scores for Each Subcomponent on the ERS [averaged over 2 reaches]. Subcomponents scores are represented on the y-axis. Subcomponents on the scale are represented on the x-axis: **Advance**: **1.** uses more than one gesture, **2.** limb moved by torso, **3.** Strong Weight Effort observed, **4.** Indirect Space Effort used at the end of the advance, **5.** Direct Space Effort not used at the end of the advance, **6.** Bound Flow Effort observed, **7.**

Shaping Qualities observed; during the **Grasp**: **8.** uses more than one gesture, multiple attempts [gestures], **9.** hand moved by the body/torso - body is engaged, **10.** hand appears stuck on the reaching platform, **11.** increased Bound Flow Effort, **12.** Shaping Qualities observed; during the **Withdrawal**: **13.** uses more than one gesture, **14.** limb moved by torso, **15.** Strong Weight Effort observed, **16.** Indirect Space Effort used at the end of the advance, **17.** Bound Flow Effort observed, **18.** Shaping Qualities observed; during the **Release**: **19.** uses more than one gesture, **20.** limb moved by torso, **21.** Strong Weight Effort observed, **22.** Bound Flow Effort observed, **23.** Shaping Qualities observed. Adapted from Foroud and Whishaw, 2006.

Non-Kinematic Components

Several inappropriate Effort Qualities, similar to PL, were observed throughout IC's gestures when reaching with his contralateral arm. Like PC, IC gave the appearance that, rather than reaching for a small food item on the Advance and Release, he was using his arm to push a heavy object [Strong Weight Effort]; and during the Advance it was as if he were reaching in the dark [Indirect Space Effort]. These types of movement qualities were accompanied with increasing constraint [Bound Flow]. IC's arm never reached the target with a pinpointed direct focus [lack of Direct Space Effort].

In addition to using inappropriate Effort Qualities, IC used Shaping Qualities that are not necessary for performing the reaching task with efficiency. During the Advance, IC displayed Rising [lifting], Spreading [expanding body volume], and Advancing [approaching] qualities. During the Grasp phase, Rising, Sinking, and Spreading Shaping Qualities were observed and seemed to interfere with the ease of grasping and lifting the target. During the Withdrawal, the subject displayed Rising, Enclosing, and Retreating; all three qualities that hinder the normal Withdrawal gesture.

Unsuccessful Reaching Trials

On the two unsuccessful reaching trials, IC performed the movements in a similar fashion as the successful trials described above. The one difference between these trials and the successful trials was observed on the one unsuccessful trial when IC dropped the target at his mouth. On the Release component of this trial, IC did not use any of the Effort qualities as he did on the other trials. Furthermore, on a third incomplete trial, IC accumulated points as he made similar inappropriate kinematic and non-kinematic movements in the Advance and Grasp components of the task to the ones made during the other trials. However, although he performed the Release component, he did not use any of the Effort qualities on this portion.

DISCUSSION

The present study produces a LMA description of skilled reaching that captures the kinematic and non-kinematic features of movements that may change after stroke in human subjects. Based on this description, a rating scale, the ERS, was created in order to measure the extraneous movements of skilled reaching-for-food. Results from the rating scale showed that the kinematic and non-kinematic changes in movement were greater in the contralateral-to-stroke limb than in the ipsilateral-to-stroke limb in the stroke subjects, and more severely in the subject with the internal capsule injury - which is known to produce severe motor impairments. These results indicate that LMA analysis and the ERS rating scale is sensitive to both the severity and the location of stroke and that the ERS provides a simple tool that can be used for diagnosis and assessment.

LMA is unique in its application because, whereas biomechanical analyses are used to quantify, simultaneously, the movements isolated body segments are making, LMA places emphasis on underlying motor patterns by notating how the body segments are moving, how they are supported or affected by other body parts, as well as whole body movement. Furthermore, LMA provides a language for describing the non-kinematic aspects of movements that cannot be captured by biomechanical analyses. This is the first study that provides a language for classifying the non-kinematic features of movements in any neurological patient, including stroke. Insights can be gained from using an analysis system such as LMA, as it identifies the underlying motor patterns [kinematic and non-kinematic] that affect actions that can be difficult to measure using biomechanical analyses. Such an understanding of the mechanisms underlying abnormal motor patterns in stroke patients is critical for designing effective rehabilitation programs [Cirstea & Levin, 2000; Lough, Wing, Fraser & Jenner, 1984].

Skilled reaching was used in the present study because reaching for objects, and especially reaching for food items to eat, is a daily activity, which, when lost or impaired, can compromise independence. The task has also been used in previous preclinical [Adkins & Jones, 2005; Hsu & Jones, 2005; Maclellan, Grams, Adams & Colbourne, 2005; Piecharka, Kleim & Whishaw, 2005; Windle & Corbett, 2005] and clinical investigations of stroke [Cirstea, Mitnitski, Feldman & Levin, 2003; Cirstea, Ptito & Levin, 2003; Harris-Love, McCombe Waller & Whitall, 2005; McCrea, Eng & Hodgson, 2005; Micera et al., 2005; Michaelsen, Jacobs, Roby-Brami & Levin, 2004; Michaelsen & Levin, 2004; Roby-Brami, Feydy, Combeaud, Biryukova, Bussel & Levin, 2003; Roby-Brami, Jacobs, Bennis & Levin, 2003] and analogous tasks are widely used in studies of motor systems [Smith & Metz, 2005; Wallace & Whishaw, 2003; Webb & Muir, 2005; Whishaw, 2003; Whishaw et al., 2002; 2003]. Furthermore, the movements of skilled reaching in both normal subjects and patients are extremely consistent from trial to trial and between limbs, thus necessitating the use of only one, or at most, a few trials of data collection [Whishaw et al., 2002]. The simplicity of the task thus lends itself to clinical studies where patient fatigue may hamper data collection and when time may be a constraint.

During the skilled reaching task, the kinematic structure [Body and Space] of movements work to support the action while the non-kinematic movements [Effort and Shape] are economized so as to minimize work effort. The kinematic structure of movement is the movement of the body through space - this creates the *scaffolding* for movement that is the functional element of any task. While non-kinematic features of movements appear to be more qualitative and expressive, there are actions that benefit from an increase in non-kinematic movements. For example, the exaggeration of intensity, shape, force, flow, rhythm and attention emerge during sport or labour as well as during the expression of emotion [e.g., joy, sorrow, aggression, play, etc.]. These non-kinematic aspects of movements, thought to be more variable between people than the kinematic aspects of movement [Bartenieff & Lewis, 1980] can not only facilitate, but also hinder the efficiency of a motor behaviour [Bartenieff & Lewis, 1980]. Changes in the behaviour of non-kinematic movements can occur after stroke due to fatigue [Jeannerod, 1988], compensatory strategies [Lough et al., 1984; Cirstea & Levin, 2000; Roby-Brami, Feydy et al., 2003; Levin et al., 2004; Michaelsen & Jacobs et al., 2004], or released movements [Jackson, 1932]. Though problems in the organization of the limbs during skilled actions after stroke are more typically described using biomechanical measures [Cirstea et al., 2003; Lang & Schieber, 2004; McCrea, Eng & Hodgson, 2002; Micera et al., 2005; Platz et al., 2001; Trombly, 1992, 1993], LMA can describe, simultaneously, both the kinematic and non-kinematic features of movement and their interaction.

Two types of changes in the kinematic structure of movement were observed in the stroke subjects. First, the stroke subjects made extraneous gestures. A gesture is one action made by one limb or one limb segment and can involve a simultaneous movement of the limb, limb segments, or articulations. During reaching, both stroke subjects made more gestures than the healthy subjects. The extra limb gestures are repeated attempts of the specific component of the reach in which the stroke subjects failed. Second, rather than making the appropriate lateral movements in normal reaching, both subjects developed a new strategy for moving the torso to aid in performance of the task. During the Advance and Withdrawal, the subjects carried the limb to the desired target by making large forward and backward movements with the torso, rather than moving the arm independently. Using the torso to carry the arm to a desired target may be due to the lost, or newly limited, ability to move the arm independently of the torso. For example, the forward and backward movements of the torso were less pronounced in PL partly because he began the Advance by lifting his arm independently of the torso, but then relied on his torso to continue to bring the arm towards the target.

Following stroke, many tasks can still be achieved; however, they are accomplished by the use of compensatory strategies [Lough et al., 1984; Cirstea & Levin, 2000; Roby-Brami et al., 2003; Michaelsen et al., 2004] such as repeated gestures with gross motor support of the torso, rather than by a series of smooth single gestures supported by subtle postural shifts as shown in this study [also see Trombly, 1992; Whishaw et al., 2002]. In this study, the stroke subjects made multiple gestures within various components of the task to compensate for the inability to guide the arm properly towards the target. Furthermore, they used forward and backward movements of the torso, during the Advance, Grasp, and Withdrawal, so as to bring the arm towards the desired location. The lost ability to gesture with the arm independently of the torso changed the function of the torso where making the appropriate lateral movements in normal reaching would have hindered the success of the overall reaching task.

There are two categories of non-kinematic features of movement that, in the stroke subjects, hindered their ability to reach for and eat a food target in a smooth manner. First, the Effort qualities listed in the ERS were inappropriate for the functional goal-directed task of skilled reaching. During reaching, both stroke subjects moved with unclear trajectories [Indirect Space] and increasing pressure [Strong Weight Effort] and tension [Bound Flow Effort] - three qualities that hinder the ability to reach efficiently. The intensity of these inappropriate Efforts was greater in the IC stroke subject, suggesting that the severity of released movement qualities and/or fatigue is related to the location of stroke. Alternatively, the greater intensity could have resulted from the expression of the difficulty of the task, or even from a perception that the task is difficult, thus further hindering the ease of the task.

Indeed, even IC’s first attempt at the reaching task appeared to be extremely difficult for him and took him a great deal of effort. By contrast, PL seemed to perform the task with much less difficulty, even though his movement lacked fluidity and smoothness. In LMA theory, it is argued that some actions move in a ‘…continuous flowing progression…’ [Bartenieff & Lewis, 1980] with no specific exertion and that the mover’s mood or particular situation can change the use of Effort qualities by reducing or increasing in intensity or exertion, or by changing in proportionality, for effective function and expression [Bartenieff & Lewis, 1980]. Skilled reaching appears to be an action where the use of Effort is minimal and restricted to being light, quick and direct. Following stroke, there appears to be a change in the type of Effort qualities used as well as an increase in the intensity. During the unsuccessful trial when the target was dropped prior to placing it in the mouth, and the incomplete trial when the target was dropped upon grasping, IC made the same kinematic movements to return his hand to his lap as in his other trials. However, he did not use the Effort qualities that were used during his other trials. This suggests that he was capable of moving his arm to place his hand on his lap without the dysfunctional use of Efforts. When moving within the framework of the task, however, he used Efforts in a dysfunctional way. Therefore, studies on the influence of performing a formal task and the use of Effort qualities may be useful. The second type of non-kinematic movement that hindered reaching, Shaping, was most striking in the IC patient. IC shaped his body into various Shaping qualities. These movement qualities looked awkward and out-of-context because they were not consistent with the direction of the movement. For example, when leaning forward, IC engaged in a *Rising* quality, which, if anything, should have been an *Advancing* quality.

The ERS is the first scale that categorizes the non-kinematic movements and summarizes the relation between non-kinematic movements and the kinematic structure of the movements. In any task, the function of movements is maximized by capitalizing on the kinematic structure of the movements required and exerting only the minimum amount of non-kinematic movements. The out-of-context, non-kinematic movements displayed by the stroke subjects during reaching may be an example of the type of released movements that occur after stroke [Jackson, 1932]. Furthermore, following brain injury, a patient frequently displays fatigue and weakness [Bourbonnais & Vanden Noven, 1989; Ingles, Eskes & Phillips, 1999; Jeannerod, 1988; McCrea, Eng & Hodgson, 2005]. Although weakness may be attributed to the damaged physiology of the motor system [Bourbonnais & Vanden Noven, 1989], the dysfunctional use of Effort and Shaping Qualities after stroke can contribute to fatigue as it requires more energy and hinders the functionality of the actions. Nonetheless, the use of non-kinematic movements becomes abnormal after stroke and this study provides the first language for the classification of such movements in any task, as well as a new diagnosis and assessment tool that captures non-kinematic movements during reaching. The ERS and LMA can be used in future studies of the organization of non-kinematic movements, as well as to provide new insights on the behavior of tics, tremors and other motor phenomena.

CHAPTER 3

Skilled Reaching after Stroke: I. Group Results

ABSTRACT

Skilled reaching and variants of the behaviour are commonly used in stroke subjects as assessment tasks for upper limb function in both laboratory and clinical settings. Current assessment and rehabilitative tools, relevant to loss of function, describe many levels of articulations and movement synergies from digit flexion through shoulder rotation to ankle flexion. It is also important to analyze how each movement is performed within the context of complete motor behaviours as it has been shown that motor behaviours are organized in terms of action rather than by muscles. Further, the organization of movement in the nervous system differs between performing single articulations to synergies to movement patterns within the context of a specific behaviour. The objective of the present study was to examine both kinematic and non-kinematic details of reaching within the context of the whole behaviour in stroke subjects. Two rating scales were used, each one derived from hand written movement notation systems that describe the particular movements of reaching within the context of the whole behaviour, thus deconstructing the movements of reaching within the context of the behaviour. Results support the idea that Advance and Withdrawal phases of reaching are coordinated by different neural organization, and that, perhaps, the Advance phase is more predisposed to rehabilitation or recovery. Finally, the role and organization of non-kinematic aspects of movements are discussed.

INTRODUCTION

Skilled reaching and variants of the behaviour are commonly used in stroke subjects as assessment tasks for upper limb function in both laboratory [Adkins & Jones, 2005; Hsu & Jones, 2005; Maclellan, Grams, Adams & Colbourne, 2005; Piecharka, Kleim & Whishaw, 2005; Smith & Metz, 2005; Wallace & Whishaw, 2003; Webb & Muir, 2005; Windle & Corbett, 2005; Whishaw, 2003; Whishaw, Gorny, Foroud & Kleim, 2003; Whishaw, Pellis & Gorny, 1992a; b; Whishaw, Suchowersky, Davis, Sarna, Metz & Pellis, 2002] and clinical [Cirstea, Mitnitski, Feldman & Levin, 2003; Cirstea, Ptito & Levin, 2003; Michaelsen, Jacobs, Roby-Brami & Levin, 2004; Harris-Love, McComb, Weller & Whithall, 2002; McCrea, Eng & Hodgson, 2005; Micera, Eng & Hodgson, 2005; Michaelsen & Levin, 2004; Roby-Brami, Feydy, Combeaudi, Biryukora, Bussell & Levin, 2003; Roby-Brami, Jacobs, Bennis & Levin, 2003] settings. Many advances have been made on the organization of skilled movement and applied therapies, however, there are four recurring problems in this type of behavioural stroke research. First, there is large variability in lesions, symptoms, and rehabilitative response between stroke subjects. In animal research, the variability is accounted for by the ability to localize the lesion to specific brain locations in a large number of subjects. To reduce within group variability in clinical research, scientists and physicians have established criteria to categorize stroke subjects into smaller groups [Cirstea & Levin, 2000; Lang, Wagner, Edwards, Sahrmann & Dromerick, 2006; Lang, Wagner, Bastian, Hu, Edwards, Sahrmann & Dromerick, 2005; Wagner, Dromerick, Sahrmann & Lang, 2007], however, this does not negate information that must be sacrificed when selecting common criteria. Scientists and therapists also have devised assessment and rehabilitative tools, relevant to loss of function that can be modified to address individual stroke patient needs.

For example, the Fugl Meyer, one of the most widely used and detailed assessment scales, describes many levels of articulations and movement synergies from digit flexion through shoulder rotation to ankle flexion [Fugl Meyer, 1980; Sanford, Moreland, Swanson, Stratford & Gowland, 1993]. Once assessment is complete, therapies can be catered to each individual based on their specific deficits. Herein lies the second problem, for though this type of analysis is important for assessing motoric deficits based on muscle function and coordination, it is also important to analyze how each movement is performed within the context of complete motor behaviours, as it has been shown that motor behaviours are organized in terms of action rather than by muscles [Graziano, Taylor, Moore & Cooke, 2002; Graziano, Taylor & Moore, 2002] and with parameters specific to the behavioural task [Graziano, 2006].

The organization of movement in the nervous system differs between performing single articulations to synergies to movement patterns within the context of a specific behaviour [Berthoz, 2000]. For example, the ability to pronate the arm while seated with arms by the side is different within the context of reaching due to body posture and alignment, and purpose [e.g., goal directed versus. exploratory]. Another example is that digit flexion on its own is one specific type of function, independent movements of digits during grasping is another specific type of motor behaviour. Third, the majority of analyses performed in skilled reaching are done by assessing the kinematic aspects of movements [Clark, Ploughman & Corbett, 2007]; however, non-kinematic aspects of movement are affected by stroke as well [Foroud & Whishaw, 2006]. Most observers see these changes however, describing them in a reliable, consistent, and universal way is challenging. For example, two people may interpret the meaning of *fluid movement* in two different ways and may even select separate criteria for defining fluid movement. You can experiment with this idea by randomly asking persons to define, or even to demonstrate *fluid movement* and observe the differences between people. Various techniques have been developed to capture non-kinematic aspects of movement in an objective manner [Lamontagne, Stephenson & Fung, 2007; McDonnell, Hillier, Ridding & Miles, 2006; van Dijk, Jannink & Hermens, 2005] though they are often un-assessable to clinical, or even research, facilities due to the cost, technical expertise, and time involved for assessment. In a previous study, Laban Movement Analysis [LMA] was used to create a rating scale for capturing the non-kinematic changes in movement after stroke whereby observer training and a videotape of the subject performing the task are the only necessary tools. Fourth, although there is a large amount of animal and human subject research on stroke, it is difficult to compare changes in movement after stroke between animal and clinical research.

The objective of the present study was to examine the fine kinematic and non-kinematic details of reaching within the context of the whole behaviour in stroke subjects. In order to address the within-group-variability problem, the stroke group was compared with healthy matched controls and then divided into smaller groups in order to compare lesion levels, and recovery stages, etc. within the stroke group. The two types of analyses selected for this study are rating scales of reaching behaviour, one of which can be applied to assessments of skilled reaching in rodent stroke models [Adkins & Jones, 2005; Alveradashvili, Foroud, Lim & Whishaw, 2008; Farr & Whishaw, 2002; Whishaw et al., 2002; 2003].

Each rating scale is derived from hand written movement notation that describe the particular movements of reaching within the context of the whole behaviour, thus providing a method for displaying various levels and patterns of movement and relationships between body parts. The purpose of this approach is to deconstruct the movements of reaching, but always within the context of the behaviour. The first scale, derived from Eshkol-Wachman Movement Notation [EWMN], quantifies the organization of moving body parts during reaching, thereby capturing deficiencies in the kinematic components of reaching. The scale was originally used to study reaching in patients with Parkinson's disease [PD], and has since been applied to animal models of PD and stroke [Whishaw et al, 2002]. It is well known that, after stroke, people not only display motor deficits, but also display extraneous compensatory, and, in some cases, disinhibited, or *released*, movements. Therefore, a separate scale is required to capture extraneous movements. This second scale, derived from Laban Movement Analysis [LMA], quantifies the extraneous kinematic and non-kinematic movements that can occur within reaching behaviour after stroke [Foroud & Whishaw, 2006].

METHODS

Subjects

Ten stroke subjects [mean = 69.60 ± [SD] 8.13, SE = 2.57 years of age, five males and five females] and ten matched control subjects [mean = 68.00 ± [SD] 7.51, SE = 2.38 years of age, five males and five females] participated in this study. Of the stroke group, five were post-acute [i.e., were within the first six months of having had a stroke], and five were chronic stroke subjects [i.e., had a stroke at least two years prior to the study]. Lesions were varied in terms of hemisphere, level, and location. Hemiplegia was diagnosed in the contralateral limb in nine subjects, and in the ipsilateral limb in one subject. A summary of the details of the stroke subjects is provided in Table 3.1.

Table 3.1 Summary of Stroke Subjects

	Cortical		Subcortical	
	Hemisphere	Hemiplegia	Hemisphere	Hemiplegia
Right	5	3	3	0
Left	2	4	0	3
Right	Parieto-Occipital		Posterior Limb of Internal Capsule	
	Frontro-Parietal		Superior Posterior Parietal	
	Cerebral medially near falx		Thalamic	
	Superior Posterior Parietal			
	Parietal Somatosensory			
Left	Frontal + Anterior Parietal			
	Deep Parietal			

Reaching Task and Video Recording

The same reaching task and method of video recording described in Chapter 2 were used for the group analysis in this chapter.

Analysis

Two rating scales were used to quantify movements performed by subjects in the reaching task. The first scale, described below, was derived from EWMN notated scores of reaching [Whishaw et al., 2002]. The scale quantifies the body’s movement during reaching in terms of the dynamic relationship between body parts during various components of reaching, thereby capturing deficiencies in the kinematic components of reaching. The second scale, described in Chapter 2, was derived from LMA notated scores of reaching [Appendix 2]. This scale defines the reach in terms of the natural divisions of the task [Advance, Grasp, Withdrawal, and Release] and quantifies extraneous kinematic and non-kinematic movements that can occur within reaching behaviour after stroke [Foroud & Whishaw, 2006].

Statistical analyses, with significance at $p < 0.05$, were done using repeated measures analysis of variance [ANOVA] with Fisher's PLSD post-hoc tests and t-tests. The data were treated as interval data as defined by Field and Hole [2003]. Due to anticipated patient fatigue in the stroke subjects potentially hampering the data collection, the first two most successful trials performed in each subject were analyzed from each limb.

EWMN Derived Reaching Scale [EW-DRS]

The EW-DRS is a scale derived from Eshkol-Wachman Movement Notations [EWMN] of the reaching task whereby the reaching act is divided into seven components, with each component further divided into two or more subcomponents, giving a total of 21 subcomponents [Whishaw et al., 2002] [Table 3.2].

Table 3.2 The Eshkol-Wachman Movement Notation - Derived Reaching Scale [EW-DRS]

EWMN - derived Reaching Scale		
Components	Subcomponents	Score
A. Orient	1. Head fixates on the target	0, 0.5, 1
	2. Eyes fixate on the target	0, 0.5, 1
B. Lift	3. Arm points to target	0, 0.5, 1
	4. Digits open	0, 0.5, 1
	5. Elbow flexion	0, 0.5, 1
C. Aim	6. Hand is carried directly to the target	0, 0.5, 1
	7. Hand ends above the target	0, 0.5, 1
	8. Contralateral shift of the torso during advance	0, 0.5, 1
D. Pronate	9. Hand is fully turned	0, 0.5, 1
	10. Elbow is extended	0, 0.5, 1
	11. Thumb and index finger are close to the target	0, 0.5, 1
E. Grasp	12. Pincer grasp is used	0, 0.5, 1
	13. Independent movements of the digits during the grasp	0, 0.5, 1
	14. Arm lifts up after grasp	0, 0.5, 1
F. Supinate	15. Hand supinates once	0, 0.5, 1
	16. Hand supinates a second time	0, 0.5, 1
	17. Head shifts to meet the hand	0, 0.5, 1
	18. Ipsilateral shift of the torso carries the head to meet the hand	0, 0.5, 1
G. Return	19. Hand pronates	0, 0.5, 1
	20. Digits release from the grasp	0, 0.5, 1
	21. Hand returns palm down and open on the lap	0, 0.5, 1
		Total = 21

Adapted from Whishaw et al. 2002.

[A] Orient. The head and eyes move in order to view the target prior to the reach.

[B] Lift. The hand is lifted from the knee with flexion of the elbow to raise the hand above the target, and the first and second digits pointing toward the target and the palm is open to shape the digits for grasping.

[C] Aim. As the hand is carried towards the target, the hand ends above it; the movement of the hand towards the target is made with the assistance of a contraversive movement of the trunk.

[D] Pronate. The hand is fully pronated above the target, the elbow opens to facilitate hand pronation, and the first and second digits are brought close to the target.

[E] Grasp. The target is grasped with a pincer grip using the first and second digits, the first and second digits move independently of the other digits during grasping, and the target is lifted upward just after being grasped [also see Wong & Whishaw, 2004].

[F] Supination. The hand supinates by about 90 degrees shortly after retrieving the food item, then supinates by about another 90 degrees to place the food into the mouth. At the same time, the head is carried by an ipsiversive movement of the torso, so that the mouth meets the hand at the end of its trajectory.

[G] Return. The digits open as the food is released into the mouth, the hand pronates, the digits open further as the open hand is placed palm down on the lap.

Expressive Reaching Scale [ERS]

The ERS is a scale derived from Laban Movement Analysis notations of reaching in two stroke cases [Foroud & Whishaw, 2006] and provides a method for quantifying the exertion of the movement by assessing the non-kinematic features of movement that have a more expressive quality than the kinematic structure of movements. The ERS evaluates four phases of the skilled reaching task: Advance, Grasp, Withdrawal, and Release. Each component is divided into two kinematic and several non-kinematic subcomponents giving a total of 23 subcomponents [Chapter 2, Table 2.2]. The 23 subcomponents of the ERS are descriptions of the inappropriate movements that contribute to reaching abnormally [as outlined in Chapter 2].

In both the EW-DRS and ERS, each subcomponent was rated on a 3-point continuous scale from “0”, the movement is absent to “0.5”, the movement is present but incomplete to “1”, the movement is present. The EW-DRS describes normal reaching movements and the higher the score, the better, whereas the ERS describes abnormal reaching movements, and the higher the score, the worse. The score for each component is the average of the subcomponent scores. The overall score for a reaching trial is the average of the 21 points on the EW-DRS, and the 23 in the ERS.

RESULTS

General Group Differences

EW-DRS

A group difference between stroke and control groups on overall scores [F [1,18] = 35.36, $p < 0.0001$], with the stroke group performing worse than the controls, on each limb [unpaired t-test, $p < 0.005$], was found [Figure 3.1A]. Differences were also found when comparing component scores, for group [F [1,18] = 35.82, $p < 0.0001$], components [F [6,108] = 8.41, $p < 0.0001$], and components by group [F [6,108] = 3.05, $p < 0.05$], with the stroke group performing worse than controls on Aim, Grasp, and Supinate when reaching with either limb [unpaired t-test, $p < 0.05$] [Figure 3.1B, C].

ERS

Similar to the EW-DRS results, a group difference between stroke and control groups on overall scores [F [1,18] = 14.46, $p < 0.005$], with the stroke group performing worse than the controls, on each limb [unpaired t-test, $p < 0.05$], was found [Figure 3.2A]. Differences were also found when comparing component scores, for group [F [1,18] = 15.19, $p < 0.005$], components [F [3,54] = 6.47, $p < 0.005$], and components by group [F [3,54] = 3.02, $p < 0.05$], with the stroke group performing worse than controls on Advance, Grasp, and Withdrawal when reaching with the ipsilateral limb, and Advance and Grasp when reaching with the contralateral limb [unpaired t-test, $p < 0.05$] [Figure 3.2B, C].

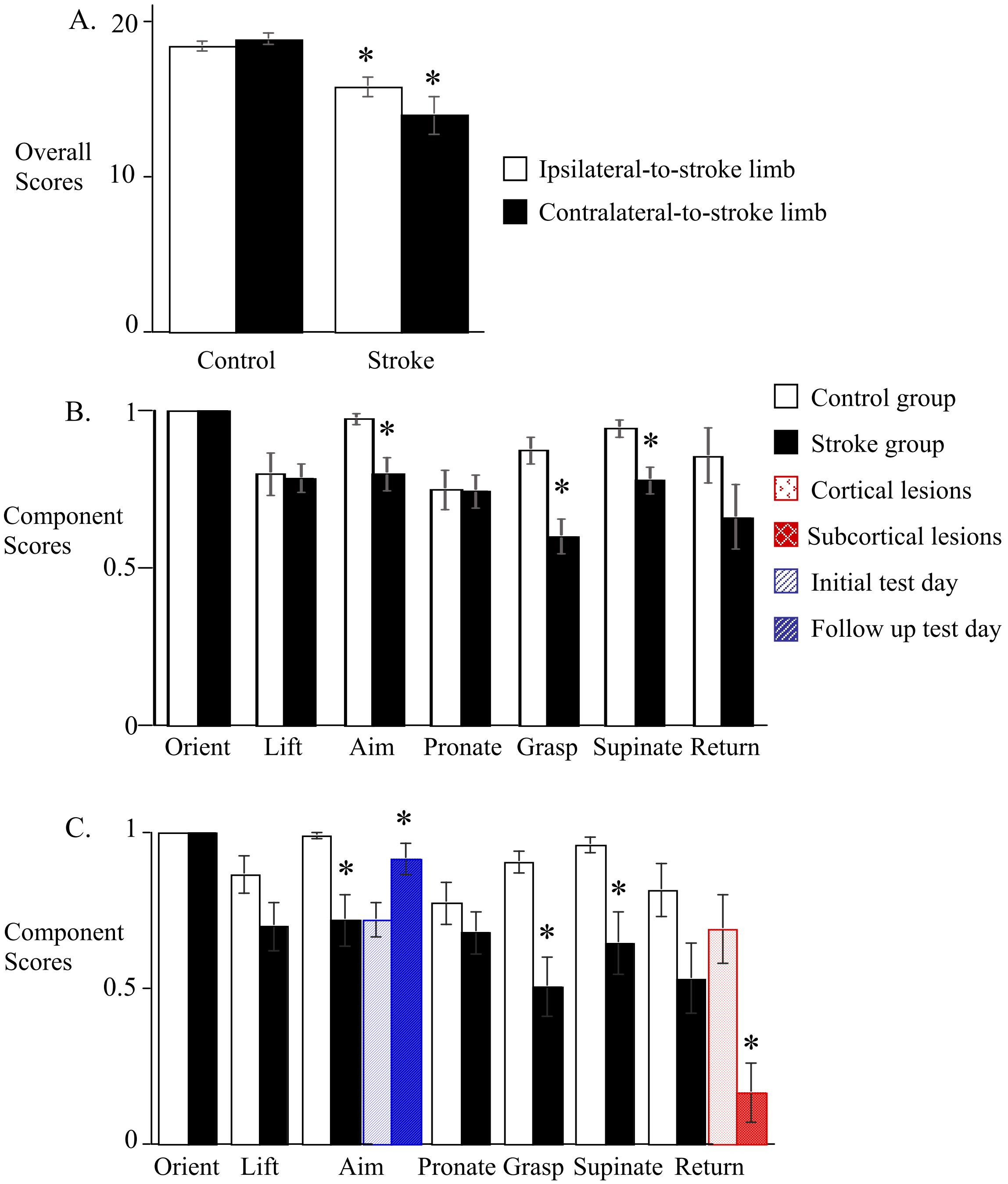


Figure 3.1 Group Results on the EW-DRS. A] Overall scores in control and stroke groups. B] Component Scores for Ipsilateral-to-Stroke Limb. C] Component Scores for Contralateral-to-Stroke Limb.

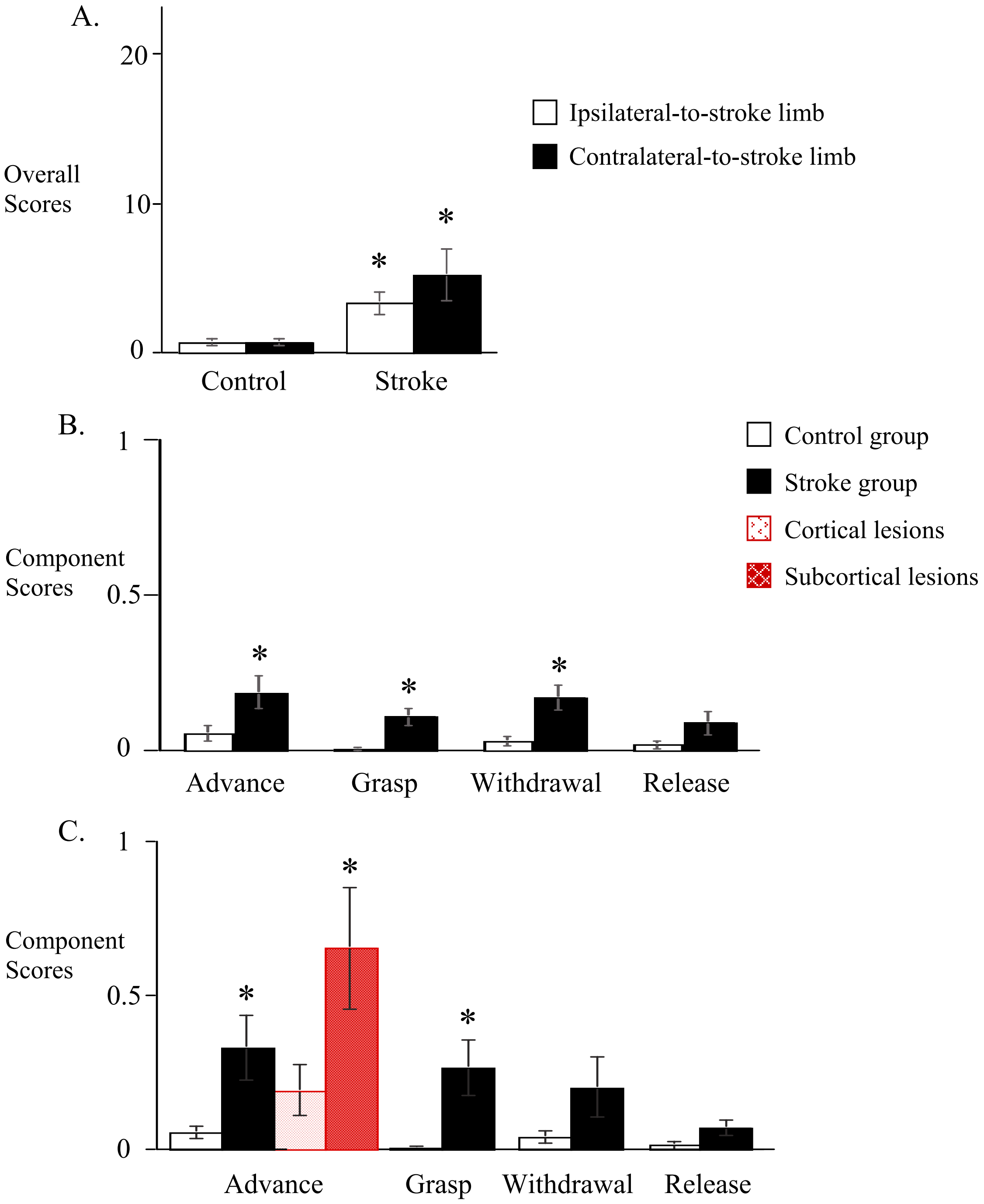


Figure 3.2 Group Results on the ERS. A] Overall scores in control and stroke groups. B] Component Scores for Ipsilateral-to-Stroke Limb. C] Component Scores for Contralateral-to-Stroke Limb.

Kinematic versus Non-Kinematic Subcomponents on the ERS

Unpaired t-tests [$p < 0.05$] comparing the eight kinematic subcomponents, as well as the fifteen non-kinematic subcomponents, of the ERS between groups revealed a significant difference in the non-kinematic subcomponents when reaching with either limb, with the stroke group performing worse than the controls. Of these subcomponents, the differences seemed to lie in the Grasp component in the ipsilateral limb, and in the Advance, Grasp, and Release components in the contralateral limb [Figures 3.3A, 3.4A].

Level of Lesion Effects

The stroke group was divided into cortical [$n = 7$] and subcortical [$n = 3$] groups.

EW-DRS

Repeated measures ANOVA showed no lesion effect on overall scores [$p > 0.05$], however, unpaired t-tests [$p < 0.05$] showed a difference in the contralateral limb with the subcortical group performing worse than the cortical group. Significant differences between components were found when comparing component scores [$F [1,8] = 8.03$, $p < 0.0001$]. Unpaired t-tests [$p < 0.05$] suggest a difference between the two stroke groups in the contralateral limb for the Return component [Figure 3.1C].

ERS

The ANOVA did not show a lesion effect on overall scores [$p = 0.05$], however, unpaired t-tests [$p < 0.05$] showed a significant difference with the subcortical group performing worse than the cortical group in the contralateral limb. Differences were found between the two groups when comparing components with limb by lesion [F [3,24] = 3.13, $p < 0.05$] and components [F [3,24] = 6.80, $p < 0.005$] effects. Unpaired t-tests [$p < 0.05$] showed a difference in the Advance component when reaching with the contralateral limb, with the subcortical group performing worse than the cortical group [Figure 3.2C].

Kinematic versus Non-Kinematic Subcomponents on the ERS

Unpaired t-tests [$p < 0.05$] between cortical and subcortical groups for overall scores revealed significant differences in kinematic subcomponents when reaching with contralateral limb. The difference was found in the Grasp component. A difference in the ipsilateral limb on Withdrawal component as well as in the non-kinematic subcomponents for Advance with the contralateral limb was also found. In all cases, the subcortical group performed worse than the cortical group [Figures 3.3B, C, 3.4C].

Effect of Time

Post-Acute versus Chronic Stroke Subject

No differences were found between post-acute [$n = 5$] and chronic [$n = 5$] groups on either scale.

Two Year Follow-Up in Post-Acute Stroke Subject

The post-acute group was tested within the first six months of their stroke initially, and two years later [note that 3 of the 5 subjects returned for follow-up, the following results compare the 3 subjects at initial and follow-up test days].

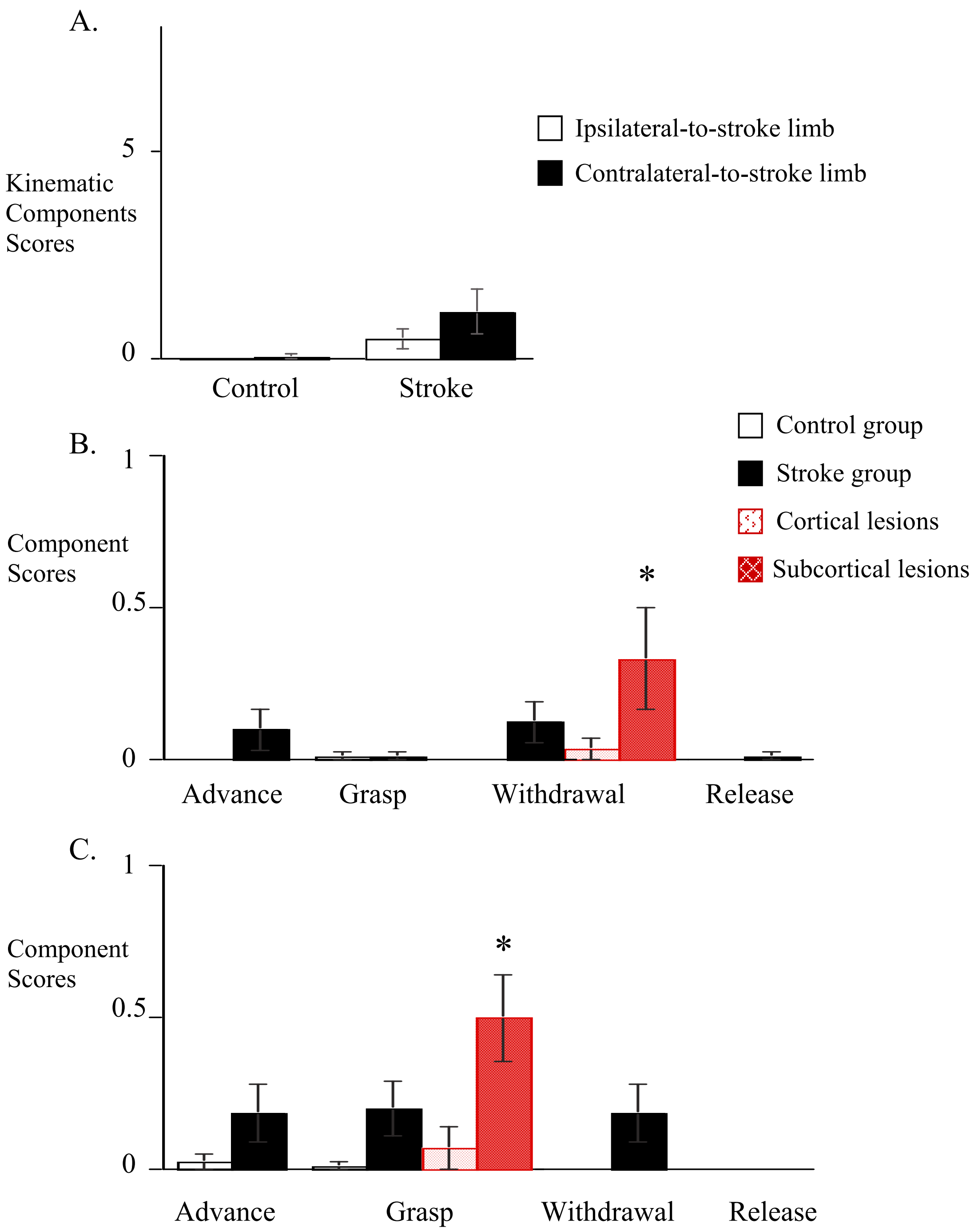


Figure 3.3 Group Results for Kinematic Subcomponents of the ERS. A] Scores in control and stroke groups. B] Kinematic Scores in Components of the ERS for Ipsilateral-to-Stroke Limb. C] Kinematic Scores in Components of the ERS for Contralateral-to-Stroke Limb.

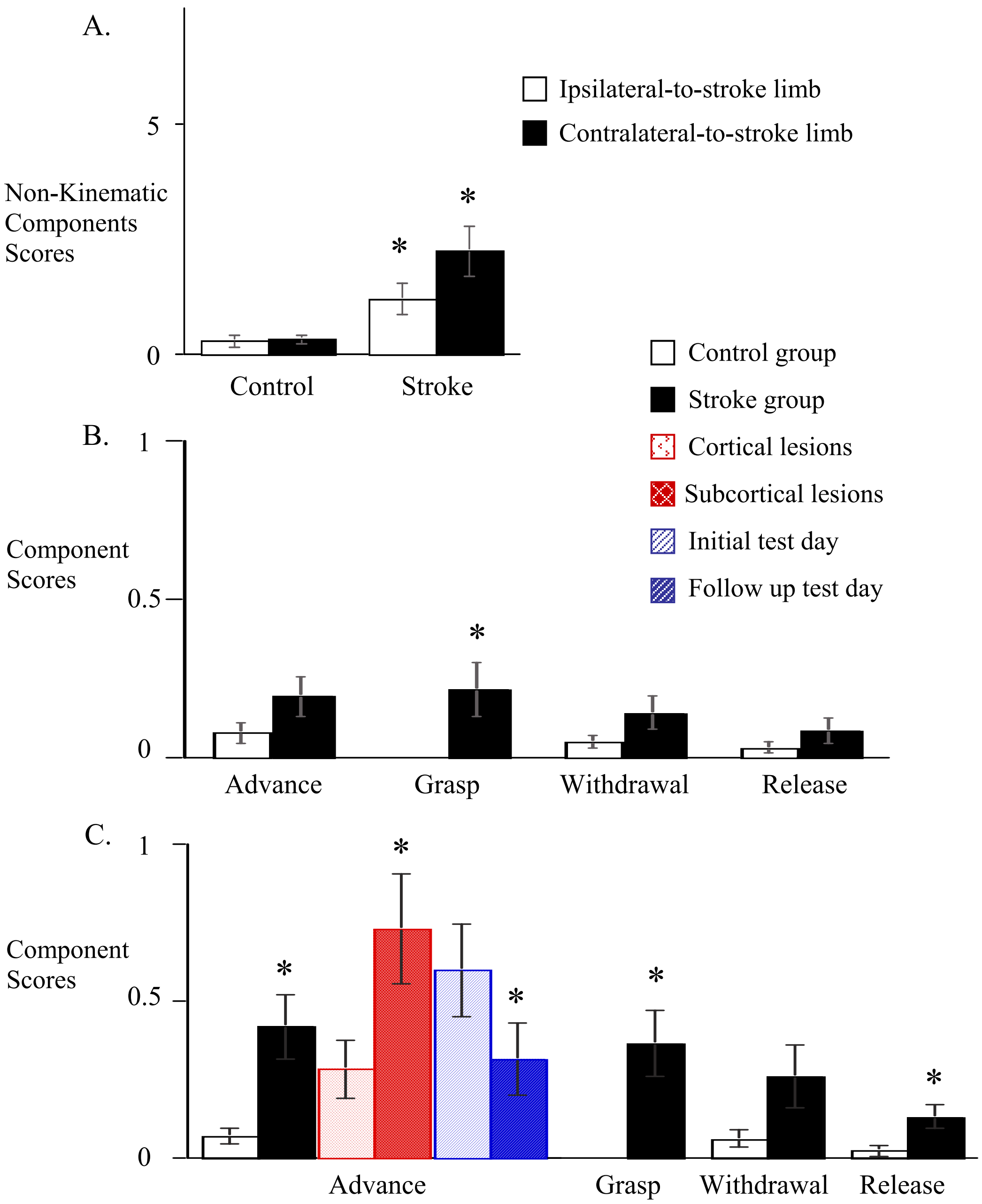


Figure 3.4 Group Results for Non-Kinematic Subcomponents of the ERS. A] Scores in control and stroke groups. B] Non-Kinematic Scores in Components of the ERS for Ipsilateral-to-Stroke Limb. C] Non-Kinematic Scores in Components of the ERS for Contralateral-to-Stroke Limb.

Table 3.3 Changes in Individual Results after Two Year Follow Up

	Subject A [Cortical]		Subject B [Subcortical]		Subject C [Subcortical]	
	Ipsilateral	Contralateral	Ipsilateral	Contralateral	Ipsilateral	Contralateral
EWMN derived reaching scale						
Orient	↑					
Lift	↑	↓*		↑	↓*	
Aim	↓*	↓*	↓	↓	↓*	↓
Pronate			↓	↓*	↓*	↑
Grasp	↓	↑	↓	↓	↑	↑
Supinate	↓	↑		↑*	↓	↓*
Return		↑	↓	↓	↑	↓
Expressive reaching scale						
Advance	↑	↓	↓*	↓	↑*	↓
Grasp		↑	↓*	↓		
Withdraw	↓	↓	↑*	↓	↓*	↑*
Release	↑	↑	↓			↑*

EW-DRS

No differences were found when comparing overall scores between initial and follow-up test days. Paired t-tests [$p < 0.05$] on component scores revealed a significant difference, with Aim being worse on the initial test day, when reaching with the contralateral limb [Figure 3.2C].

ERS

No differences were found when comparing overall or component scores. Paired t-tests did show a difference between initial and follow up test dates on the non-kinematic subcomponents within the Advance component in the contralateral limb [$p < 0.05$] [Figure 3.4C].

Changes in individual subjects

Upon taking a closer look at component scores, on both reaching scales, between initial and follow-up test days within each individual subject, it was found that the changes that occurred between the test days varied between subjects. Further, the changes can be in both positive and negative directions [Table 3.3].

DISCUSSION

In summary, the stroke group performed worse on both scales when reaching with either arm than the control group at component and subcomponent [in kinematic and non-kinematic] levels. Performance with contralateral limbs were consistently worse than performance with ipsilateral limbs, however, ipsilateral limb scores were worse in stroke subjects when compared to controls in certain components. Differences were repeatedly found when comparing subgroups within the stroke group, with subcortical lesions worse than cortical, and post-acute group worse on initial test day than follow up on Aim and Advance components. This study did not completely remove the effects of variability in the stroke group, as some components are not significant though the means are far apart. Further, although the scores between test days at the post-acute stage and two years later at the chronic stage did not show differences except in Aim and Advance, there were many changes, in both positive and negative directions that were variable between subjects that likely cancelled each other out, thus resulting in similar overall scores. The next step will be to examine the data on individual levels in order to gauge any commonalities and differences and is examined in greater detail in the following chapter. In the meantime, we can gain insight in how the movements of reaching change within the context of the whole behaviour from the results in this study.

Aim, Pronate, Grasp, and Supinate are consistently problematic throughout all levels of the stroke subgroups. The data suggest that Aim and Pronate, two components that are part of the Advance phase, improve with time, while Grasp and Supinate, two components of the Withdrawal phase, do not. The Advance and Withdrawal phases may be coordinated by different neural organization. Studies have shown that different stimulation of various motor sites in the cortex in monkeys evoked multi-joint movements of the limb towards a final posture, regardless of starting point, each specific to the site of stimulation [Graziano, Taylor & Moore, 2002; Graziano, Taylor, Moore & Cooke, 2002], and that outward reaching movements are evoked by different cells to inward hand-to-mouth movements [Graziano, 2006]. The Advance phase may be organized in such a way that it is more readily malleable via cellular plasticity or reorganization of redundant neural systems than the Withdrawal phase. It has been well established that the motor nervous system is both redundant [Boyd, Vidoni & Daly, 2007; Dancause, 2006a; b; Dove, Eskes, Klein & Shore, 2007] and adaptable [Berthoz, 2000; Graziano, Aflalo & Cooke, 2005]. It could be that movement of a limb towards a target is more adaptable than movements of the limb toward the body, as moving the limb towards a target encompasses a wider range of behaviours, such as bracing for impact, protection against invasive objects [something falling on, or thrown at, you], and balance during motor activities.

Certain aspects of the reaching movements appear to change over time after stroke. It is possible that certain components of movement, such as released movements, emerge early in the recovery phases. The motor system encompasses inhibitory circuits [Berthoz, 2000; Llinás, 2002], as a mover must inhibit many movements throughout the body in order to perform a specific voluntary action. After stroke, inhibitory pathways during normal skilled reaching may be damaged. Other aspects of movement could be developed throughout rehabilitation, or even with experience gained over time, as compensatory strategies. For example, if lifting the arm has become difficult because the way in which the nervous system organizes the synergistic movements of the shoulder, elbow, and torso is damaged, exerting more force, or Strong Weight Effort, may make the task possible. Functional tasks can adopt expressive qualities for support in the healthy nervous system as well. Athletes know that it is not enough to move the arm along a specified and efficient trajectory to throw a ball, they must also exert a certain amount of force, weight, and spatial attention [Strong Weight and Direct Space Efforts] in order to be successful in achieving distance and accuracy.

Now that non-kinematic aspects of movement can be characterized alongside the kinematic aspects within the same motor behaviour, an investigation on how the two are mutually organized and integrated within the motor nervous system would prove insightful. Non-kinematic aspects of movement appear in every body part as well as during movement synergies. It is unlikely that they are regulated by modular areas within the motor system. If they were, preparation for every voluntary action would require feedback loops with the dedicated area. Rather, it may be that non-kinematic aspects of movement are intricately woven into multiple neurological and behavioural layers of motor organization and that cells involved in other aspects of movement also modulate non-kinematic aspects. For example, non-kinematic aspects of movement appear during 1. functional actions such as hammering a nail versus powdering your nose; 2. expressive actions during thought and communication; and 3. sport and play behaviour. Furthermore, it may be that non-kinematic aspects of movement are modulated at subcortical as well as cortical levels. The motor nervous system makes fine adjustments during action based on proprioceptive information fed back to the cerebellum. It is possible that both kinematic and non-kinematic information are integrated in their afferent neural pathways, as non-kinematic adjustments must not only be made, but must be made in harmony with kinematic adjustments. The control of non-kinematic aspects of movements is relevant within the context of skilled reaching behaviour and should therefore be considered in both research and clinical settings.

CHAPTER 4

Skilled Reaching after Stroke: II. Individual Results

ABSTRACT

A persistent problem in human stroke research is that lesions caused by stroke are often unique. In clinical research, stroke subjects are placed in groups according to previously selected criteria [e.g., middle cerebral artery stroke, or contralateral hemiplegia]; however, this does not negate information that must be sacrificed when selecting common criteria. The problem of variability between stroke subjects can be a benefit to the study of skilled movement if analysis can be applied to individuals and later compared between them. This approach, though detailed and time consuming, provides insight into the organization of skilled movement and for the design of personalized rehabilitation programs. The purpose of this study was to examine skilled reaching in individual subjects in order to gauge the commonalities and differences between lesion types. Three conclusions are made for the way that skilled reaching breaks down after stroke, with variation in details being lesion dependent: 1. body-limb disintegration [disinhibition and/or compensatory]; 2. inappropriate use of Efforts [disinhibition of Bound Flow Effort and lack of Indirect Space Effort due to compensation for loss of control]; and 3. disruption in the temporal aspect of the phases of reaching.

INTRODUCTION

Different Strokes for Different Folks

A persistent problem in human stroke research is that lesions, or combinations of lesions, caused by stroke are typically unique. Although vasculature and neural structure are similar across individuals, personalized deviations occur; the evidence for this lies in plasticity of cortical motor maps after use, discontinued use, learning, or injury [Dancause 2006a]. Contributing to this cause, the location, type [e.g., ischemia versus hemorrhagic], and duration of stroke, is variable and rarely predictable. To reduce within group variability in clinical research, stroke subjects are often placed in groups according to previously selected structural or behavioural criteria [e.g., middle cerebral artery stroke, or contralateral hemiplegia], however, information is sacrificed when selecting common criteria. Further, variability subsists in rehabilitative response between stroke subjects as each person has a unique combination of life skills and experience, personality traits, including attitude and approach to illness, and medical complications.

In addition to variability between individuals, the details of recovery may be subtle. In the previous chapter, subjects in the post-acute group were examined two years after their stroke. Although their overall scores on the rating scale did differ from their post-acute scores, changes in positive and negative directions were observed that likely cancelled a statistical effect [Chapter 3, Table 3.4]. These changes would have been missed if not for examination at the individual level.

The problem of variability between stroke subjects can be a benefit to the study of skilled movement if analysis can be applied to individuals and later compared between them. This approach, though detailed and time consuming, provides insight into the organization of skilled movement as well as for the design of personalized rehabilitation programs. The purpose of this study is to examine the data previously collected in the stroke group [described in Chapter 3] in terms of individual scores in order to gauge the commonalities and differences between lesion types.

METHODS

Subjects

Comparisons between individual subcomponent scores, from both the EW-DRS and the ERS scales, in the ten stroke subjects described in the group study [Chapter 3] were made. As the present analysis is an examination of individual subjects, two additional subjects who did not fit the group criteria in the previous chapter due to the bilateral nature of their lesions, were added here. The subjects are two, right handed females [43 years of age, bilateral parieto-occipital, right posterior frontal and right cerebellum lesions; 66 years of age, bilateral cerebellum and brainstem lesions], one of whom [brainstem involvement] had paresis in both limbs and performed the reaching task with her less affected limb only.

Analysis

Subcomponent scores from both the EW-DRS and ERS were compared. Each subcomponent was rated on a 3-point continuous scale from “0”, the movement is absent to “0.5”, the movement is present but incomplete to “1”, the movement is present. The EW-

DRS describes normal movements for reaching with high scores indicating a strong performance, whereas the ERS describes abnormal and extraneous movements during reaching with high scores indicating weak performance.

Means for subcomponent scores were calculated for the matched control group [including the additional matched controls for the two stroke subjects added in this analysis] and the stroke group [Table 4.1]. Unpaired t-tests confirmed significant differences between the two means in each limb on each scale [$p < 0.0001$]. Stroke subjects were then marked for scores of less than 0.75 on each subcomponent of the EW-DRS and more than 0.21 on each subcomponent of the ERS.

Table 4.1 Group Means from the EW-DRS and ERS

	Ipsilateral to Stroke Limb	Contralateral to Stroke Limb
Control Group		
EW-DRS	0.89	0.91
ERS	0.03	0.03
Stroke Group		
EW-DRS	0.75	0.64
ERS	0.16	0.21

RESULTS

The following is a description of the most commonly affected subcomponents on each scale when reaching with either limb [Table 4.2]. In addition, certain subcomponents were affected by fewer subjects and are highlighted in Table 3.[35]

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[35] Results from each subject are presented in Appendix 3.

Table 4.2 Affected Subcomponents in Most Subjects

	Ipsilateral Limb	Contralateral Limb
Components	Subcomponents	
A. EW-DRS		
Lift		Opening of digits
	Flexion of the elbow	
Aim		Hand carried directly to target
		Hand ends above target
	Trunk moves with hand on advance	Trunk moves with hand on advance
Pronate	Elbow opened	Elbow opened
Grasp	Independent movement of digits	Independent movement of digits
	Lift up on grasp	Lift up on grasp
Supinate		Supination I
	Supination II	Supination II
	Trunk moves with hand on withdrawal	Trunk moves with hand on withdrawal
Return	Frees digits from grasp	Frees digits from grasp
	Hand open on lap	Hand open on lap
B. ERS		
Advance		Limb moved by torso
	Indirect Space Effort used	Indirect Space Effort used
		Direct Space Effort not used at the end of Advance
	Bound Flow Effort used	Bound Flow Effort used
Grasp	Bound Flow Effort used	Bound Flow Effort used
Withdrawal	Indirect Space Effort used	
		Limb moved by torso
	Bound Flow Effort used	Bound Flow Effort used
Release	Bound Flow Effort used	Bound Flow Effort used

EW-DRS

All stroke subjects had perfect scores for each of the subcomponents on Orient when reaching with either limb.

Ipsilateral-to-Stroke Limb

When reaching with the ipsilateral limb, most stroke subjects performed poorly on the following subcomponents: *Flexion of elbow* [Lift], *Trunk moves with hand on advance* [Aim], *Elbow opened* [Pronate], *Independent movement of digits* and *Lift up on grasp* [Grasp], *Supination II* and *Trunk moves with hand on withdrawal* [Supinate], *Frees digits from grasp* and *Hand open on lap* [Return].

Other than subcomponents for Orient, the only subcomponent not affected in any stroke case is *Point at target* [Lift].

Contralateral-to-Stroke Limb

When reaching with the contralateral limb, most stroke subjects performed poorly on the following subcomponents: *Opening of digits* and *Flexion of elbow* [Lift], *Hand carried directly to target* and *Hand ends above target* [Aim], *Elbow opened* [Pronate], *Independent movement of digits* and *Lift up on grasp* [Grasp], *Supination II* and *Trunk moves with hand on withdrawal* [Supinate], *Frees digits from grasp* and *Hand open on lap* [Return].

ERS

Ipsilateral-to-Stroke Limb

When reaching with the ipsilateral limb, most stroke subjects performed poorly on the *Indirect Space Effort used at the end of Advance* for the Advance component and the *Bound Flow Effort* subcomponents for all four components.

Subcomponents not affected in any stroke case include *Uses more than one gesture*, *Limb moved by torso*, and *Shaping Qualities observed* for the Grasp component and *Limb moved by torso* for Release.

Contralateral-to-Stroke Limb.

When reaching with the contralateral limb, most stroke subjects performed poorly on the *Indirect Space Effort used at the end of Advance* and the *Direct Space Effort not used at the end of the Advance* subcomponents for Advance, and the *Bound Flow Effort observed* subcomponents for Advance, Grasp, and Withdrawal components.

Subcomponents not affected in any stroke case were limited to the Release component and include *Uses more than one gesture*, *Limb moved by torso,* and *Shaping Qualities observed.*

Table 4.3 Affected Subcomponents in Fewer Subjects

A. EW-DRS			
Ipsilateral Limb		Contralateral Limb	
Component	Subcomponent	Component	Subcomponent
Lift	*Opening of Digits*	*Lift*	*Point at target*
	Right Parieto-Occipital		Right Superior Posterior Parietal
	Right Cerebral medially near falx		Right Internal Capsule
	Bilateral Cerebellum + Brainstem		Right Subcortical
	Hand carried directly to target		*Elbow Flexion*
	Right Cerebral medially near falx		Right Somatosensory
	Bilateral Cerebellum + Brainstem		Right Cerebral medially near falx
	Hand ends above target		Right Fronto-Parietal
	Left Deep Parietal		Bilateral Parieto-Occipital + Right Posterior Frontal and Cerebellum
	Right Somatosensory		
	Right Cerebral medially near falx		
	Bilateral Cerebellum + Brainstem		
Pronate	*Hand fully turned*	*Pronate*	*Hand fully turned*
	Left Deep Parietal		Left Frontal and Anterior Parietal
	Right Somatosensory		Left Deep Parietal
	Right Cerebral medially near falx		Right Somatosensory
			Right Internal Capsule
	Thumb and index finger close to target		*Thumb and index finger close to target*
	Bilateral Cerebellum + Brainstem		Right Internal Capsule
Grasp	*Uses pincer grasp*	*Grasp*	*Uses pincer grasp*
	Left Deep Parietal		Right Fronto-Parietal
	Right Thalamic		Right Thalamic
	Right Cerebral medially near falx		Right Internal Capsule
	Bilateral Cerebellum + Brainstem		Right Subcortical
Supinate	*Supinate I*		
	Left Deep Parietal		
	Right Somatosensory		
	Right Subcortical		
	Bilateral Cerebellum + Brainstem		

Table 4.3 [*continued*]

A. EW-DRS [*continued*]

Ipsilateral Limb		Contralateral Limb	
Component	Subcomponent	Component	Subcomponent
[Supinate]	*Head to meet hand*	*[Supinate]*	*Head to meet hand*
	Right Thalamic		Left Frontal + Anterior Parietal
	Bilateral Cerebellum + Brainstem		Left Deep Parietal
			Right Internal Capsule
			Right Subcortical
Return	*Hand pronate*	*Return*	*Hand pronate*
	Left Frontal + Anterior Parietal		Right Thalamic
	Right Thalamic		Right Internal Capsule
	Bilateral Cerebellum + Brainstem		Right Subcortical

B. ERS

Ipsilateral Limb		Contralateral Limb	
Component	Subcomponent	Component	Subcomponent
Advance	*Uses more than one gesture*	*Advance*	*Uses more than one gesture*
	Bilateral Cerebellum + Brainstem		Right Internal Capsule
			Bilateral Parieto-Occipital + Right Posterior Frontal and Cerebellum
	Limb moved by torso		
	Right Cerebral medially near falx		
	Right Subcortical		
	Strong Weight Effort used		*Strong Weight Effort used*
	Arsec		Right Superior Posterior Parietal
	Right Internal Capsule		Right Internal Capsule
	Right Subcortical		Right Subcortical
	Direct Space not used at end		
	Right Fronto-Parietal		
	Left Deep Parietal		
	Right Cerebral medially near falx		
	Bilateral Cerebellum + Brainstem		
	Shaping Qualities used		*Shaping Qualities used*
	Right Cerebellum + Brainstem		Right Internal Capsule
			Right Subcortical

Table 4.3 [*continued*]

B. ERS [*continued*]			
Ipsilateral Limb		Contralateral Limb	
Component	Subcomponent	Component	Subcomponent
Grasp		*Grasp*	*Uses more than one gesture*
			Right Fronto-Parietal
			Left Deep Parietal
			Right Thalamic
			Right Internal Capsule
			Limb moved by torso
			Right Fronto-Parietal
			Right Internal Capsule
			Right Subcortical
	Hand appears stuck on pedestal		*Hand appears stuck on pedestal*
	Right Internal Capsule		Right Fronto-Parietal
	Right Subcortical		Right Internal Capsule
			Right Subcortical
	Shaping Qualities used		*Shaping Qualities used*
	Right Subcortical		Right Internal Capsule
			Right Subcortical
Withdrawal	*Uses more than one gesture*	*Withdrawal*	*Uses more than one gesture*
	Right Internal Capsule		Right Internal Capsule
	Limb moved by torso		
	wmj		
	Right Subcortical		
	Strong Weight Effort used		*Strong Weight Effort used*
	Right Superior Posterior Parietal		Right Superior Posterior Parietal
	Right Internal Capsule		Right Internal Capsule
	Bilateral Cerebellum + Brainstem		
	Shaping Qualities used		*Shaping Qualities used*
	Bilateral Cerebellum + Brainstem		Right Internal Capsule
Release	*Uses more than one gesture*	*Release*	
	Right Internal Capsule		
	Strong Weight Effort used		*Strong Weight Effort used*
	Right Cerebral medially near falx		Right Parieto-Occipital
	Right Parieto-Occipital		Right Internal Capsule
	Right Internal Capsule		
	Shaping Qualities used		
	Bilateral Cerebellum + Brainstem		

DISCUSSION

In summary, both ipsilateral and contralateral skilled limb movements are vulnerable to stroke. In skilled reaching, the flexion and extension of the elbow, ipsiversive and contraversive postural adjustments of the trunk, independent movements of the digits during grasping, and freeing the digits from the grasp upon release of target, are affected in the ipsilateral limb in most stroke subjects. In terms of the non-kinematic aspects of movements, most subjects use Indirect Space and Bound Flow Efforts. The same abnormal kinematic and non-kinematic movements occur in the contralateral limb and extend to the loss of ability on opening the digits on approach, bringing the hand to a position above the target, supinating the limb and bringing the hand towards the mouth, and using Direct Space Effort at the end of the Advance. Furthermore, it seems that placing the palm flat on the lap at the end of the task is affected in both limbs. This loss of movement may be a preservation of energy as it is an instructional, rather than a behavioural, part of the task. In addition to commonly affected subcomponents in the stroke group, certain components were affected in fewer subjects. For example, the subject with a superior posterior parietal lesion displayed abnormalities that include the use of Strong Weight Effort, and the subject with a posterior internal capsule lesion showed dysfunction in all kinematic and non-kinematic aspects except in the use of the pincer grasp.

It is well known that skilled reaching, a voluntary motor behaviour, involves motor areas of the frontal lobe along with their projections to and from the basal ganglia and cerebellum. It is not surprising here that lesions in the cerebellum, internal capsule, and right subcortical areas show more severity of dysfunction globally than cortical lesions. Lesions to the parietal cortex must be considered in the neural control of skilled reaching as various lesions in the right and left parietal lobes display dysfunction in this study.

Both EW-DRS and ERS rating scales were used in the present study because where one scale provides a measure for motor deficits, the other provides a measure for abnormal extraneous movements. After stroke, deficits and extraneous movements are correlated [Appendix 2] as stroke often causes a combination of lost and released movements. Further, loss of function is often correlated with compensatory motor strategies [Cirstea & Levin, 2000]. Comparative studies on skilled reaching using both rating scales in disorders characterized by either lost movements [Parkinson's disease] or extraneous movements [Huntington's disease] would provide further evaluation on the correlations between the two rating scales, as well as insight on the relations between motor deficits and extraneous movements during skilled actions.

This study provides four new insights on the way that skilled reaching breaks down after stroke, with variation in details being lesion dependent. First, Bound Flow Effort is consistently used in all subjects throughout all phases of skilled reaching, suggesting that there is either a disinhibitory release in the tension exerted throughout a movement, or a maladaptive compensatory strategy in the force exerted on the muscles in use. Bound Flow Effort, the increase of pressure, or tension, exerted throughout a movement is likely a separate phenomenon from spasticity.[36] The posterior internal capsule subject has spasticity in the contralateral limb; however, it was noted that during repositioning of the limb, between

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[36] Spasticity is defined as hypertonic muscles due to loss of inhibitory synapse in the central nervous system resulting in the continuous contraction of affected muscles [Kandel et al., 2000].

failed attempts at the task, the subject's limb, though spastic, did not use Bound Flow Effort [Foroud & Whishaw, 2006].

Second, Indirect Space Effort is used in most subjects during their approach towards the target or mouth, suggesting a lack of control, and, perhaps, a compensatory strategy for the loss of control. By increasing the hand's motor attention [Indirect Space Effort] towards the surrounding space of the target, a subject increases the chance of approaching the target without knocking it over. The only subjects who did not use Indirect Space Effort are the ones with left frontal/anterior parietal, and right somatosensory [anterior parietal] lesions.

Third, most subjects display some form of body-limb disintegration. Either the trunk does not make supporting ipsiversive or contraversive postural adjustments during the Advance or Withdrawal phase, or it moves forward and backward in order to bring the limb towards and away from the point of target. For example, during supination and withdrawal, the trunk may lean backwards in order to move the hand away from where the target was placed. In doing so, the distance between the trunk and limb is maintained for a while, thus making it temporarily impossible for the hand to meet the mouth. Subcortical lesion subjects display a combination of body-limb disintegration symptoms, however, most cortical lesion subjects display body-limb disintegration in one form or another. Body-limb disintegration may be disinhibitory, compensatory, or a combination of both effects. The ability to inhibit trunk movements during limb actions may be lost [as is probably the case in subcortical lesions]. Using the trunk to move the limb forward may be a compensatory strategy for the loss of range of motion in the limb, as might be the case in both subcortical and cortical lesions.

Fourth, the temporal aspect of skilled reaching defined by a rhythmic quality between the phases is disrupted. The ERS divides skilled reaching in terms of phases to be performed by single gestures in healthy subjects [Foroud & Whishaw, 2006] that flow from Advance to Grasp to Withdrawal and finish with Release. In some stroke subjects, the gesture[s] from the previous phase is in the process of becoming complete as the actions for the next phase begin. That the hand appears stuck to the pedestal upon grasping the target, and the digits do not release from the grasp as the food is placed in the mouth, are two examples of a lack of motor disengagement. This may be related to a loss in the ability to transition between different phases of the motor behaviour due to an inability to disengage from a motor pattern. Only three subjects, each with parietal involvement [superior posterior parietal, parieto-occipital, deep parietal], did not display one of these two symptoms, which suggests that the inability to disengage, motorically, from a movement phase of skilled action might be modulated primarily in frontal and/or subcortical areas.

Skilled reaching is a behaviour that generates a temporal and hierarchical sequence of acts and neural modulation that involves orienting towards a stimulus, approaching it, grasping it, withdrawing it towards, and releasing it into, the mouth, with supporting movements of the head and torso and a multitude of kinematic postural and non-kinematic inhibitory functions that facilitate the ability to disengage from one phase, in order to engage in the next with efficiency. The simple and generally vital behaviour of reaching is one that integrates the whole body, kinematically and non-kinematically, into an efficient, articulated behaviour. The more it is studied, the more questions arise on its behavioural and neural organization. It makes sense that, in order to understand how such a densely efficient behaviour disintegrates with disease or injury, we must look to how it develops in the first place.

PART II

EARLY ONTOGENY OF REACHING

The richness of the observational evidence is in sharp contrast to the poverty of scientific knowledge.

Frank Beach
Current Concepts of Play in Animals.
The American Naturalist, 1945

CHAPTER 5

Movement Patterns of Skilled Reaching Acquisition in Infants: An Integration from the Parts to the Whole

ABSTRACT

Developmental studies of skilled reaching often begin when the infant is capable of completing the task, which is usually between four and five months of age. The developmental sequence of the behaviour prior to this point remains unknown. The purpose of the present study was to examine the development of reaching movements in infants as young as one month of age. Videotapes of the visually guided reaching behaviour of infants, from the age of four weeks, were analyzed. Notated scores describe four developmental patterns that are positively correlated with increasing age. Results suggest there are four developmental stages of skilled reaching, two of which occur prior to the infants' ability to grasp the target, and that developmental patterns assemble, disassemble, and reemerge in an integrated fashion as the whole behaviour progresses towards a crystallized action. Implications for the evolution of skilled reaching, etiology of neurodevelopmental disorders, recovery of function after neural injury in adults, and parallels with cognitive development are discussed.

INTRODUCTION

One theory for the organization of social and cognitive processes is that they are built upon the development of perceptual-motor integration [Bainbridge-Cohen, 1993]. For example, language is a complex social-cognitive process that is thought to have evolved from reaching movements [Rizzolatti & Arbib, 1998]. Reaching itself is an articulate and sophisticated motor behaviour that serves diverse functional and expressive behavioural outcomes. Developmental studies of skilled reaching often begin when the infant is capable of reaching out, grasping, and withdrawing the target to the mouth, which usually begins around four months of age [Thelen, Corbetta & Spencer, 1996]. Indeed, there are studies that have examined limb movements prior to four months of age where the behaviour of interest was either reflexive [Twitchell, 1969, 1970], or spontaneous [Twitchell, 1970; Wallace & Whishaw, 2003]. Twitchell [1970] described an ontogeny for prehension that begins with the grasping reflex [a synergistic flexion of fingers and all the joints of the limb that can be stimulated through proprioception] that gradually disappears as crude voluntary grasping movements emerge and increases in dexterity with maturation. He demonstrated that during maturation, two opposing reflexes, avoiding [withdrawal] and grasping [approach], overlap in evolution and argued for an effect on the development of posture and movement. Many advances have been made in categorizing the progression from reflexive to purposeful movements. However, a concrete understanding of the development of reaching, from the point at which the infant is incapable of, to capable of, performing the behaviour, has yet to be made.

Smith and Thelen [2003] suggest that ‘development is about creating something more from something less’ and describe three, necessary developmental progressions for the capability of reaching. First, infants must become capable of stabilizing the head; there is a stage at which the developing system is actively working on posture stabilization while maintaining reaching as a goal. Second, infants begin selecting appropriate muscle patterns in order to achieve the reaching goal. Third, reaching, as with all motor development, progresses through a continuous interaction between the nervous system, the body, and the environment [Thelen & Spencer, 1998]. More recently, they have found evidence that suggests reaching movements in infants are not organized by muscles [Clearfield, Feng & Thelen, 2007], a finding that coalesces with the electrophysiological work done on macaques by Graziano [2006]. Studies in recent years have shown that direct pyramidal connections to motor neurons are established before birth, which suggests that the neural capability of visually guided movements of the upper limbs are present long before the emergence of the behaviour. It is possible that the movements that make up reaching are present, although fragmented, early in infancy. Indeed, von Hofsten [1979] has shown that upon the presentation of a target, infants make forward aiming movements while maintaining visual contact with the target.

It may be that through the natural progression of spontaneous movements and their proprioceptive feedback, plus the infant’s sensory, and eventually, motor interactions with the environment, that the movements of reaching become integrated into one efficient and functional skilled action. The question is what is happening between birth and the emergence of skilled reaching; how is reaching put together? The purpose of this study was to examine the behavioural ontogeny of reaching movements in infants from as early as four weeks of age. An ethological approach was used to study the movements performed by infants upon presentation of a visual target.

METHODS

Subjects[37]

A total of twenty-two subjects participated in the study. Four healthy, full term infants [2 males, 2 females] were followed from approximately seven to thirty-six weeks of age. Eighteen subjects participated in the cross sectional analysis, where one male and one female per each four week age interval, beginning at four weeks of age, was made.

Video Recording

Subjects were video recorded weekly in their homes by the experimenter with a Canon 2R40 digital video camcorder at 30 frames per second.

Behaviour

Infants were videotaped while being presented with one of their own toys as a target. Targets were selected, and changed often, depending on the infant's interest and motivation. For example, at thirty-six weeks, one of the infants stopped reaching for the standard toys presented, but engaged in many reaches when presented with a plastic spoon [which had recently joined her toybox]. Targets were presented to subjects at an approximate distance of the infants arm's length; variation in distance occurred at times in order to capture the

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[37] Informed consent to participate in this study was provided by the mothers of all the subjects. The study was conducted with the approval of the University of Lethbridge Human Subjects Ethics Committee.

infant’s gaze. Once the infant saw the target, it was held in place. The analysis on the targets that were presented was made at mid-line. Trials with targets presented from the left, right, or above the child were also completed. However, the behavioural patterns of the infants remained the same as when the targets were presented at midline. Until infants were capable of sitting independently [at which point they participated in the study in a seated position], they were videotaped in the task while lying supine on a blanket and while seated with support by cushions or a standard infant seat [not a car seat] – one that did not encumber the infants’ bodies.

Analysis

Videotapes were analyzed by the experimenter who has an expertise in two, hand-written movement notation systems: Eshkol-Wachman Movement Notation [EWMN] and Laban Movement Analysis [LMA]. Shorthand forms from both movement notations were used to describe gestures [single non-weight bearing actions involving the torso, head, limbs and limb segments], postural movements [weight bearing movements of the body], and the phases of skilled reaching in the infants upon presentation of the target.

EWMN describes the relations and changes in relation between body segments [Eshkol & Wachman, 1958] and has been applied to numerous ethological and behavioural neuroscience studies [Golani et al., 1981; Golani & Fentress, 1985; Pellis, 1981; 1982; 1983]. LMA describes kinematic and non-kinematic [intensity of movement] features of movement and their interaction, thus emphasizing how motor actions are made [Bartenieff & Lewis, 1980; Laban, 1960]. Scientific validity of LMA has been made [Fagen et al., 1997] and it has been used in research in the behavioural neurosciences [Foroud & Pellis, 2003; Whishaw, Gorny, Foroud & Kleim, 2003; Foroud, Whishaw & Pellis, 2004; Vasey, Foroud, Duckworth & Kovacovsky, 2006; Foroud & Whishaw 2006].

Body Organization during Skilled Reaching

The organization of the relationships between body parts during skilled reaching has previously been described in children [e.g., Thelen and colleagues, 1996, 1998, 2007] and adults [Foroud & Whishaw, 2006; Whishaw, 2003; Whishaw et al., 2002]. In both cases, movements involve synergistic movements of the limb segments of the arm toward the target and the mouth with supporting postural movements of the torso. The movements of skilled reaching, and their categorization for two assessment scales, are described in the preceding chapters. Notation systems were used to describe the movements of skilled reaching made by infants in this study. Comparisons with previously defined movements of the task in older age groups, where movement organization may take age-specific forms, may compromise accurate descriptions in young infants.

Phases of Reaching

Previous studies on skilled reaching have described what appear to be phases, or natural divisions, in the behaviour. In the present study, the phases of reaching, as defined below, are evaluated in the development of skilled reaching. [1] Orient: visually and physically orienting the body towards the target; [2] Advance: lifting, aiming, and bringing the limb towards the target; [3] Grasp: grasping the target between the digits; [4] Withdrawal: using the limb to bring the target towards the mouth; and [5] Release: releasing grasp of target while placing it in the mouth and returning the limb to the starting position. Typical skilled reaching in healthy adults involves the use of one gesture to complete each phase [Foroud & Whishaw, 2006].

RESULTS

In the present study, four movement patterns were identified and are described below [Figure 5.1]. Three of the four longitudinal infants progressed sequentially through the four developmental patterns. Video from one male began when he was twenty weeks old and showed that he passed through two of the four movement patterns identified in this study [Table 5.1]. A cross sectional analysis verified the observations made in these four infants [Table 5.2].

Four Developmental Movement Patterns of Skilled Reaching

Movement patterns A and B were performed bilaterally in some cases, unilaterally in pattern C, and both bilaterally and unilaterally, in pattern D. Phases of skilled reaching are present in some form in each of the four patterns.

Developmental Pattern of Reaching A: Movement in Parts

Components of reaching movements of the torso, head, mouth, arms and hands occur independently of one another, in a manner akin to movement babbling.[38] Small contractions and extensions of the torso are made: the contractions cause the head and upper body to move slightly forward towards the target. The head moves up and down on the vertical axis

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[38] Movement babbling is the seemingly spontaneous and random repetition of the small components of a movement which is analogous to the vocal babbling of infants during the development of speech and language.

and is accompanied with opening and closing movements of the mouth. The lips form an "O" shape, similar to sucking movements. The limbs do not move far from the body as they do not lift away from the body; however, small flexions and extensions of the elbow are made, and the limbs sometimes meet at the infant's midline. Partial supinations and pronations with rotatory movements of the limb occasionally accompany elbow flexions and extensions, and occur independently of elbow movements. Random movements of the digits as well as various forms of grasping movements are made.

The phases of reaching behaviour are evident, although they are temporally out of sequence. First, the infant visually Orients towards the target. As a whole, the movements described above appear to be aimed toward the target [Advance phase]. However, when broken down, various fine components can be divided out between Advance and Withdrawal. For example, elbow flexion is a movement component in both Advance and Withdrawal phases and elbow extension is a component of Advance phase. Pronation of the limb is a component of both Advance and Withdrawal phases, and supination of the limb is a component of the Withdrawal phase. Further, the infant moves forward [Advance] and then relaxes backward slightly [Withdrawal], before moving forward again [Advance]. Digit and grasping movements are part of the Grasp [grasp target] and Release [free digits from grasp upon placement in the mouth] phases. Throughout all the movements, visual gaze remains fixed on the target, however, at certain points, the infant simultaneously looks away and stops the movements described above. This could be a Release phase, although in this context, it could be more appropriately referred to as a *disengage* phase. If the target is jiggled in place, or removed and returned to the infant’s midline, the infant will Orient towards the target and begin the sequence of movements described above.

Developmental Pattern of Reaching B: Whole Body Movement

The whole body engages as one motor unit in reaching towards a target. Finer motor components of skilled reaching are no longer visible; instead, the torso contracts, bringing the head, upper torso, and limbs toward the target in one, simultaneous motion. In addition, the limbs sometimes pronate and even extend past the target. When the limbs pass the target, or are sometimes held near enough the target so there is physical contact, the torso continues to contract and the body continues to reach towards the target. The hands make grasping movements, although they are held mostly in the form of a fist. Sometimes, there is flexion and extension of the wrist. At the same time, the mouth is open and appears to be leading the head forward, as though the infant is reaching for the target with the mouth.

Phases of reaching behaviour appear in a similar way, as during pattern A. The infant visually Orients towards the target. Then, the torso, upper body, limbs and mouth reach toward the target, and though they are not making the fine components of reaching, the body is approaching the target as the limb does during the Advance phase. Although the infant does not hold a static posture, time is spent in this forward leaning position with minor perturbations. This could be a precocial Grasp phase, and within this phase, the infant leans back slightly and relaxes this posture before re-establishing the forward leaning motion. This could be a precocial Withdrawal phase of skilled reaching. Similar to pattern A, throughout all the movements, visual gaze remains fixed on the target. However, at certain points, the infant simultaneously looks away and stops the movements described above [Release/disengage]. Again, if the target is jiggled in place, or removed and returned to the infant's midline, the infant will Orient towards the target and begin to engage the whole body as one motor unit, and will reach towards the target all over again.

Developmental Pattern of Reaching C: Integration

Reaching movements of the torso, head, mouth, arms and hands occur in synchrony with whole body movements reaching towards a target. Thus, movement components of skilled reaching and whole body reaching are integrated into a functional behaviour. The limb lifts away from the body, sometimes with flexion and extension of the elbow; at the same time, the body moves towards the target. The infant grasps the target and moves the mouth, head, and torso toward the target in hand. Movements of the limb do not take a direct path toward the target. When the infant's back is not supported by a seat, the path towards the target is even less direct. When the back is supported, the torso remains still while the hand and arm reaches toward the target, grasps it, and brings it towards the mouth. At this point, if the mouth and target are not aligned, the head may lift as the mouth opens and together, the head and mouth close down on the target.

All phases of skilled reaching, except for Release, are clearly visible as the infant Orients towards the target, leans towards the target with the upper torso, head and limbs for Advance, Grasps the target, Withdraws the target to the mouth with a flexion of the elbow and by leaning the torso and head backward and slightly downward into the target as the mouth closes unto it. At this point, the infant does not release the target. The target is held hostage in the infant’s hands and mouth until the experimenter gently nudges the target away and presents it to the infant again, at which time the infant visually Orients towards the target and begins to repeat movement pattern C of skilled reaching.

Developmental Pattern of Reaching D: Inhibiting and Mastering

Discrete targeted and coordinated movements of the arm and hand emerge that are supported by postural adjustments of the torso. Upon orientation, the infant lifts the limb by elbow flexion, extends the limb along a trajectory towards the target, grasps the target, synergistically supinates the limb as it is withdrawn, by elbow flexion, towards the mouth. The mouth closes around the target where it stays. As with pattern C, the hand does not release the target. During these movements, the torso, though not stationary, maintains its posture. The torso makes small movements on its rotatory axis and it looks as though the infant is wobbly.

Similar to pattern C, all phases of skilled reaching, except for Release, are clearly displayed in the behaviour. The infant Orients towards the target, Advances the limb towards the target, Grasps the target, Withdraws the limb with the target to the mouth. Once again, at this point, the infant does not release the target until the experimenter gently nudges the target away and presents it to the infant again. The infant then visually Orients toward the target and repeats the behaviour.

Individual Differences

Female I

12 weeks. While lying supine, upon presentation of the target from the left receptive field, the subject oriented head and eyes, made grasping movements with left hand, and repetitively opened and closed the mouth. The legs and other hand [right] made planar movements, but these were not directed toward the target. The right hand maintained a closed fist position. When the left hand was in a closed position, the subject made planar movements originating from the wrist. When the left hand was open, the left arm made planar movements while the mouth engaged in sucking movements. When the toy was placed in her hand so that she could grasp it, she maintained a firm grasp, and held it at arm's length while continuing to make pattern A types of movements toward the target with her head and mouth.

13 weeks. While seated in an infant chair, the subject still made pattern A types of movements, however, the movements were now more distinct. The head made many more movements in the sagittal plane, which could be a response to movements originating in the torso. The infant used Shapeflow and this quality of movement in the torso may have affected the stability of the head. There are some moments, before the torso became engaged, when the torso was still and the head clearly launched forward towards the target. The mouth was also making opening and closing movements as though she were reaching towards the target with her mouth. Although at this point in development, the phases of reaching blur together, Orient, and Release/disengage were distinct.

14 weeks. The first observation of pattern B is was made. While seated, the entire body moved towards the target. The hands met in the middle across the infant's torso, grasped each other and moved toward the mouth - which was still reaching towards the target. Upon contacting the mouth with the hands, the subject relaxed briefly and, at this point, could suck on her hands prior to beginning to reach towards the target with the entire body once again.

16 weeks. The first observation of pattern C is made. While seated, the infant successfully reached out with the limbs, grasped the target and brought it to her mouth. Although the torso was stable, it was supported by a chair.

19 weeks. The infant sat in a new chair that did not offer back support. She still made pattern C types of movements. This time, her torso moved forward, with the limbs reflecting her inability to inhibit the torso while the limbs moved away from the body. Her limb movements were curve-like and did not follow a direct path toward the target. When withdrawing the target towards her mouth, the torso moved forward, and, at the same time, she reached for the target with her mouth. The hand and mouth moved toward each other.

26 weeks. The first observation of pattern D was made. The infant was seated in a chair that did not offer back support. The limb took a direct path towards the target and the torso was maintained in a stable posture while performing the task, though it made small movements by circling on its axis.

Female II

7 weeks. While lying supine, the subject made pattern A types of movements with the arms, hands and legs, but rather than opening and closing the mouth and moving the head towards the target, she engaged in the rooting and sucking reflex while maintaining a fixed gaze on the target.

9 weeks. Still made pattern A types of movements. The hand occasionally contacted the target, but continued to make pattern A movements. She did not grasp onto the target or withdraw the hand to the mouth.

10 weeks. Movements performed seemed to be between patterns A and B. Upon presentation of the target, the infant moved in a pattern A style. However, through the course of the movement, the pattern changed, and it appeared as though the whole body was engaged in movement towards the target in a fashion similar to pattern B types of movement.

12 weeks. The first observation of pattern B was made and was similar to Female I, but with less intensity. If the target were placed in the infant's hand, she continued to make pattern B types of movements.

16 weeks. First observation of pattern C types of movements, which were similar to movements performed by Female I at 16 weeks.

26 weeks. First observations occurring in which the subject could sit without support. She still used pattern C types of movements and was reaching bilaterally.

35 weeks. The first observation of pattern D was made. The infant was seated on the floor, independent of support, performing the reach unilaterally. She continued to organize her movements in a typical pattern D fashion while reaching for toy rings [~ 5.7 x 3.2 x 0.6 cm] as well as rice puffs [~ 0.5 x 0.3 x 0.3 cm]. Although her actions were the same, unlike when reaching for the toy rings, she did not seem to get many rice puffs into her mouth.

Male I

20 weeks. The first observation of pattern C was made. The infant was seated in an infant's chair with back support. His torso was stable and the limbs followed a direct path toward the target. Unfortunately, this was the first video sample of this infant for this study. He may have initiated pattern C types of movements in earlier weeks.

31 weeks. The subject was capable of sitting on the floor, independent of support, however, upon initiating the task, he attempted to crawl away. When seated in his high chair with the tray removed, he used pattern D types of movements when reaching for toy rings and rice puffs. As with Female II, though his actions were the same as when reaching for the toy rings, he did not seem to get many rice puffs into his mouth.

Male II

7 weeks. The first observation of pattern A was made. The subject engaged in all the characteristics of pattern A described above [see Female I], but with less intensity. As movements of the torso were made toward the target, they seemed to be led more by the pelvic girdle than by the head and mouth.

10 weeks. Similar to Female II, upon presentation of the target, the infant briefly made pattern A movements, followed by pattern B movements.

14 weeks. The first observation of pattern B was made. All the characteristics of pattern B were present, including head and mouth movements. However, they were performed with less intensity than by the two female subjects. If the target were placed on the belly, the hands would grasp it - although there was no withdrawal upon grasping.

15 weeks. The first observation of pattern C was made. When seated in an infant's chair, he reached unilaterally. However, when seated on the floor with cushions placed behind him for soft support, he performed the reach bilaterally.

31 weeks. The first observation of pattern D was made. The subject sat in his high chair with the tray removed. He performed the task bilaterally upon presentation of a toy ring, and unilaterally for rice puffs. In both cases, he used pattern D types of movements. Again, although his actions were the same, he did not seem to get many rice puffs into his mouth.

Cross Sectional Analysis

All four movement patterns of reaching were observed in the cross sectional group, thus verifying that the patterns observed are not limited to the four infants described above [Table 5.2]. Pattern A types of movements were observed in five infants, pattern C in six infants, and pattern D in two infants. Some infants displayed movements that involved two patterns. Three infants performed the task with patterns A and B types of movements, however, in each case, the B pattern of movement, where the whole body moves as a unit towards the target, was more clear than pattern A movements. Two infants performed a combination of patterns C and D types of movements. In both cases, pattern D was dominant and it appeared as though pattern C versus D patterns depended upon the body parts [e.g., arm versus torso] and phase of reaching [e.g., Advance versus Withdrawal]. Regardless, there appears to be a positive correlation between the movement patterns described in this study and age. Patterns A and B are likely to be performed by younger infants and patterns C and D in older infants [$r = 0.957$; $p < 0.0001$] [Figure 5.2].

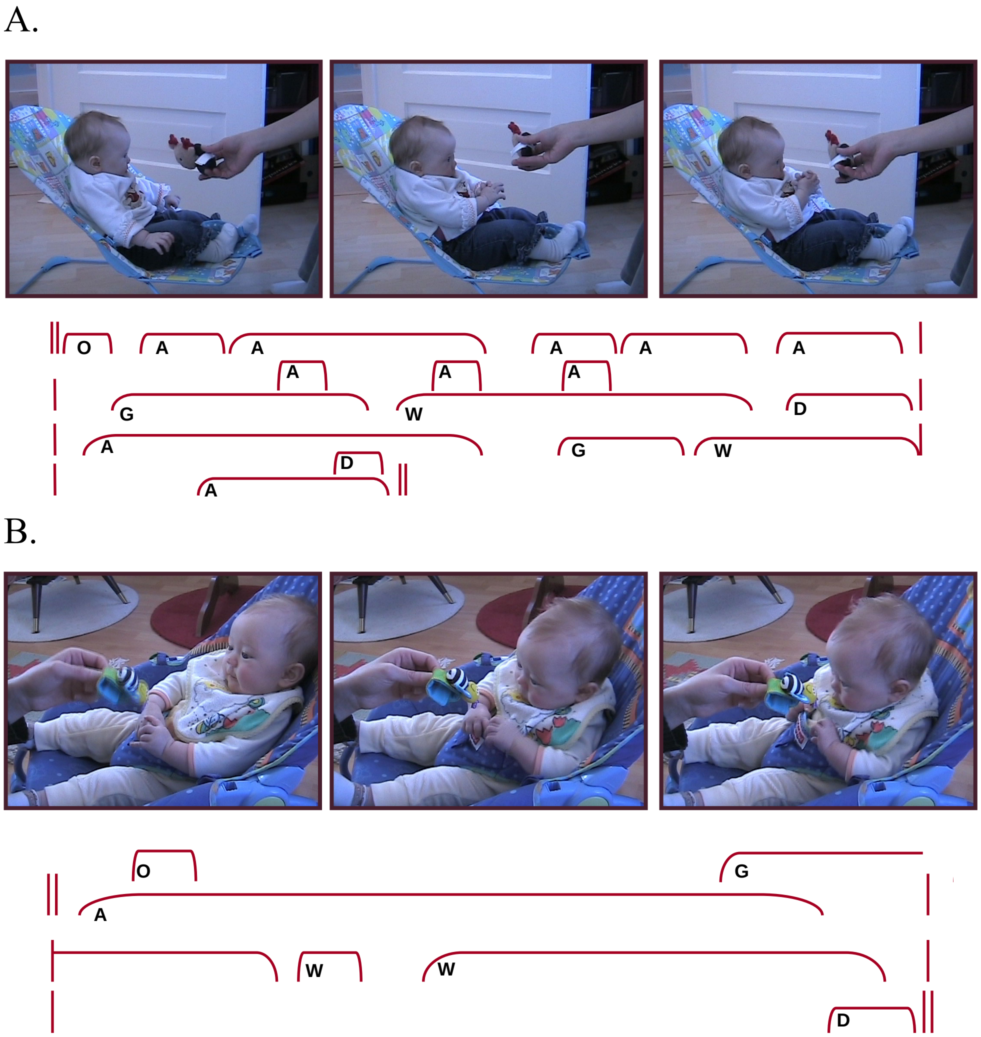


Figure 5.1 Phases of Skilled Reaching in Four Developmental Patterns. Photographic

sequences are taken from video frames of one of the females in the longitudinal group, are read from left to right, and are from a single trial in each of the developmental patterns. Notated scores of the phases of reaching, O- Orient, A- Advance, G- Grasp, W- Withdrawal, D- Disengage/R- Release, are read from left to right and begin and end with double bar lines. Single bar lines at the beginning and ending of columns within the notated scores connect the sequence. The length of the bows reflect the time spent during the representative phase. A] Developmental Pattern of Reaching A: Movement in Parts [12 weeks]. B] Developmental Pattern of Reaching B: Whole Body Movement [14 weeks].

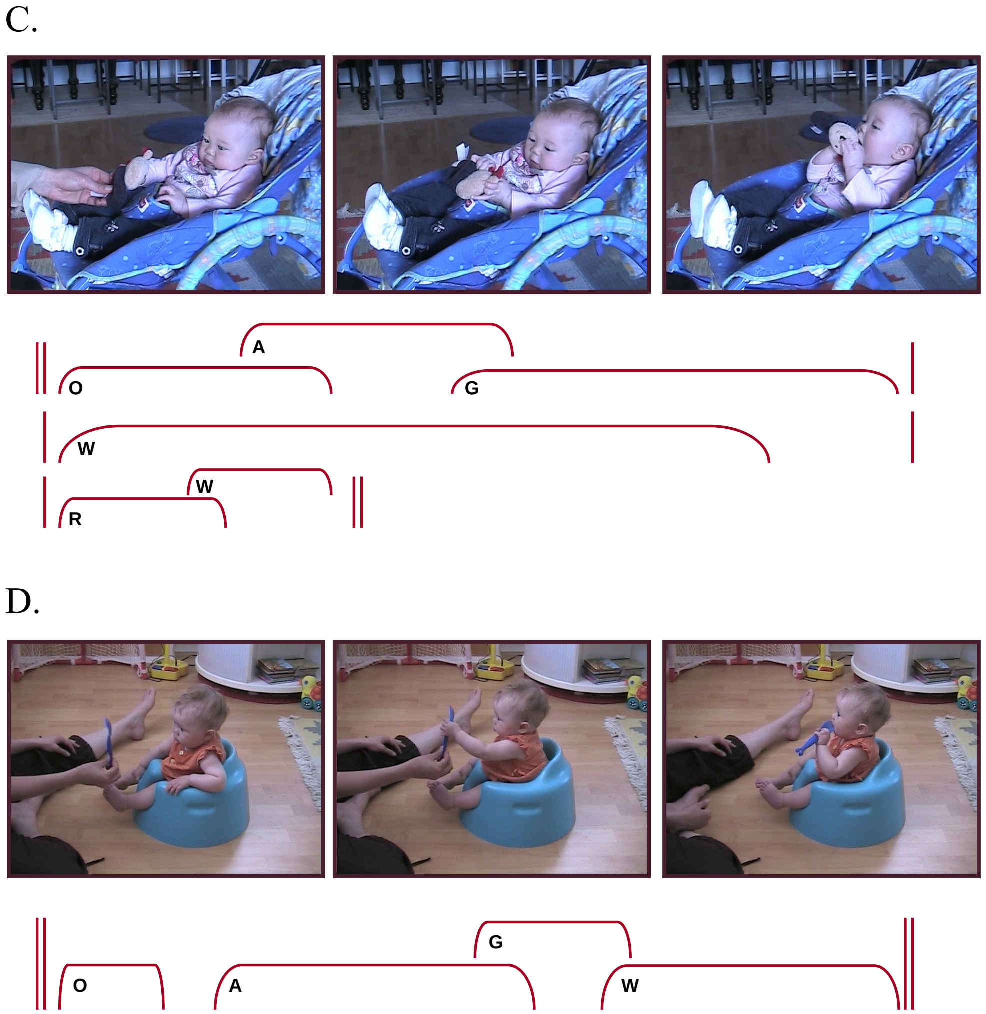


Figure 5.1 [*continued*] C] Developmental Pattern of Reaching C: Integration [16 weeks]. D] Developmental Pattern of Reaching D: Inhibiting and Mastering [26 weeks].

Table 5.1 Movement Patterns of Skilled Reaching in Infants from the Longitudinal Group. Movement patterns of skilled reaching [A, B, C, or D] observed in infants from the longitudinal group marked at the age of first observation. Data previous to 20 weeks is missing from Male I.

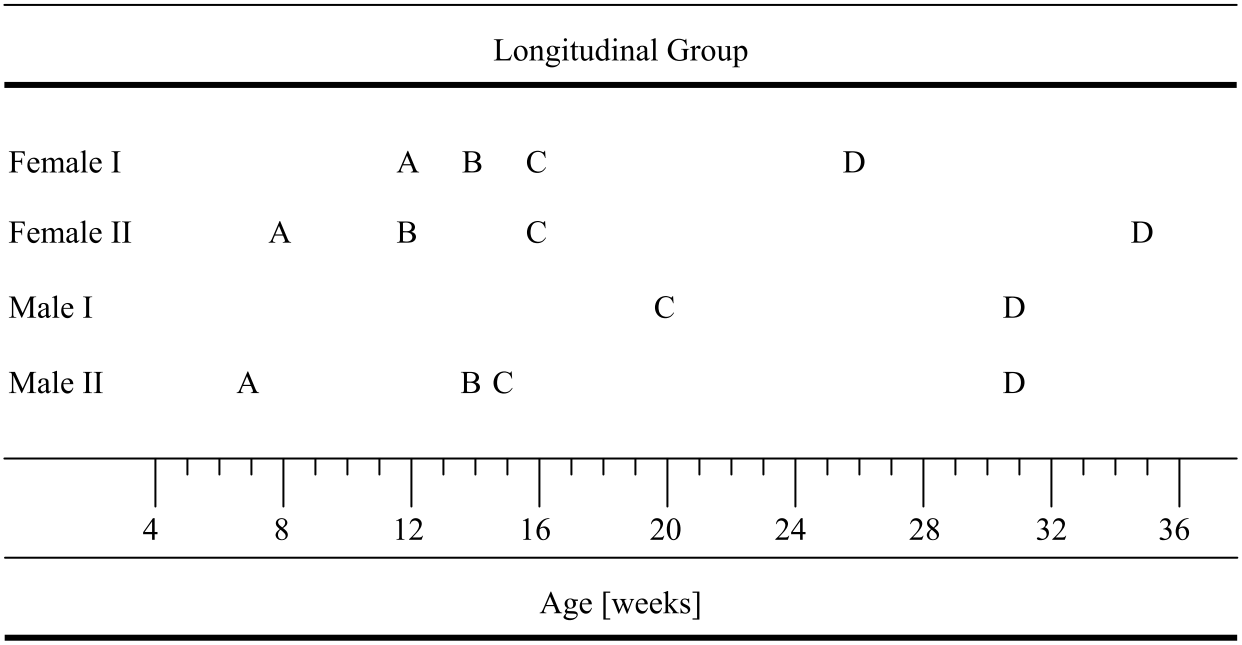


Table 5.2 Movement Patterns of Skilled Reaching in Infants from the Cross Sectional Group. Where two patterns are marked [e.g., B/A], both are observed within single trials and the pattern marked first [i.e., B] predominates.

Cross Sectional Group	4	8	12	16	20	24	28	32	36
Female									
1	A								
2		A							
3			B/A						
4				B/A					
5					C				
6						C			
7							C		
8								D/C	
9									D
Male									
1	A								
2		A							
3			A						
4				B/A					
5					C				
6						C			
7							C		
8								D/C	
9									D
Age [weeks]	4	8	12	16	20	24	28	32	36

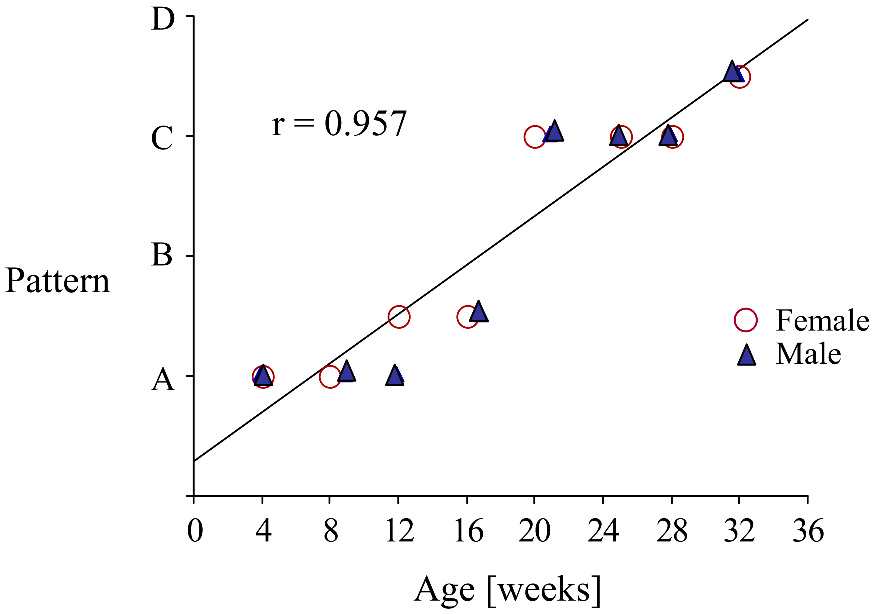


Figure 5.2 Correlations between the Movement Patterns of Skilled Reaching in Infancy and Age

DISCUSSION

The present study identifies a natural progression of skilled reaching that can be classified by four movement patterns, all of which begin with visual orientation. In pattern A, many incomplete and fragmented movement components of skilled reaching occur. In pattern B, movement components of reaching are no longer visible; instead, the infant moves the entire body as a single unit towards the target. A combination of movements from patterns A and B occur in the pattern C, where movement components of skilled reaching and whole body reaching integrate into a functional behaviour for what appears to be the first time. Even so, when reaching from a seated position with no back support, the body is not fully inhibited in its movements and tends to flop forward with the advancement of the limb. Finally, in pattern D, the infant reaches for, grasps, and withdraws the target to the mouth with the limb while maintaining relative postural stability.

Each of the four movement patterns can be divided into the phases of reaching where Advance, Grasp, and Withdraw are all present in some form. In patterns A and B, the Release phase seems to be present as well; if left alone, the infant will eventually disengage from the task by looking away and will either stop moving, or begin to squirm. Finally, the movement patterns appear in a developmental sequence that could potentially be classified as the developmental stages of skilled reaching acquisition. Infants in the longitudinal study progress sequentially through patterns A to D and there is a positive correlation between movement patterns and age in the cross sectional analysis. It may be that patterns A, B, C, and D are movement patterns that are part of the four developmental stages of skilled reaching.

Specific motor patterns within each developmental movement pattern may peak and recede. For example, von Hofsten [1979] described a developmental progression for reaching that matches with pattern A movements from the present study. On presentation of an object, infants made more forward movements aimed at the target than other types of movements while maintaining visual contact. Concurrently, infants extended the arms with an open handed posture. The number of reaching movements upon object presentation decreased gradually with age until reaching a minimum in frequency by seven weeks of age. This was then followed by a dramatic increase. Further, as the number of reaching movements changed with age, so did the concurrent hand postures; infants used more open postures until seven weeks of age when more closed fisted postures were observed. Finally, as the number of reaching movements increased, open hand postures were used more often than closed fisted ones [von Hoften, 1979; 1980; 1982; von Hofsten & Lindhagen, 1979].

The temporal relationship between the natural phases of skilled reaching appears to have a developmental progression as well. Notations from previous studies [Alveradashvili, Foroud, Lim & Whishaw, 2008; Foroud & Whishaw, 2006] describe little to no overlap in the phases of reaching. If there is overlap, the movements for one phase end as the movements for the second phase begin. After lesions to the motor cortex in rats, the sequence and timing between the phases change [Alveradashvili et al., 2008]. This was observed in the first two developmental stages of reaching in the present study as the phases of reaching occurred within each other. For example, there may be an Advance phase followed by another Advance phase in which two Withdrawal phases occur. Although there was overlap between the phases of reaching in Stages 3 and 4, the overlap was relatively short in temporal duration compared to earlier stages and the phases were clearly defined.

A temporal overlap may also occur in the stages in ontogeny. Both Female II and Male II infants progressed through the stages, however, movements from the previous stage lingered after a new stage began. During this transition, patterns from the previous stage [e.g., pattern A] were observed, though not with the same intensity or duration of the newly acquired pattern [e.g., pattern B]. Further, it seemed that the infants became better at their current stage [e.g., Stage 2] each week until the emergence of the following stage [e.g., Stage 3]. The progression and recession of patterns in body organization and phases of skilled reaching within developmental patterns A to D, along with the temporal overlap between developmental Stages 1 to 4, suggest a cyclical and repetitive nature to the development of skilled reaching. Specific components of skilled reaching assemble, disassemble, and reemerge in an integrated form, as the whole behaviour progresses towards a crystallized action [Figure 5.3].

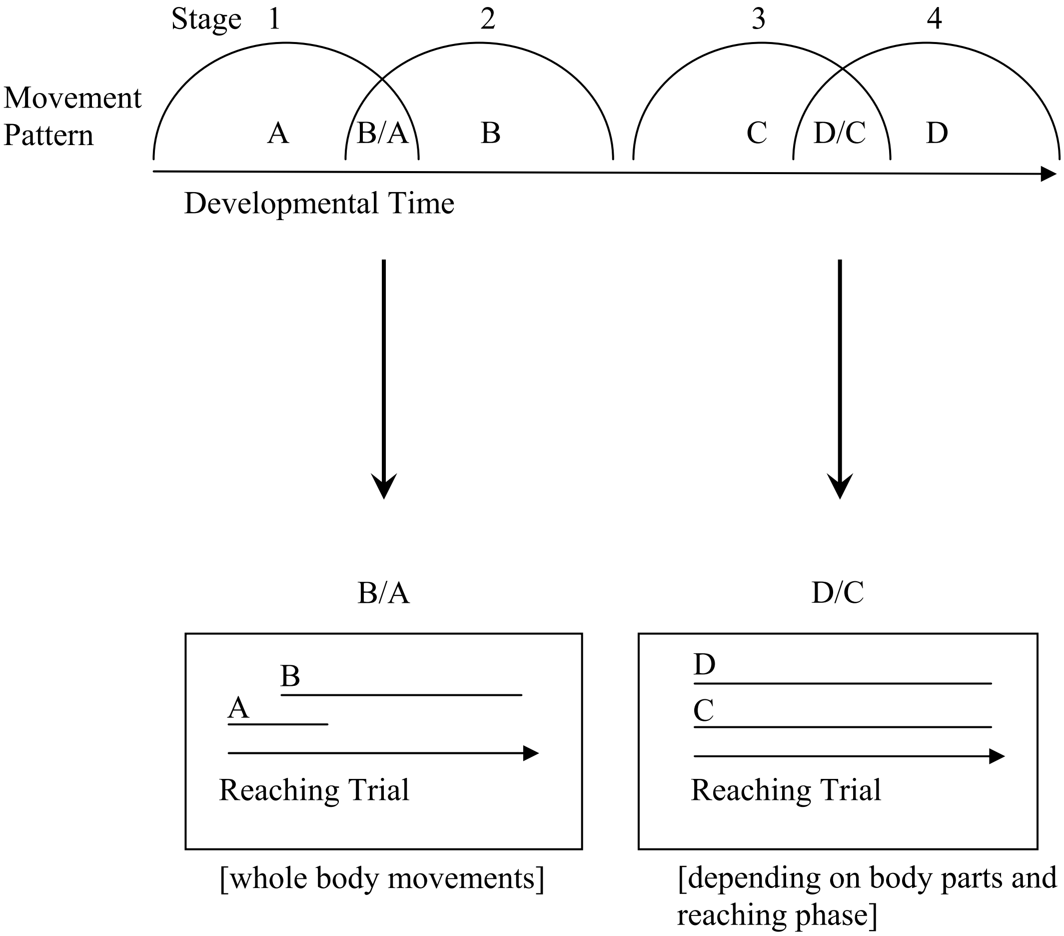


Figure 5.3 Proposed Model for the Progression of the Developmental Sequence of Skilled Reaching. A temporal overlap between the ontogenetic stages of reaching between movement pattern A, typical of Stage 1, and movement pattern B, which emerges at the onset of Stage 2. During the transition between Stages 1 and 2, movement pattern A occurs at the beginning of the task and gradually change to pattern B types of movements within the same trial. During the transition between Stages 3 and 4, patterns C and D co-occur and depend on the body part or the phase of the reaching behaviour [e.g., Advance, Grasp, or Withdrawal].

One principle of movement described in LMA theory known as Action-Recuperation states that for every action, the body requires a recuperative reaction. Recuperation prepares the body to return efficiently to, and perform, the former action. In actions that are maintained at a high intensity for long periods of time, small recuperative movements emerge and even cycle through the action in order to support the intensity of the action. This cyclic pattern was observed in the first two developmental stages of reaching. Although the infant's movements were continuously aimed toward the target, small withdrawing movements [i.e., extension of the torso during pattern A] were made without sacrificing the global advancing movements.

Movement patterns specific for the acquisition of skilled reaching described in the present study encompass the three, necessary developmental progressions for enabling reaching as described by Thelen and Spencer [1998]. In the first stage [pattern A], the infant makes many single and synergistic movements that are components of reaching, though not temporally sequenced. Postural movements of the head and torso are included in these movements and are not similar to the adult expression of supporting postural movements for reaching [Whishaw et al., 2002]. They are, however, similar to those exhibited in the second and third stages [patterns B and C] of reaching described in this study. Such postural movements may serve as an opportunity to explore stabilization of the head during movement. Furthermore, during this time, the movements of the mouth, limbs, and upper torso are focused toward the target. That is, it appears that the infant is engaged in posture stabilization while maintaining reaching as a movement goal. In the third developmental stage of reaching, infants use the limb to reach for, grasp, and withdraw the target at the same time that the torso and head lean in toward the target and sink downward as the limb withdraws to the mouth. This stage may be a period in which infants begin selecting appropriate muscle patterns in order to achieve the reaching goal. Finally, throughout all four developmental stages, the infant is continuously engaged in interactions between the senses, the body, the environment, and the nervous system. This may in part be the driving progression through the stages. Movements in the fourth stage [pattern D] become refined with experience in the next few months and throughout childhood, the details of which have been described in several studies [e.g., Armbrüster & Spijkers, 2006; Konczak, Jansen-Osmann & Kalveram, 2003; Olivier, Hay, Bard & Fleury, 2007; Schneiberg, Sveistrup, McFadyen, McKinley & Levin, 2002; Thelen & Spencer, 1998].

Inhibitory pathways form a critical component of the motor nervous system. Consider an adult reaching for a glass of water: the movements seem limited to those of the limb, head and mouth. A closer look reveals subtle lateral movements of the torso that support limb movements. Concurrent, and perhaps coupled, movements of the torso, legs, head and opposing arm remain invisible - they are inhibited so as to allow for the creation of a smooth and efficient reaching act [Llinás, 2002]. Indeed, after neural injury, such as stroke, some inhibitory pathways may be damaged causing the movements under their regulation to *release* [Jackson, 1932]. Uninhibited movements are abundant in the earlier stages of the four developmental stages of reaching described in this study. It may be the case that inhibitory pathways are established as the infant progresses through the four stages. That is, inhibitory pathways that are specifically relevant to reaching are laid down as the infant engages in incomplete, goal directed movements of the whole body, and become solidified in the latter stages of reaching when the torso is relatively still during the behaviour. In the fourth stage, the infant's torso circles on its own axis without contracting or leaning forward. At this stage, the infant appears to be wobbly, and this may be the emergence of the inhibitory torso movements during skilled limb movement.

In the first two stages, movements of the mouth and head are striking and are still exaggerated in the third developmental stage of reaching as compared to the fourth. In the first two stages, it appears as though the infant is reaching with the mouth. This observation suggests that reaching may be organized for movements made by the mouth and transitions to the limb throughout development. There are five major movements involved in breastfeeding [Bainbridge-Cohen, 1993]. The infant must reach for the nipple with the mouth, grasp it [with the mouth], make sucking movements, swallow, and finally release the nipple. These movements parallel limb reaching, as the mover must reach for the target, grasp it, withdraw it to the mouth, receive it into the mouth as the hand releases the target, all of which is followed by chewing and swallowing movements of the mouth.

Developmental motor sequences within a behaviour are both hierarchical and temporally sequential [Pellis, Pellis, Chen, Barczi & Teitelbaum, 1989]. Developing neural correlates of a motor sequence may be dominant, even suppressive, over other sequences, and such dominance may shift through the course of development [Pellis, Pellis & Teitelbaum, 1991]. No doubt such shifts in dominance of motor sequences would be present in the transition from reaching with the mouth to reaching with the limb. Reaching may be driven by different systems that fluctuate in dominance through the course of development, with earlier stages driven by the mouth, and may be reflective of phylogeny.

This study demonstrates that various patterns in motor organization of reaching wax and wane throughout development and eventually integrate into the adult typical behaviour, at which point, subtle components of the skill may be refined. This knowledge could potentially be applied to establishing markers for motor development as well as for the assessment of childhood and adult disorders. Teitelbaum and colleagues [1998; 2002; 2004] have shown that developmental motor patterns in children with autism are abnormal in infancy specifically due to dysfunctional reflexes. Such abnormal motor patterns in early development result in different sensorimotor experiences compared to non-autistic children. Together, the abnormal reflexes and affected sensorimotor experiences contribute to later motor, social and cognitive development [Teitelbaum et al., 2002; 2004].

The sequential progression of motor patterns observed in this study may be present in a variety of behaviours for motor development and may even be relevant for the development of cognitive processes - which often follow the same developmental patterns of motor development. The developmental stages of locomotion described by Thelen and Fisher [1982] follow a similar motor sequence where the movements occur in parts in early stages, then as a whole in following stages, and, finally, integrate into the typical adult patterns that become smoother with age. The same developmental progression seems to exist in the perceptual-motor abilities of speech in infancy that ‘bootstrap’ speech production [Vouloumanos & Werker, 2007; Werker, 2003; Werker & Tees, 1992; 1999].

An investigation of skilled reaching in infants and children with autism could be useful for the classification of the disorder and the design of early markers for diagnosis and therapeutic interventions. Further, principles for the development of skilled reaching can be applied to investigations of diseases where skilled limb movements are lost, such as Parkinson’s disease, Huntington’s disease, and stroke. Indeed, parallels between the evolution of behaviour in development and that of degenerative disorders, as well as recovery after brain injury have been demonstrated [Denny-Brown, 1958; Denny-Brown & Chamber, 1958; Hines, 1942; Georgopoulos, 1986; Golani, Bronchti, Moualem & Teitelbaum, 1981; Lakke, 1985; Pellis, 1995; Pellis et al., 1989; Teitelbaum, 1967; Teitelbaum, 1971; Teitelbaum, Cheng & Rozin, 1969a; b; Teitelbaum, Wolgin, DeRyck & Marin, 1976; von Hofsten, 1979].

PART III

ONTOGENETIC MOVEMENT PATTERNS for REACHING after STROKE

Observe the wonders as they occur around us.

Rumi
The Essential Rumi [Translated by Coleman, 1995]

CHAPTER 6

Motor Patterns Typical of Early Development Occur after Stroke in Adults

ABSTRACT

The hypothesis that recovery from brain injury recapitulates ontogeny has been supported by animal studies on brain function and behaviour. Twitchell [1957] described parallels between natural human development of limb movements and recovery after stroke. Recent studies on the development of skilled reaching have identified a series of developmental stages that commence prior to the acquisition of the skill. In light of these new findings, the purpose of this study was to investigate whether skilled reaching performed by adult stroke patients can be characterized by the normal developmental stages in infancy. Results suggest that various parameters that organize skilled reaching such as the temporal sequence of the phases, nature of postural support, inhibition of non-kinematic features of movement, and integration between torso and limb movements can change after stroke. These changes can be due to compensatory strategies or released phenomena, thus adding new dimensions to the organizational rules for the behaviour after stroke. Further, stroke patients can be characterized differently, depending on a choice of measures.

INTRODUCTION

Studies in mammals have shown parallels between behavioural characteristics typical of development and recovery after brain damage in a variety of behaviours including postural support, locomotion, feeding, exploration, and limb movements. Adult rats and cats with lateral hypothalamic lesions will cling to a vertical surface for long periods of time and gradually droop downward rather than climb up and out of the position. This pattern changes, upon wrapping the head with a bandage so that the head falls backward, causing hyperextension of the neck and limbs and eventually leading to a release in grasping [Chen, Pellis, Sirkin, Potegal, & Teitelbaum, 1986; Teitelbaum, Wolgin, DeRyck & Marin, 1976; Van Harreveld & Kok, 1935]. This phenomena, termed bandage backfall, is likely the inhibition of vestibular and propioceptive reflexes [Schallert & Teitelbaum, 1981] during vertical clinging, and also occurs in healthy rat pups, kittens, puppies, infant rabbits, monkeys and humans as well as in adults with severe Parkinson's disease [PD] [Teitelbaum et al., 1976]. Locomotion and posture recover after stroke in rhesus macaques in a similar fashion as their developmental progression [Hines, 1942]. In rats, recovery of feeding behaviour from lateral hypothalamic lesions progresses through developmental stages of feeding specific to the species [Teitelbaum, 1971; Teitelbaum, Cheng & Rozin, 1969a; b], and recovery from akinesia follows the developmental sequence of warm up for exploratory behaviour [Golani, Bronchti, Moualem & Teitelbaum, 1981]. The development of forelimb placement and its recovery from lateral hypothalamic lesions in cats follow the same motor sequelae in both sensory and motor modalities [Wolgin, Hein & Teitelbaum, 1980]. Rats with lateral hypothalamic lesions recover righting [turning from supine to prone] systems in a similar fashion as the progression of such systems during ontogeny [Pellis, 1996; Pellis et al., 1989]. Further, this serial gain in righting systems during both development and recovery in rats appears to be the opposite in the successive deterioration of PD in humans. The degenerative progression of the disease leads to axial apraxia - the inability to use proximally driven movements to initiate voluntary righting [Lakke, 1985; Pellis, 1996]. Finally, acceleration of movement is discontinuous in reaching limb movements in healthy adults, however, in infants, it develops gradually with a series of smaller movements. Larger amplitudes in movement are achieved with age as movement acceleration becomes discontinuous [von Hofsten, 1979]. This progression gradually disassembles in PD as the disease progresses [Georgopoulos, 1986].

Humans recovering from stroke to the motor system will display a variety of symptoms specific to the site of the lesion, personal experience, and compensatory strategies acquired after the event [Cirstea & Levin, 2000]. One common problem after stroke is the loss of inhibition where the higher levels in the brain that exude control over the lower levels of which they are built upon become lost [Jackson, 1884; Teitelbaum, 1967]. By studying intrinsic reflexive behaviours in newborn infants that wane as voluntary movements develop, and comparing them with the motor abnormalities after brain damage in adulthood, Teitelbaum demonstrated how the ‘disappearing reflexes’ of infancy are cortically inhibited and thus *released* upon cortical brain damage [Denny-Brown, 1958; Denny-Brown & Chamber, 1958; Teitelbaum, 1967].

Twitchell [1957] described parallels between natural human development and recovery from hemiplegia after stroke in adults. In limb actions, movement progresses from gross, whole body engagement to proximal control of synergistic movements in the arm, which emerge as infantile reflexes become inhibited. Finally, finer skillful articulations of the distal portions of the limb, such as the hand and fingers, may occur, depending on lateral corticospinal tract involvement. Previous studies of skilled reaching have defined natural divisions, or phases, in the behaviour [Alveradashvili, Foroud, Lim & Whishaw, 2008; Foroud & Whishaw, 2006; Whishaw, Suchowersky, Davis, Sarna, Metz & Pellis, 2002]. In normal adult behaviour, the phases of skilled reaching are defined by a single gesture [a gesture often includes multiple body parts moving in a synergistic way] that is required to complete the phase and the timing between each phase. Prior to the acquisition of reaching behaviour, infants from approximately two to five months of age progress through four developmental stages where each stage can be characterized by how the phases of reaching are organized. The purpose of the present study was to investigate whether the developmental stages of skilled reaching appear in adults after stroke. Results show that after stroke, the phases of reaching can become blurred, interrupted, repetitive, and even out of order. This study thus provides new information on the global aspects of what the constituents are of reaching, such as sequence, rhythm, and flow, and how they can fall apart after stroke.

METHODS

Subjects

Videotaped data from the twelve stroke subjects [mean = 69.91 ± (SD) 7.78, SE = 2.35 years of age, six males and eight females] and their matched controls [mean = 68.27, ± (SD) 7.19, SE = 2.17 years of age, six males and eight females] from Chapter 4 were examined in this study. Of the stroke group, five were post-acute [i.e., were within the first six months of having had a stroke] and seven were chronic stroke subjects [i.e., had had a stroke at least two years prior to the study]. Lesions were varied in terms of hemisphere, level, and location. Hemiplegia was diagnosed in the contralateral limb in 9 subjects, and in the ipsilateral limb in 1 subject. Two subjects had bilateral lesions, one of which had cerebellar and brainstem lesions with paresis in both limbs and one who was hemiplegic with lesions at both cortical and subcortical levels.

Reaching Task

For the reaching task [Whishaw et al., 2002], subjects were asked to reach for a piece of food and withdraw it to the mouth to eat. Subjects were comfortably seated on a chair with a pedestal, with an adjustable post positioned directly in front of them at a distance of approximately 10 cm beneath their outstretched palm. Subjects were instructed to place both hands on their thighs, with their palms flat and to reach for a food item that was placed on the pedestal. Subsequent instruction consisted simply of telling the subject when to begin and which hand to use. All subjects were asked to perform the task with each arm. Subjects were given a choice of one of the following food items: Smartie, raisin, dried cranberry, jellybean, gumdrop, or shelled peanut.

Video Recording

Two Canon 2R40 Digital Video Camcorders [30 frames/second] were used. One camera was placed in front of the subject to capture a whole body view. The second camera placed in front of the subject captured a close up of the subject's hand when grasping the food item. Video was uploaded onto a G4 Macintosh computer and viewed in iMovie for frame-by-frame analysis.

Analysis

For this study hand written movement notations from each stroke subject were compared to the control group and with the developmental stages of reaching. Notations are derived from the Eshkol-Wachman Movement Notation system [Eshkol & Wachman, 1958] and were used to describe the phases of reaching.

Phases of Skilled Reaching

Number of frames for each phase of reaching, Advance, Grasp, Withdrawal, and Release, were counted [Table 6.1].

Table 6.1 The Phases in Skilled Reaching.

Phases of Skilled Reaching	
Orient	visually and physically orienting the body towards the target
Advance	lifting, aiming, and bringing the limb toward the target
Grasp	grasping the target in the hand, or between the digits
Withdrawal	using the limb to bring the target towards the mouth
Release	releasing grasp of target while placing it in the mouth and returning the limb to the starting position

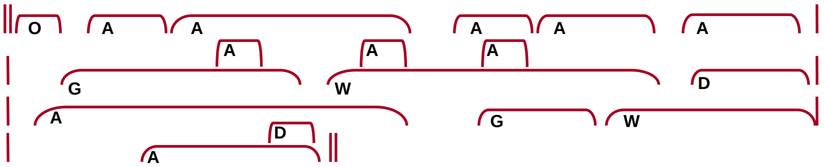
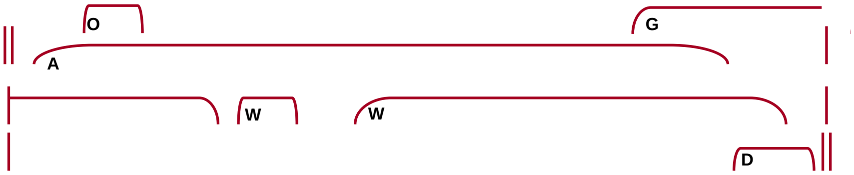
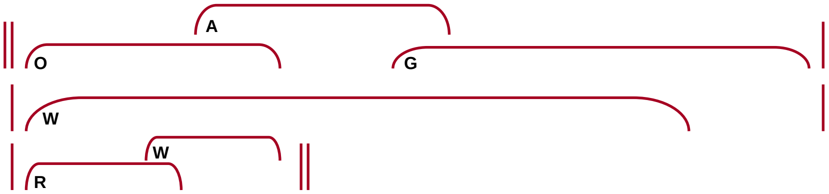
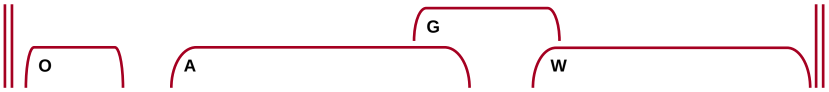
Duration Between Phases

Number of frames between Advance and Grasp [A-G], Grasp and Withdrawal [G-W], and Withdrawal and Release [W-R] phases were counted. In instances of temporal overlap between phases, for example, if the subject continued to Advance during the first two frames of the Grasp phase, the number of frames of overlap were calculated negatively, for example, -2.

Developmental Stages of the Phases in Skilled Reaching

Stroke subjects who deviated from the control group were compared with notations of reaching phases in the four developmental stages of reaching [Table 6.2].

Table 6.2 Developmental Stages on the Phases in Skilled Reaching

Developmental Stages of the Phases in Reaching		
Stage 1	Phases vary in duration, are repetitive, temporally out of sequence, and some phases occur within other	
Stage 2	Phases are typically long in duration, overlapping, and repetitive.	
Stage 3	Phases are long in duration and overlapping.	
Stage 4	Phases are shorter in duration than in Stage 3 and have less overlap.	

Stage 1. Phases vary in duration, are repetitive, temporally out of sequence, and some phases occur simultaneously. For example, Advancing and Grasping movements, though functionally unsuccessful, may co-occur.

Stage 2. Phases are typically long in duration, overlapping, and repetitive. However, they are generally less repetitive than in Stage 1.

Stage 3. All phases of skilled reaching are clearly visible and in sequence, though they are long in duration and overlapping. A phase may be repeated on occasion.

Stage 4. All phases of skilled reaching are clear; they are shorter in duration than in Stage 3 and have less overlap.

RESULTS

Control Group

Phases of Reaching

Repeated measures ANOVA were used for number of frames for each reaching phase by sex and by limb. There were no significant differences [p always > 0.1] except for comparisons between phases [$F [3,36] = 28.525$, $p < 0.0001$]. This suggests that the duration of each phase varies. Posthoc Fisher's PLSD showed differences in all phases [$p < 0.005$] except when comparing the Withdrawal and Release phases [$p > 0.1$] [Figure 6.1A].

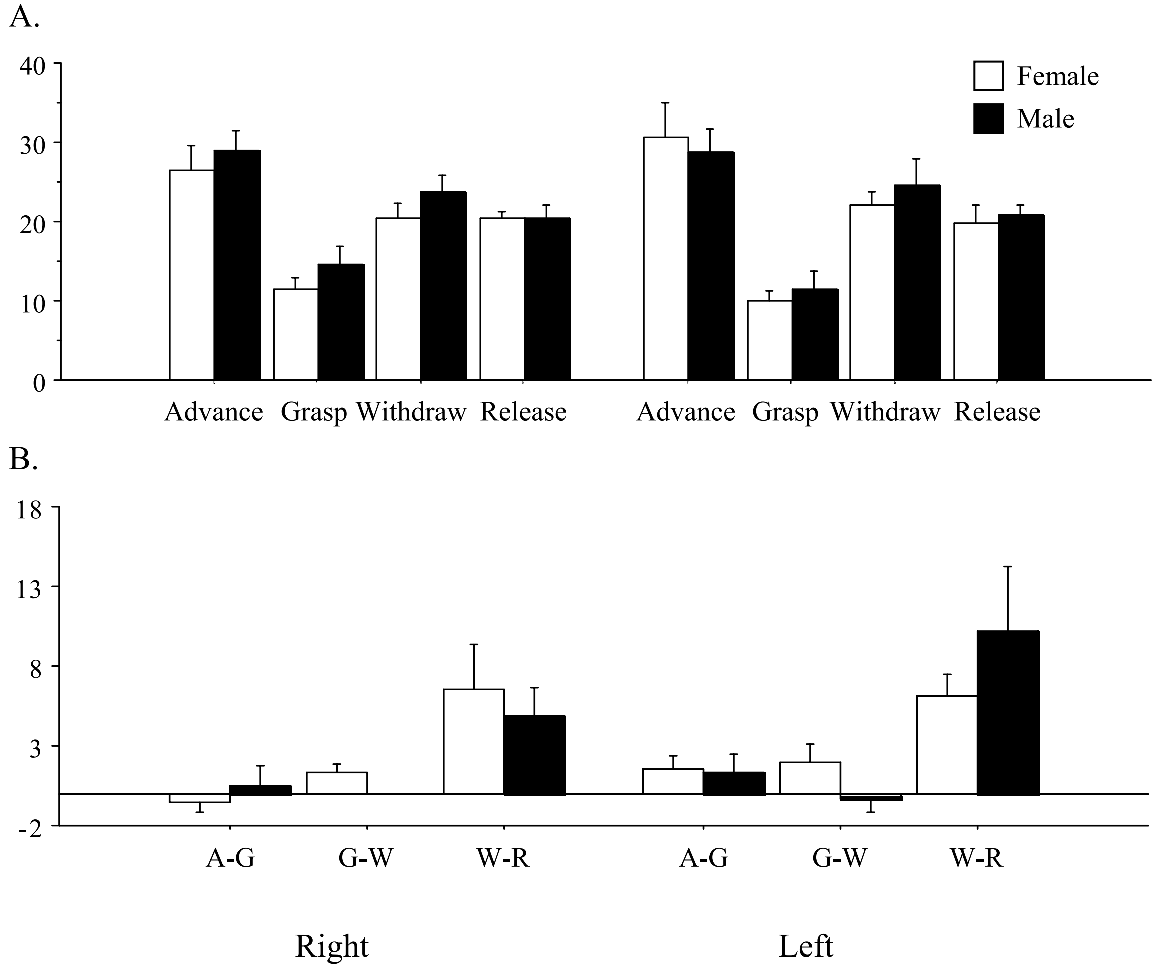


Figure 6.1 The Phases in Skilled Reaching in the Control Group. Y-axes represent number of frames [i.e., time] and the X-axes represent the limb used to perform the reach. A] The Mean Time Duration [number of frames] for Each Phase of Reaching. B] The Mean Time Duration between the Phases of Reaching; A-G, number of frames between Advance and Grasp; G-W, between Grasp and Withdrawal, W-R, between Withdrawal and Release. Negative numbers indicate the number of frames that overlap between the phases.

Duration Between Phases

The same pattern was found in repeated measures ANOVA for duration between phases by sex and by limb [p always > 0.1] except for comparisons between the duration between phases [F [2,24] = 15.179, $p < 0.0001$]. Fisher's PLSD revealed significant differences between A-G and W-R, and G-W and W-R [p<0.0001, p = 0.0001] and no difference between A-G and G-W [Figure 6.1B].

Since there are no differences between males and females, or between right and left limbs, the mean number of frames for each reaching phase, and for the duration between phases, were used to create a representative notation [Figure 6.2]. Data from the stroke group were compared to the representative control notation. Table 6.3 shows which stroke subjects matched the representative notation when reaching with the ipsilateral and contralateral limbs. Repeated measures ANOVA was then used to compare the matching stroke subjects' notated scores with the representative notation from the control group.

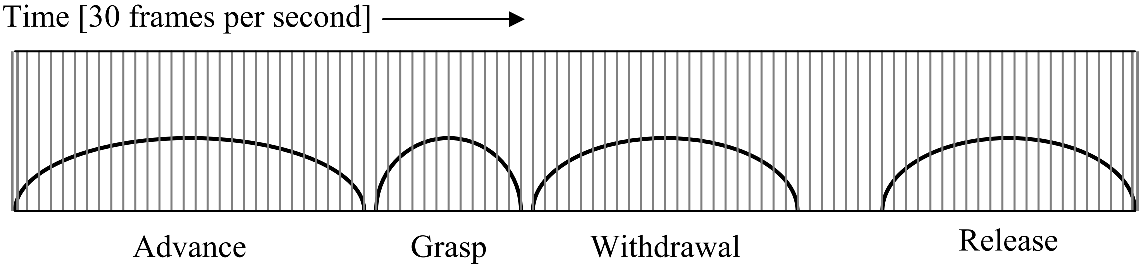


Figure 6.2 Representative Notation of the Phases in Skilled Reaching from the Control Group. The notation begins and ends with double bar lines and is read from left to right. Each bar line indicates that one video frame has passed, thus representing time. The bows represent the duration of the reaching phases presented. This shorthand, notated score was created to illustrate the timing of the phases of reaching. The mean number of frames for the duration of phases, and the duration between phases, in the control group were used to create the notation.

Stroke Group

All stroke subjects performed the task with each limb. One subject, with bilateral cerebellar and brainstem lesions, used her least affected limb to manipulate her more severely affected limb to complete the task. Since this changed the nature of the task, only data from her least affected limb were collected. A second stroke subject with right subcortical damage performed the task with each limb independently, but was unsuccessful in bringing the food item to her mouth when reaching with the contralateral-to-stroke limb. She completed all the phases of reaching and data from both limbs were collected.

Reaching Phase and Duration Between Phases

Data from the stroke subjects who matched with the representative control notation were compared to the control group. Repeated measures ANOVAs did not show significant differences at any level except for Phase [F [3,36] = 25.374, $p < 0.0001$] and for duration between phases [F [2,24] = 10.023, $p = 0.0007$]. Again, posthoc Fisher's PLSD revealed differences in phases [$p < 0.0005$] except when comparing the Withdrawal and Release phases [$p > 0.1$], and differences in duration between phases [$p \leq 0.0001$] except when comparing A-G and G-W [$p > 0.1$].

Developmental Stages of Reaching

In the instances where the notated score from a stroke subject, or from one limb from a stroke subject, did not match the representative control notation, the notations were compared with that of the developmental stages in infancy [Table 6.3].

When reaching with the ipsilateral-to-stroke limb, most stroke subjects matched the control representative notation. Subjects who matched with developmental Stage 1 in terms of phase and duration between phases, were limited to the two subjects with bilateral cerebellar involvement. Two subjects, one with an internal capsule lesion and one with right subcortical damage, matched with the developmental Stage 4 in terms of phase and duration between phases.

Table 6.3 Comparisons between Individual Stroke Subjects with the Control Group and the Developmental Stages of Reaching. * Indicates a match in the temporal phases, and durations between phases, between the stroke subject [represented by lesion] and corresponding control group or developmental stage.

A. Ipsilateral-to-Stroke Limb

	Phase and Durations between Phases				
	Control	Stage 1	Stage 2	Stage 3	Stage 4
Right Hemisphere Lesions					
Parietal Somatosensory	*				
Superior Posterior Parietal	*				
Parieto-Occipital	*				
Fronto-Parietal	*				
Cerebral medially near falx		*			
Posterior limb of Internal Capsule					*
Thalamic	*				
Subcortical					*
Left Hemisphere Lesions					
Frontal + Anterior Parietal	*				
Deep Parietal	*				
Bilateral Involvement					
Right and Left Parieto-Occipital + Right Posterior Frontal and Cerebellum		*			
Cerebellar and Brainstem		*			

Table 6.3 [*continued*]

B. Contralateral-to-Stroke Limb

	Phase and Durations between Phases				
	Control	Stage 1	Stage 2	Stage 3	Stage 4
Right Hemisphere Lesions					
Parietal Somatosensory		*			
Superior Posterior Parietal				*	
Parieto-Occipital	*				
Fronto-Parietal			*		
Cerebral medially near falx	*				
Posterior limb of Internal Capsule			*		
Thalamic	*				
Subcortical			*		
Left Hemisphere Lesions					
Frontal + Anterior Parietal		*			
Deep Parietal	*				
Bilateral Involvement					
Right and Left Parieto-Occipital + Right Posterior Frontal and Cerebellum					*
Cerebellar and Brainstem	N/A	N/A	N/A	N/A	N/A

Fewer subjects matched the control notation when reaching with the contralateral-to-stroke limb. The two subjects who matched with developmental Stage 1 had parietal damage, one in the right hemisphere and the other in the left. The three subjects matching with developmental Stage 2 had right hemisphere lesions with fronto-parietal damage, internal capsule lesion, and subcortical damage, respectively. The subject with superior posterior parietal lesion matched with developmental Stage 3. One subject with bilateral cerebellar involvement matched with developmental Stage 4, the other subject with cerebellar involvement did not perform the task properly with the right limb.

DISCUSSION

The present study compares skilled reaching in individual stroke subjects with varying lesions, severity of damage, and symptoms, with the four developmental stages of the behaviour. The analysis demonstrates how the motor components of the developmental stages of reaching are evident in the adult after stroke. Whether the emergence of developmental patterns in the behaviour is to due to reorganization as a result of released phenomena, compensatory needs, or a combination of both is not clear. Further, since the sample size is small and lesions highly variable, the effects of specific lesions, or even neural contributions in the process of development for each stage, remains unknown.

The description of the parallels between natural human development and recovery from hemiplegia after stroke in adults made by Twitchell [1957] are supported in this study. In Stage 1 of reaching, infants make many of the movements required for the behaviour, although the movements seem to occur independently of one another. What is remarkable is that they are all directed toward the target. In Stage 2, infants make whole body movements – again, directed toward the target. The pattern from Stage 2 is similar to the early developmental and recovery patterns described by Twitchell. Infants progress through a third stage in which the first two stages become integrated and they are able to bring the hand to the target where it is grasped and brought to the mouth. Although they are successful in bringing the target to the mouth, the actions are proximally, rather than distally driven – another phenomena described by Twitchell for both development and recovery patterns of limb movements. During this stage, there is a transition between postural disinhibition and inhibition as the infant becomes better in the task – again, the same pattern was observed by

Twitchell in stroke subjects. Twitchell explained that during recovery after stroke, finer skillful articulations of the hand and fingers may reappear, depending on lateral corticospinal tract involvement. Fine hand and digit movements have been observed in infants at the first stage, as well as in previous studies [Wallace & Whishaw, 2003], although the function was not evident as such movements and are not coordinated with shoulder and elbow movements until the third stage.

Reaching can be characterized in several ways. Both temporal phases and the coordination between body parts have been detailed throughout development [Chapter 5], and the temporal phases have been compared with stroke subjects in the present study. These results are complimentary, with scientific demonstrations on how the control of limb movements can be characterized in several ways at neuronal and topographical levels in the nervous system [Graziano, 2006]. Further, one or more levels of categorization for a single behaviour within an organism can disassemble depending on lesion. Subjects who could be characterized with developmental patterns of reaching in terms of phases could be classified by different developmental patterns when observing the organization of their body parts during movement.

Stroke subjects who participated in the present study were initially assessed using rating scales specifically designed to quantify deficits and extraneous movements during skilled reaching. These scales, derived from notations of reaching, capture organizational and expressive components of reaching [Chapter 3 and 4]. Temporal phases, or natural divisions of reaching behaviour, are one way of breaking down the components of the motor task.

However, the way that individual body parts become organized into a synchronous behaviour occurs in addition to the phases of reaching. Further studies are required to compare the organization of body parts between stroke subjects and infant development. As a pilot investigation, the results from the reaching scales of Chapters 3 and 4 were compared with the infantile developmental stages. Preliminary results suggest that, depending on the measure used, some of the cases described above [in this chapter] change when, instead of comparing the phases of reaching, the organizational structure of the moving body parts are compared [Table 6.4].

By comparing the movements of skilled reaching after stroke with the developmental stages, conclusions can be made on the nature of the motor impairment. At certain stages in development, infants do not have inhibitory control over their postural movements and the torso falls forward as the limb advances towards the target. Many of the stroke subjects in the present study make similar movements with their torso upon advancing the limb; however, when examining the details of the movement [i.e., notations in Chapter 2 and assessment with the Expressive Reaching Scale], it becomes clear that the torso is advancing the limb. This subtle contrast between developmental torso-limb relations and those of the stroke subjects suggests that in the case of stroke, this type of postural movement is compensatory for the loss of individuated control of the limb. In contrast, the emergence of infantile patterns can explain, at times, impairments displayed in the stroke subjects. In the case of an internal capsule lesion, the stroke subject uses Shapeflow in movements made by the body during all phases of the reach. This is similar to Stage 1 in development, and suggests that reaching is disrupted by the loss of ability to inhibit the non-kinematic aspects of movement during reaching. When performing the reaching task, the subject with bilateral brainstem lesions began by making grasping movements with her hand and followed by advancing movements of the limb in a similar fashion as in developmental Stage 1. In this subject, the phases of reaching may be disrupted by the emergence of the infant-typical organizational parameters for the temporal sequence of the task.

Table 6.4 Preliminary Results for Alternative Measures on the Comparisons between Individual Stroke Subjects with the Developmental Stages of Reaching. * Indicates a match between the stroke subject [represented by lesion] and corresponding developmental stage.

	Phases & Duration between Phases				Organization of Body Parts			
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 1	Stage 2	Stage 3	Stage 4
Ipsilateral Limb								
Cerebral medially near falx	*							*
Contralateral Limb								
Parietal Somatosensory	*							*
Fronto-Parietal		*					*	
Posterior limb of Internal Capsule		*			*			

Brief Description of the Organization of Body Parts during the Development of Reaching
Stage 1. Various motor components of skilled reaching, such as movements of the torso, head, mouth, arms and hands, occur independently and are often incomplete. The behaviour is disfragmented.
Stage 2. The whole body engages as one motor unit in reaching toward a target. Finer components of reaching are not clear.
Stage 3. A combination of movements from the first two stages occur in an integrated fashion whereby movement components of skilled reaching and whole body reaching begin to integrate into a functional behaviour. Movements of the limb are initiated proximally rather than distally, and movement of one body part often evokes movement in other body parts. For example, forward movement of the limb does not occur without forward movement of the torso.
Stage 4. Discrete targeted and coordinated movements of the arm and hand emerge that are supported by postural adjustments of the torso. The torso makes small movements on its rotatory axis and looks as though the infant is wobbly. Individuated limb movements, as well as the integration between gestural movements of the limb and postural movements of the torso, occur in an organized fashion though not yet polished.

That various levels of organization of movement are characterized during development and after stroke suggests that there are several movement parameters for the behaviour of skilled reaching, including rhythmic phases of action, the integration of torso and limb movements, and postural disinhibition. That changes can be due to compensatory strategies or released phenomena adds new dimensions to the organizational rules for the behaviour after stroke. Future studies are needed to investigate the role of the location of lesion on the emergence of developmental patterns of reaching in adults, to determine which patterns occur as a result of disinhibition or compensation, and whether the progression of recovery follows the motor sequence found in development. These studies can significantly contribute to designing therapies for stroke patients, for example, whether the therapist should focus on inhibition and/or integration of movement, rhythmic phases and/or body organization, and at what phase during recovery would one be more efficient over the other. At the very least, they can provide insight on the neural organization of reaching during development.

<u>CHAPTER 7</u>

General Discussion:

Movement Parameters for the Behaviour Skilled Reaching

…'Watching and wondering' about behaviour… [a *'revived'* methodology] *can indeed contribute to the relief of human suffering…*

Niko Tinbergen
Ethology and Stress Disease.
<u>Nobel Lecture,</u> 1973

General Discussion:
Movement Parameters for the Behaviour Skilled Reaching

The purpose of this thesis was to describe the organization of the movements of skilled reaching. This was accomplished by studying the development of reaching in infants and the changes in reaching that followed brain injury produced by stroke in adults. For the study of infants, the movements of reaching for objects that they then placed in their mouth were video recorded and analyzed with movement notation. For the studies in stroke patients, a formal task was used in which subjects reached for an item of food that they placed in their mouth for eating. The methods used in the study included the Expressive Reaching Scale [ERS], for quantifying extraneous movements and compliments a previously designed system and the Eshkol-Wachman Movement Notation Derived Reaching Scale [EW-DRS], for quantifying deficits in the movements of reaching.

The main findings of the research were that skilled reaching is a product of interactions between: 1. the spatial-temporal relations of the body; 2. the integrative organization between torso and limb movements; 3. the inhibitory control and postural support; 4. the sum of the parts and the whole of the behaviour; 5. the limited and specific use of Effort aspects of movement, and 6. the rhythmic quality between the temporal phases of the behaviour. Thus, the thesis shows that behaviour is assembled in such a way that these interactions are integrated through development, yet they can become dismantled in one area alone or generally throughout multiple levels of what constitutes the behaviour reaching. Furthermore, with brain damage, additional parameters, such as compensatory strategies and integration of disinhibited movements, contribute to the modulation of the behaviour.

On the Relevance of Reaching Behaviour

An investigation of the movements that compose the behaviour skilled reaching to eat was made for three reasons. First, the inability to reach and grasp objects in the environment and bring them toward oneself, such as when one reaches to eat or to groom, has severe effects on a person's independence and quality of life. Reaching is affected by a variety of disorders and injuries including cerebral palsy [Stavness, 2006; Utley & Steenbergen, 2006], multiple sclerosis [Solaro, Brichetto, Casadio, Roccatagliata, Ruggiu, Mancardi, Morasso, Tanganelli & Sanguineti, 2007], Huntington's disease [Fellows, Schwarz, Schaffrath, Dömges & Noth, 1997; Tibben, 2007], Parkinson's disease [Leiguardia, 2001; Whishaw, Suchowersky, Davis, Sarna, Metz & Pellis, 2002], and stroke [Krakauer, 2005; McCrea, Eng & Hodgson, 2002]. Knowledge of the organizational movement patterns of skilled reaching can be applied directly to the designing of effective therapy and rehabilitative programs for people with impaired reaching ability. Many researchers have focused on impaired reaching in a variety of populations. The objectives for the majority of such research are narrowed to certain aspects of the behaviour, such as shoulder and elbow joint synergies [Cirstea, Mitnitski, Feldman & Levin, 2003; Micera, Carpaneto, Posteraro, Cenciotti, Popovic & Dario, 2005], or force grip during grasping [Boissy, Bourbonnais, Carlotti, Gravel & Arsenault, 1999]. Though these studies have been fruitful, insight on the integration of the components of the behaviour are limited. Thus, this thesis addresses the need to examine the movement patterns of skilled reaching within the full context of the behaviour.

Second, reaching is commonly used to measure motor function, degeneration and rehabilitation in clinical studies, and as a means by which to investigate cognitive tasks in infants and non-human animals. Clinical studies make use of the natural, simple and easy to train attributes of the task in order to assess upper limb function. Studies on cognition apply the task in their methodology in order to make inferences on memory and other cognitive abilities in infants and non-human animals. In these studies, experimenters design tasks that involve a subject's use of reaching movements to identify targets or objects to test for attention, memory, and conceptual understanding. Knowledge of the organizational features of the movements of reaching can be instrumental in providing an understanding, and sometimes a more accurate interpretation, of a subject's performance.

For example, consider the A not B task. Subjects first observe the experimenter placing an object under one of two identical and visible locations, such as in upside-down cups. The cups differ in location only - that is, cup A is to the left of the subject and cup B to right. Each time, the subject must correctly identify the cup under which the object is hidden by reaching, grasping, and lifting cup A. Upon three successful trials, the experimenter hides the object under cup B. The subject must then correctly identify cup B. Infants between the ages of eight to twelve months fail the task – a finding that led to the theory that infants do not possess a conceptual knowledge of object permanence. That is, infants do not understand that an object still exists even when it is out of sight [Piaget, 1954]. This conclusion has been refuted upon examination of the motor aspect of the cognitive task - the movements of reaching for and grasping the cup. It has been demonstrated that several inhibitory motor patterns not yet accessible in the infant interfere with the ability to perform the appropriate movements to complete the task successfully [Diamond, 1985; 1988; 1990]. This knowledge has led to new studies and discoveries on the developing motor system [Diamond, 1988;

1990] as well as to the design of new methods of investigation on cognitive ability in infants [Diamond, 1985; 2000]. Thus, where once the A not B task was traditionally used to gauge object permanence [Ahmed & Ruffman, 2000; Diamond, 1985; 1988; Piaget, 1954] it is now used to measure attention, inhibition, motor memory, or conceptual abilities in infants [i.e., Berger, 2008; Goldberg, Dineva, Feng, Gregor, Thelen & Spencer, 2008].

Third, reaching is both neurologically and behaviourally linked to the evolution and ontogeny of language. Electrophysiological studies between species suggest that language evolved from the basic mechanisms for the capacity to execute, recognize, and imitate skilled actions of the arm and hand [e.g., reaching and grasping movements] as well as the mouth and face [e.g., ingestion] [Arbib, 2002, 2005; Arbib & Bota, 2003; Jeannerod, Arbib, Rizzolatti & Sakata, 1995]. It is argued that language emerged from the same brain mechanisms – the mirror neuron system - involved in grasping. The theory is that hand and facial gestures eventually synchronized with vocalizations and gestures of other body parts. The evolving mirror neuron system enabled the recognition, imitation, and interpretation of the integrated gestures and vocalizations. With time, a vocabulary of morphemes developed where the same sounds and movements were made for the same events by different individuals. Once a vocabulary of morphemes and related actions that consistently depicted the same events developed, a set of generic structures for making actions and observations set the scaffolding from which language evolved [Rizzolatti & Arbib, 1998].

There is evidence that motor areas in the non-human brain are precursory to language areas in the human brain. Area F5, an area in the cortex of non-human primates, known for its control of hand movements, is thought to be the phylogenetic precursor for Broca's area – the area involved in speech production in humans [Kohler, Keysers, Umiltà, Fogassi, Gallese & Rizzolatti, 2002].[39] The two areas are homologous in topographical location and cellular structure [Rizzolatti & Arbib, 1998], and both have mirroring properties [Kohler et al., 2002]. Both area F5 and Broca's area modulate oral-laryngeal and oral-facial movements [Rizzolatti & Arbib, 1998] and, Broca's area, the human speech area, is involved in hand movements [Iverson & Thelen, 1999].

Neuroimaging studies in humans have shown that movement and mirror neurons are involved in language [Aziz-Zadeh, Wilson, Rizzolatti & Iacoboni, 2006; Tettamanti, Buccino, Saccuman, Gallese, Danna, Scifo, Fazio, Rizzolatti, Cappa & Perani, 2005]. Listening to spoken sentences that describe actions stimulate the same visuomotor circuits involved in the execution and observation of that action [Tettamanti et al., 2005]. Observing another's actions forms sensorimotor images in the premotor areas of oneself. For example, if the actions are object related, mirror neurons in the parietal lobe, which is involved in articulating the hand to the shapes of objects, are activated. Further, behavioural studies have shown that the hand and mouth function in a synchronous way during language from early development, and that listeners rely on both when available [Iverson & Thelen, 1999].

The investigation of the organizational movement patterns of reaching can provide insight on the evolution and development of language. This thesis has identified the

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[39] There is some debate as to the true monkey anologue for Broca's area. For example, Petrides and colleagues [2005] suggest an area rostral to F5 is the likely candidate for a monkey analogue of Broca's area. Further studies are required to identify whether this candidate area, also known for its involvement in orofacial movements, shares common ancestry with Broca's area in humans.

developmental sequence of movement patterns for the acquisition of skilled reaching that follows a similar progression to the developmental sequences of perceptual-motor patterns for language acquisition [Werker & Tees, 1992; 1999].

On the Investigation of the Movement Patterns for Skilled Reaching

Two types of movement notation, Eshkol-Wachman Movement Notation [EWMN] and Laban Movement Analysis [LMA],[40] were used. Common forms of analysis for motor function include endpoint markers, electromyography [EMG], and the use of computer digitized motion analysis systems. Endpoint markers offer measures for checklists, success rate, or frequency. In the analysis of reaching, rating scales can be used as checklists to mark whether various components of the task are performed. Each point on the scale is an endpoint measure. In rats, reaching is often used as a measure of forelimb motor function where the endpoint measure is simply counting the number of successful trials completed within a previously set number of trials offered. Endpoint measures can also be used to quantify the frequency of a selected behaviour in order to identify the number of times a subject performs a task within a given time frame. EMGs record directly from the motor unit and provide a robust method for investigations on the activity of muscles during motor tasks. There are several computer digitized motion analysis systems available, each with unique advantages, all of which provide quantitative measures on velocity and trajectory of a selected point on a subject's body. These forms of analyses are used in clinical studies of motor disabilities such as in Parkinson's disease [Leiguardia, 2001; Whishaw et al., 2002], cerebral palsy [Stavness, 2006; Utley & Steenbergen, 2006], and stroke [Krakauer, 2005; McCrea, Eng & Hodgson, 2002].

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[40] Refer to Chapters 1 and 2 for descriptions of the two notation systems.

Movement notations are languages designed to communicate the integrative nature of movement. Using movement notation to describe behaviour is analogous to using written language to articulate a thesis. Thoughts can be quantified and classified, and the entire compilation provides an integrated and multilayered work. In addition, the act of writing provides further insight on an idea and the relations between supporting arguments. While components of a single movement can be characterized in various forms [e.g., using EMG to record muscle activity during a task, or computerized systems to capture joint torques during synergistic movements], movement notation captures a complete description of the observed movement. The act of writing movement notation also provides the experimenter with a deeper understanding of the movement. The result is a written document that can be read and describes the patterns of movement and their relations. The notations can be referred to as needed and meaningful measures can be derived for further analysis.

For this thesis, LMA was used to describe how two stroke subjects, one with a mild lesion, and one with a severe lesion, organize their movements for reaching and how they compare to their matched controls. The LMA notated scores highlighted several patterns in the movement from which a rating scale [ERS] was derived. The rating scale was used to investigate whether the patterns identified in the two initial stroke subjects are evident in a sample population of stroke survivors. This methodological approach was modelled after a previous study on skilled reaching in subjects with Parkinson's disease [PD] [Whishaw et al., 2002]. PD subjects were videotaped while performing the reaching task described in this thesis [Chapter 1]. EWMN was used to notate the movements of the reaching behaviour. The patterns described by the notation described impoverished movements and abnormal orienting fixations. The EW-DRS rating scale was created in order to facilitate the quantification of the movement deficits, or losses, in skilled reaching that was described by the notation.

During administration of the reaching task in the stroke study, it was evident that stroke patients make extraneous movements during reaching. While the question of whether there are deficits in the movements of skilled reaching after stroke remained, it was clear that an analysis of extraneous movements was also necessary. The components on the EW-DRS rating scale are derived from EWMN and provide a way to measure whether the movements that are necessary to perform the task properly are present. Although there is overlap between the two movement languages, LMA uniquely provides a language to describe the non-kinematic aspects of movement as well. Initial observations during both the administration of the task and the first few viewings of the captured video led to the hypothesis that the extraneous movements presented in the stroke subjects embodied non-kinematic aspects of movement. Thus, LMA was selected as the notation for describing reaching after stroke, and the ERS was derived from the notations.

The ERS provides the first classification of the combined kinematic and non-kinematic aspects of movement in stroke subjects that is sensitive to both the severity and the location of stroke. A negative correlation between the EW-DRS and ERS rating scales was found in the stroke group [Appendix 2]. When subjects had low scores on the EW-DRS, they had high scores on the ERS, indicating a poor performance by both rating scales. This correlation suggests that either rating scale will provide an endpoint measure on the severity of skilled reaching after stroke. Both scales were used to evaluate reaching because the purpose of the thesis was to examine what the changes were in movement after stroke. The methods for determining the loss of function have been investigated in other studies and several reliable assessment scales have been well established [Bobath, 1990; Fugl Meyer, 1980; Levin, Desroisier, Beauchemis, Bergeron & Rochette, 2004; Sanford, Moreland, Swanson, Stratford & Gowland, 1993]. The two rating scales used in this thesis are not redundant in the type of information they provide and their correlation may change in other populations. In diseases that lead to akinesia [i.e., when movements slow down and perish as in PD], the correlation might be lost as a decrease in the ability to initiate movements would likely not result in extraneous movements. Thus, subjects would likely score poorly on the EW-DRS and do well on the ERS. In contrast, in diseases that lead to other forms of dyskinesias [e.g., released movements as in Huntington's disease], the extra production of movements might result in a high score on the ERS that measures extraneous movements, but it is not known whether there would there be deficits in reaching as well [Figure 7.1]. Studies comparing the results of both rating scales for the reaching task in a variety of motor disorders would provide further evaluation on the correlations between the two rating scales, as well as insight on the relations between motor deficits and extraneous movements during skilled actions. Such studies would help to evaluate whether compensatory strategies due to impaired motor ability are the same across a variety of disorders. This information would be useful in understanding the different ways movements for skilled reaching are organized depending on the type of disorder.

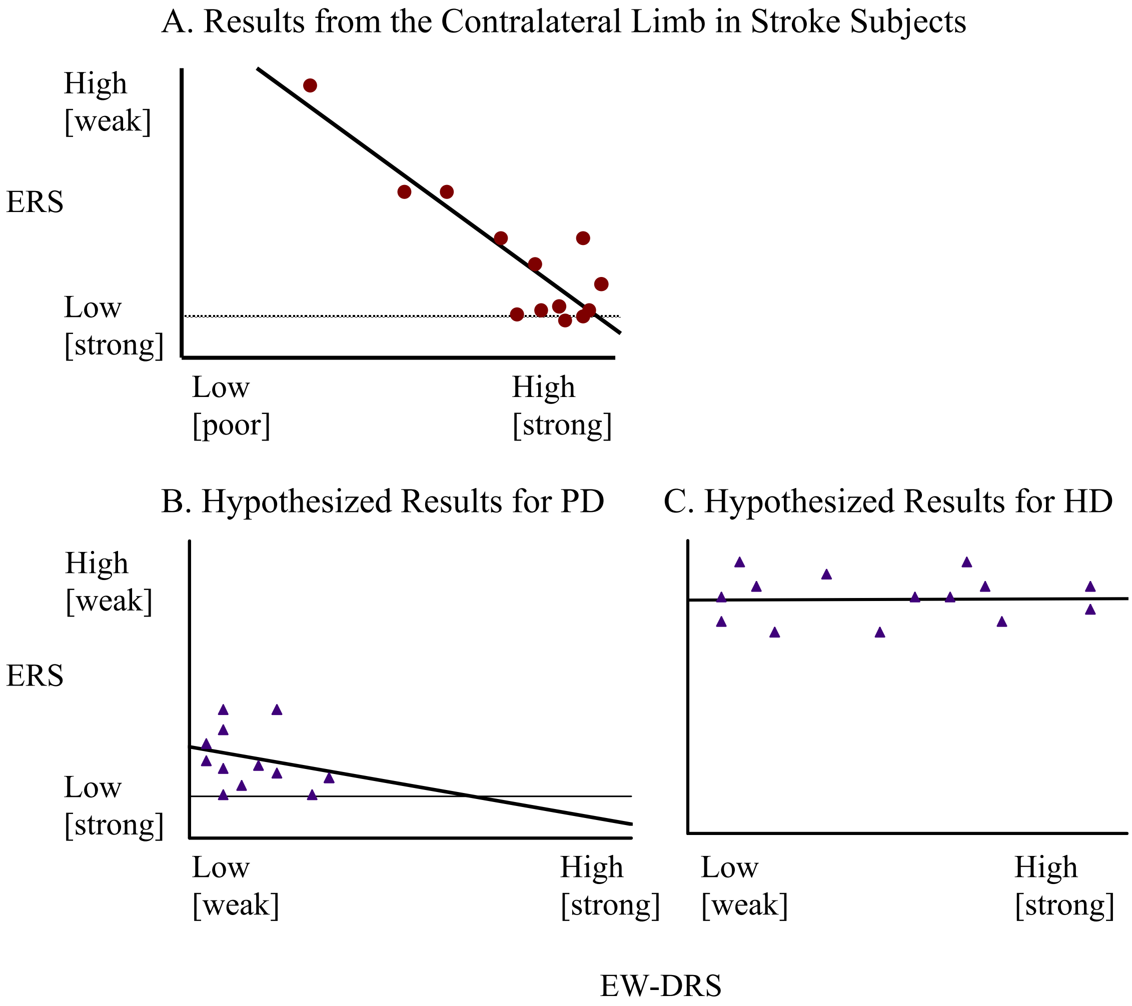

Figure 7.1 A Hypothesis on the Relationship between the ERS and the EW-DRS in Different Disease Populations. A] Contralateral Limb in Stroke Subjects. A negative correlation between the EW-DRS and ERS rating scales was found in the stroke subjects from Chapter 3. B] Parkinson's Disease [PD]. Hypothetical correlation between the two rating scales in PD. A decrease in the ability to initiate movements would likely not result in extraneous movements. Subjects would likely score poorly on the EW-DRS and do well on the ERS. C] Huntington's Disease [HD]. Hypothetical correlation between the two rating scales in HD. The extra production of movements in HD might result in a high score on the ERS, but it is not known whether there would there be deficits in reaching as well [which would result in low scores on the EW-DRS].

For this thesis, both rating scales were used to compare the stroke and control groups. Then, comparisons within the stroke group were made depending on the level of the lesion, and the time period since the stroke. Finally, a comparison between individual stroke subjects was made. Movement patterns that contribute to impaired reaching were identified and led to the question of whether such patterns are strictly organized due to injury in adulthood, or if they are part of the developmental progression of organizing movements for skilled reaching that are reverted to after injury in adulthood. Thus, an investigation on the early ontogeny of skilled reaching was made and compared with the stroke subjects.

The Stroke Studies

Results from the stroke studies suggest that changes in the components of skilled reaching after stroke are not static or unidirectional. This was observed in the two year follow-up on post-acute stroke subjects. Although their overall scores on the assessment scales did not imply changes in their movements, an examination at the components level [e.g., Aim, Pronate, and Supinate] showed that in some components subjects improved, and in others, the same subjects became worse. There was no apparent trend between the subjects. Future studies on the long term changes in movement after stroke would be valuable in determining relationships between the components of reaching. It may be that the components of reaching influence, or compete with, each other after stroke. Identifying such interactions would provide greater insight on the organization of skilled reaching as well as on the effects of therapeutic interventions.

The way that the movements of skilled reaching assemble after stroke suggest that normal reaching is a behaviour that is greater than the sum of its parts as it involves the whole body to produce isolated actions of the arm and hand. The relationship between the structural kinematic aspects of movement with the expressive non-kinematic aspects changes after stroke. Non-kinematic aspects of movement, such as Effort and Shaping, hinder the goal of reaching as they are either irrelevant or detrimental to the function of the task. The emergence of inappropriate Effort and Shaping qualities may be due to fatigue in motor exertion, compensatory strategies, and released movements, the nature of which is probably lesion dependent.

Impairments in skilled reaching movements after stroke involve the torso as well as both ipsilateral and contralateral limbs. Postural support and a loss of individual digit movements can be impaired when reaching with either limb. There are a number of ways in which the integrative actions of the torso and limb during reaching unravels after stroke. The torso may compensate for the loss of control in limb movements by moving the body towards the goal. Compensatory movements cause additional problems, such as shoulder and neck pain [Cirstea & Levin, 2000; Levin, 1996b], but they also change the behaviour in a very basic way. That is, by moving the torso forward, the nature of support for the reaching limb changes. In normal reaching movements, the torso supports the limb by making subtle lateral movements. This type of support provides a means for the isolated action of the limb. Stroke subjects move the torso forward in order to aid in advancing the limb, however, this change in torso-limb relationship has a ripple effect throughout the task. Once the torso is leaning forward, it acts as a constraint for pronating the limb in order to prepare for grasping the target. Alternatively, the torso may not move as the arm reaches out to grasp the target. In this case, arm movements are not supported and the degrees of freedom of its limb segments become limited. The relationship between the torso and the limb can be affected in either, or both, the Advance and Withdrawal phases of the reach.

Individual stroke subjects did not always have the same impairments [e.g., postural support] in both the Advance and Withdrawal phases during reaching with the same arm. Thus, the organizational parameters for the Advance and Withdrawal phases may differ within the single behaviour of skilled reaching. The Advance and Withdrawal phases can be categorized as two, separate, ethologically relevant actions in the macaque motor system [Graziano, 2006]. The Advance phase is an outward limb action and the Withdrawal phase an inward limb action. The outward limb action of Advance is specific for reaching, unlike generalized outward limb movements. It is organized in a way that anticipates the need to aim for and grasp a target that will then have to be Withdrawn towards the mouth within one smooth motion.

The Advance and Withdrawal phases of reaching provide natural divisions of the behaviour. Each phase is defined by a specific gesture. Notations of gestures alone show that there is a rhythmic quality to reaching in which each gesture can be defined in terms of the duration and pause after completion [Figure 7.2]. The temporal rhythm of the phases of reaching - Advance, Grasp, Withdrawal, and Release - are likely abnormal in stroke subjects due to deficits, compensatory actions, and abnormal postural support during reaching. In addition, the non-kinematic aspects of movement likely interfere with timing. Effort is defined as changes in the intensity, force and rhythm of movement – all of which can influence the timing of actions.

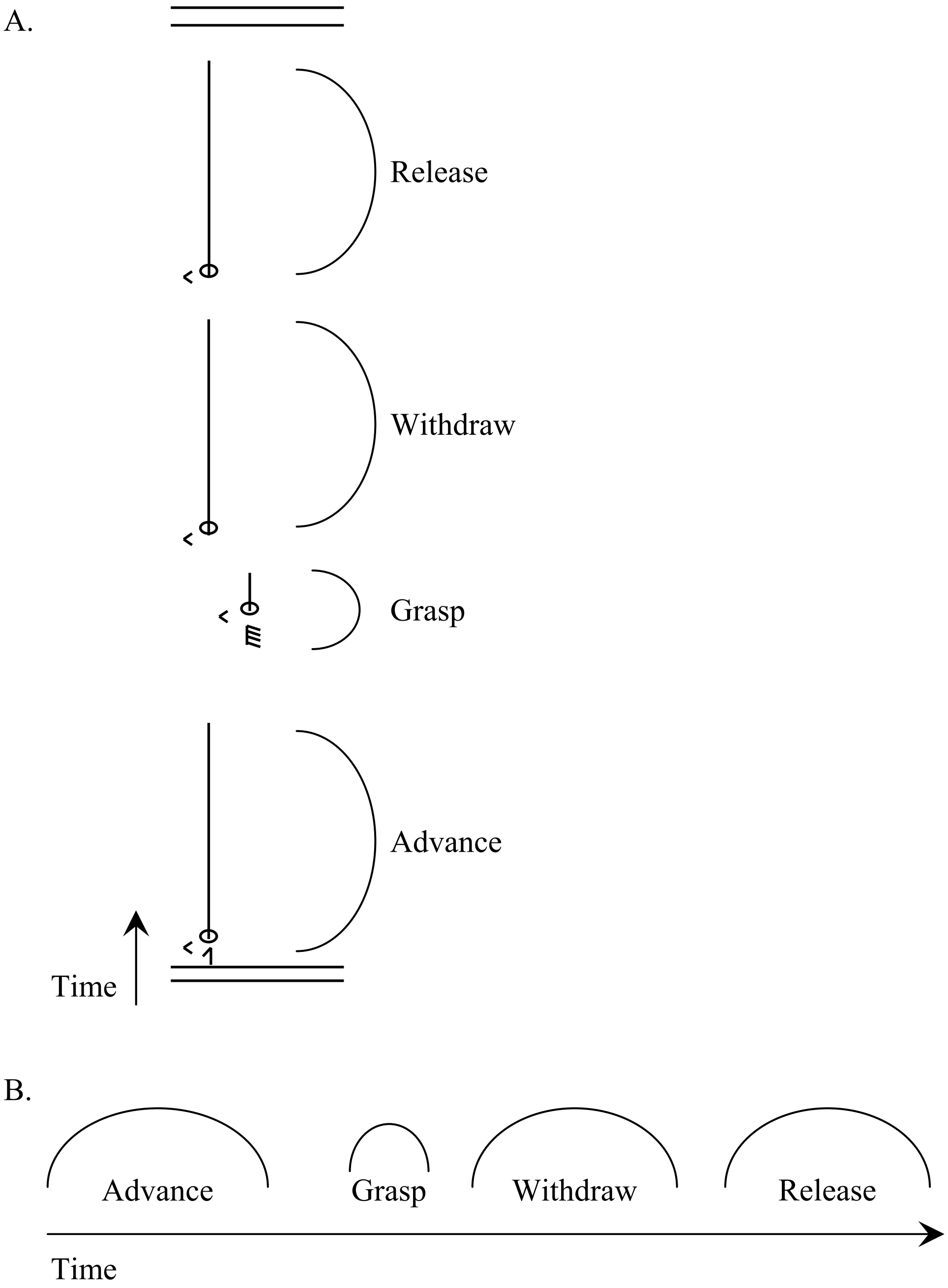

Figure 7.2 The Rhythmic Quality of Gestures During Skilled Reaching. Each gesture can be defined in terms of the duration and pause after completion. A. Vertical Motif of Gestures for Reaching. The first column describes gestures of the limb and the second column gestures of the hand. B. Interpretation of Motif in Figure 7.2A highlighting the duration and timing between of phases.

It is not surprising that lesions involving subcortical levels produce low scores in the reach-to-eat movement [Leiguardia, 2001], yet it is surprising that all of the stroke subjects displayed some impairment. Thus, damage to cortical and subcortical regions of the brain that largely spared corticospinal pathways did produce impairments in limb use. The reaching task and rating scale is also sensitive to the subtle motor impairments from brain regions not typically thought to be related to limb movement, including the ipsilateral-to-stroke hemisphere [Yarosh, Hoffman & Strick, 2004]. Limb impairments were most pronounced in the contralateral-to-stroke limb, however, impairments were captured in the ipsilateral limb as well. By comparing commonly affected components between limbs, insight can be gained into the underlying motor mechanisms responsible for deficits of reaching behavior after stroke. For example, by evaluation at the subcomponent's level, Aim was affected in the ipsilateral limb as a result of abnormal synergy between the trunk and limb. This, as well as the abnormal upper/lower limb coordination, which resulted in a poor trajectory of the limb, was affected in the contralateral limb. One possibility is that both limbs show an effect of stroke at varying degrees, or in differing ways. Another possibility is that, since neural reorganization, which depends on the relevant unaffected areas of the brain, is necessary for functional recovery [Boyd, Vidoin & Daly, 2007; Dancause, 2006a; b], as patients recover in the contralateral limb after stroke, the ipsilateral limb experiences a compromised loss of function. It is therefore recommended that assessment and rehabilitation therapies involve both limbs. This recommendation is further supported by observations of case studies for stroke on motor rehabilitation [Foroud, unpublished work] as well as studies on rehabilitation for spatial neglect [Dove, Eskes, Klein & Shore, 2007].

The movement patterns described in the human stroke subjects are visible during the ontogenetic progression towards the acquisition of skilled reaching in infants.

The Development Study

The developmental study revealed motor patterns for reaching in infants as early as four weeks of age that wane with age as other patterns appear, and finally integrate together, as the skill becomes accessible. The main finding is that reaching first develops in parts, then as a whole, and that the parts and the whole eventually synergize. Through all these stages, temporal phases of reaching are observable and progress in parallel to the organization of bodily movements.

Movement patterns in the first developmental stage of reaching are limited to a series of incomplete components of reaching, For example, upon presentation of a stimulus, infants make incomplete pronating limb movements and supinating limb movements, individual digit articulations, grasping movements, opening and closing movements of the mouth, and seem to reach for the stimulus with the mouth. These components of reaching wane with the emergence of the second stage, when infants move their whole body towards the stimulus. In this stage, infants still appear to be reaching for the stimulus with the mouth, yet rather than making a series of component movements, the whole body, as one unit, moves towards the target. Eventually, the third stage emerges, when infants move their whole body towards the target as well as incorporate limb actions, such as lifting and pronating the arm, grasping the target, supinating, and withdrawing the limb towards the mouth. In the fourth stage, the movements of the arm are isolated. Although the torso stays in place as the arm lifts away and advances towards the target, it is unstable and small perturbations are observed.

The temporal phases of reaching are repetitive, and sometimes co-occur in the earlier stages of reaching and mature in the later stages. By the fourth stage, infants perform the reach in a similar way to adults, yet the fine details, such as smooth trajectories and velocity, have yet to mature.

Results from the developmental study suggest that the movements and patterns of movement that constitute reaching behaviour progress in a cyclical fashion where they emerge, disappear, and re-appear as they become integrated with one another. It may be that critical periods for specific motor components peak as other motor components wane. As each component becomes established in the infant's behavioural repertoire in a way that is specific to reaching behaviour, it must then disassemble in order to become integrated with other components. That is, specific movements for reaching begin with disconnected fragments, the experience of performing and combining these movements eventually crystallize into a functional and complete action. This form of development can allow for establishing inhibitory pathways and for transitions in motor dominance for the behaviour. For example, it may be that reaching behaviour begins with the mouth and transitions to the arm and hand.

Motor Patterns Typical of Early Development Occur after Stroke in Adults

The study comparing reaching in stroke subjects with the development of reaching in infants shows that developmental patterns of reaching are evident in the adult after stroke.

The study compared the temporal phases of reaching in individual subjects with the stages of development, and each developmental stage was represented by at least one person in the stroke group.

The relationship between the torso and the limb changes after stroke, in some cases, in a similar way to development. In reaching during development, the torso moves forward towards the target - a pattern that was similar to several subjects in the stroke group who moved their torso forward in order to advance the limb. During development, the forward action of the torso disappears by the fourth stage. In contrast, this pattern persists in stroke survivors and causes additional chronic problems in the body [Cirstea & Levin, 2000; Levin, 1996b].

After stroke, the non-kinematic aspects of movement interfere with the task. Most stroke subjects use irrelevant Effort qualities [e.g., Bound Flow Effort] and lose Effort qualities that aid in the task [e.g., Direct Space Effort]. Effort qualities were not observed in the infant group. Whether infants are capable of Effort qualities is not yet clear. LMA theorists suggest Efforts are the qualities that crystallize an action and that this is lacking in infants, even though they can engage in pre-Effort qualities [Saxton, personal communication, 1998[41]].

In the first two stages of reaching in the infant group, shaping qualities were observed at the point at which they could not yet grasp the target though they were reaching toward it.

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[41] Saxton, N. was one of the visiting instructors for the certification program in Laban Movement Analysis and the Bartenieff Fundamentals at the Université du Québec à Montréal.

Some of the stroke subjects, particularly subjects with subcortical lesions, used Shaping qualities in their movements as they worked to complete the task. LMA theory describes Shaping as the dynamic means for connecting the inner mover to the outer world. Reaching is one action that facilitates such a connection, as the goal of skilled reaching is to bring something from the environment toward the self. Infants in the early ontogenetic stages of reaching are incapable of completing the task, yet the intention appears to be embodied in the Shaping qualities expressed. The role Shaping plays in the acquisition of the task is not yet understood.

Both stroke and developmental studies demonstrate that reaching is greater than the sum of its parts. The debate between *individuation* – in which the whole behaviour is present at or prior to birth - and *reflex integration* – in which the fragments of behaviour are present, yet assemble through the process of development - is ongoing [Brown, 1975]. In this context, individuation refers to:

> ‘the behaviour pattern from the beginning expands throughout the growing normal animal as a perfectly integrated unit, whereas partial patterns arise within the total patterns, and by a process of individuation acquire secondarily varying degrees of independence… always under the supremacy of the individual as a whole.’ [Coghill, 1929].

Reflex integration is considered to be in opposition to the individuation view and argues that behaviour emerges in partial and incomplete patterns that later integrate into ‘coordinated behaviour patterns’[42] [Windle, 1940]. It may be that individuation and reflex integration are in competition, thus resulting in species-specific organization and, depending on the behaviour, occurring simultaneously during ontogeny. The work from this thesis has led me

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[42] Quotation ‘coordinated behaviour patterns’ from Brown, 1975.

to view individuation and reflex integration as parts of a greater process. Infants experience the parts of reaching and the whole [gestalt] of reaching at different phases in development before they become integrated. After stroke in adults, the integration between the sum of the parts and the whole behaviour becomes unsynchronized where subjects perform the task with extraneous and missing components.

Other developmental patterns were also observed in the stroke group. During the developmental progression towards the acquisition of skilled reaching, the movement components for reaching emerge, disappear and re-emerge, suggesting that components are competing with one another. This pattern was found in the post-acute group upon examination two years later.

There appears to be relationship between *function* and *loss of function* during development and after stroke in adults. Developing neural modulates of a motor sequence may be dominant, even suppressive, over other sequences, and such dominance may shift through the course of development [Pellis, Pellis & Teitelbaum, 1991]. This may be a critical process for ontogeny. If it were the case that everything develops at once, there would be problems in integrating the parts that make up a whole. Further, there would be less opportunity to perfect basic movement components [i.e., the parts] that constitute an action. This process is essential, as it leads to an automation of the motor behaviour, thus freeing cognitive processes. The developmental study in this thesis describes movement patterns that emerge in pieces early on, then disappear and reemerge in an integrated way. During the disappearances of early movement patterns, infants engage in less specific movement patterns as the whole body performs the behaviour as one unit. The modulation for movement may be similar after stroke. As suggested above, neural reorganization is necessary for functional recovery [Boyd, Vidoin & Daly, 2007; Dancause, 2006a; b], so improvement may compromise function. For example, as patients recover in the contralateral limb after stroke, the ipsilateral limb experiences a compromised loss of function [Levin, 1996b]. Thus, the parameters identified in this thesis for skilled reaching during development and after stroke could lead to the designing of rehabilitative therapies that take advantage of the relationship between function and loss of function. Indeed, future studies can evaluate whether the components of reaching that compete with each other during development are the same as the components that compete with each other after brain injury.

Conclusions and Future Directions

This thesis describes how skilled reaching to eat is the product of interactions between 1. the spatial-temporal relations of the body; 2. the integrative organization between torso and limb movements; 3. the inhibitory control and postural support; 4. the sum of the parts and the whole of the behaviour; 5. a limited use of Effort and Shaping aspects of movement; and 6. a rhythmic quality between the temporal phases of the behaviour. The behaviour assembles in a way that integrates these interactions through development, yet can become dismantled in one area alone or generally throughout multiple levels of what makes the behaviour reaching. Furthermore, with brain damage, additional parameters, such as compensatory strategies and integration of disinhibited movements, contribute to the modulation of the behaviour. Future studies on comparing the rules that organize for reaching with the rules that organize other movements can deepen the understanding of skilled reaching, movement, and how the nervous system instigates one set of parameters over another for a given behaviour within the animal's repertoire.

The findings in this thesis demonstrate that skilled reaching constitutes motor parameters that may not be visible in a healthy adult, but that function through development and inhibitory systems in adults, to create the smooth and finely articulated action. Future studies can provide deeper insight on the specific neural contributions to each parameter as well as provide guidance in the design of rehabilitative studies.

Some of the patterns described in the stroke studies in this thesis have been observed in skilled reaching by rats [Appendix 5; Alveradashvili et al., 2008] and vervet monkeys [Appendix 6; Foroud, unpublished work]. Briefly, LMA notated scores of skilled reaching in rats prior to and after motor cortex stroke describe changes in the relationship between the postural movements of the torso and limb actions as well as in the temporal phases of the behaviour. After stroke, rats made abnormal movements with the torso that changed the alignment of the limb towards the target. Exactly which components of the movements of the torso are direct effects of the stroke, or are due to compensation for abnormal limb movements, is not yet established. Nonetheless, the relationship between the torso and limb changes after stroke. The temporal aspects of reaching also changes after stroke, the gestures defining the phases of reaching are repeated and there is greater overlap between the phases compared to reaching before the stroke.

Vervet monkeys performing a skilled reaching task organize their movements in a different way to rats and humans; this is likely due to the anatomy of the forelimb which has an effect on the way the monkeys travel across the floor and the way that they can articulate the limb in order to grasp a target. Even so, vervet monkeys organize their reaching movements in such a way that the torso supports the actions of the limbs. After modelling PD, the relationship between the torso and limb movements disintegrates and limb movements are no longer supported by the torso.

Current assessment scales and therapies provide excellent analysis and treatment of deficits in specific muscles, limb joints and actions. Research in recent years has demonstrated that motor behaviour develops and is organized in the nervous system by integrated movements rather than by muscles or simple actions such as flexion. Further, the findings in this thesis suggest several motor parameters are involved in organizing skilled reaching. These findings led to the pilot study in which a therapy program based on the Bartenieff Fundamentals[43] was implemented in one case [Figure 7.3]. The therapy program focused on promoting inhibition of adjacent body parts during movement of specific body parts, thus integrating whole movement patterns rather than improving single articulations in isolation from the rest of the body. Particular concentration was placed on modifying the emergent non-kinematic aspects of movements in order to facilitate, rather than hinder, functional movements. The subject improved in the therapeutic task over the course of ten weeks. Increased mobility was notable and resulted in direct improvement in daily activities [e.g., putting glasses away after washing] and, subsequently, the quality of life in general.

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[43] Refer to Chapter 1 for a description of the Bartenieff Fundamentals.

Figure 7.3 Movement Therapy based on the Bartenieff Fundamentals

An analysis on the organization of skilled reaching in various disorders can provide further insight on the natural behaviour as well as on the nature of the disorders studied. As suggested above, these implications are evident in disorders of the motor system such as cerebral palsy, PD, and Huntington's disease. Yet, there may be benefits in examining reaching in disorders that are traditionally characterized as social or cognitive disorders, such as developmental disorders of the frontal-striatal system [e.g., autism[44] or schizophrenia[45]].

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[44] People with autism have gross and fine motor abnormalities [Leary & Hill, 1996; Teitelbaum, Teitelbaum, Nye, Fryman & Maurer, 1998; Bradshaw, 2001], including problems with planning goal directed actions [Hughes, 1996], as well as deficits in the mirror neuron system [Oberman, Hubbard, McCleery, Altschuler, Pineda & Ramachandran, 2005; Ramachandran & Oberman, 2006]. They have a variety of social and cognitive deficits that include language deficits, an inability to understand the actions and emotions of others, and difficulty in expressing their own emotions, desires, and needs. It is difficult for people with autism to make social inferences or to be spontaneous. People with autism rely on routine and have difficulty making predictions about what is about to happen. The dance/movement therapist's perspective of autism is that children with autism have difficulty understanding the boundaries between self and other. That, for them, everything in their surrounding environment is an extension of self. This perspective is harmonious with neurological theories for autism. Dance/Movement Therapy [DMT] and creative movement therapy have benefited children with autism. Janet Adler, a pioneer in DMT, was the first person to work with children with autism in a way that presented the children with opportunities to approach and embrace others. Since then DMT therapists have researched the effects of DMT on autism finding benefits [i.e., Hartshorn, Olds, Field, Delage, Cullen & Escalona, 2001].

[45] People with schizophrenia are dysfunctional in the way they perceive the actions of the self and the other. They may move or speak themselves, yet attribute such actions to others. Alternatively, they may perceive the actions and speech of others as their own. This disorganization of action and perception is considered to be a

These disorders of the fronto-striatal system encompass abnormalities in the motor, emotional, and language systems, yet the parallels between the anomalous systems remain unknown. It is has been shown that the many systems of the human function together in the healthy adult [Diamond, 2007]. The interwoven relationship between motor and cognitive development is evident in human neuroimaging studies, brain damaged patients, and in people with neurodevelopmental disorders. Such studies have repeatedly shown that an interrelation exists between the cerebellum and dorsolateral prefrontal cortex [Diamond, 2000]. Traditionally, the cerebellum is known to be involved in motor coordination and learning, and the dorsolateral prefrontal cortex [DLPFC] in cognitive functions. Phylogenetic studies have shown that the cerebellum and DLPFC evolved in concert [Dow, 1942; Diamond, 2000]. Imaging studies have shown that cognitive tasks requiring DLPFC also activate the cerebellum, in that when activity in DLPFC decreases so does the activity in the cerebellum. Further, lesions in one area cause hypometabolism in the other [Diamond, 2000]. Cognitive disorders are often defining features of children with neurodevelopmental disorders such as autism and attention deficit hyperactivity disorder [ADHD]. In recent years, studies have shown that children with autism and ADHD also exhibit movement disorders. DLPFC and cerebellum have projections to and from each other – there is communication in both directions. Diamond [2000] notes that cognitive functions dependent on the DLPFC are also important for organizing and executing skilled movement. Such functions include the ability to keep relevant information in mind so as to be able to keep on task – to ‘remember

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basis for the hallucinations and delusions created by the schizophrenic mind [Arbib & Mundhenk, 2005]. Arbib describes that for the ability to have language, a person must know what the self is doing, as well as what others are doing, and that this mirror system functions abnormally in people with schizophrenia. Language and thought patterns are disorganized in people with schizophrenia. Arbib postulates that verbal thoughts are created through verbal pathways, yet once sensed, or put into action by speaking, the self perceives them to be created from outside the self as there is no working memory record of the creation of the verbal thoughts. Hence, people with schizophrenia fabricate that these are the actions of others - even if the others do not in fact exist.

what it is we are supposed to do' [similar to prediction]; to continually organize and reorganize the information as needed, to resist distractions and temptations in order to resist responding too early, and to inhibit one's first action/reaction when another might be more appropriate.

One hypothesis is that the combined physical, social, and cognitive experiences in infancy are critical in developing the creative intelligence that is characteristic of human behaviour [Smith & Gasser, 2005]. Interactions between abnormalities in one system may affect the development of other systems. For example, if the motor system develops abnormally, it may have abnormal effects on developing cognitive systems. Language is thought to have evolved from experiences related to skilled reaching and it has been demonstrated that gestural movements of the arm and hand develop in synchrony with vocalizations for language development [Gentilucci & Corballis, 2006; Hadar, Wenkert-Oleniks, Krauss & Soroka, 1998; Iverson & Thelen, 1998; Krauss, 1998; McNeill, 1992]. The findings from this thesis contribute to the knowledge of the organization of skilled reaching and can lead to investigations to the relationship between movement and language. This can, in turn, set the groundwork for investigations of skilled reaching movements in disorders of the frontal-striatal system and its interactions with the developing language system.

Today, scientists are at the beginning of a renaissance in the study of movement, in which the focus is not limited to motoricity alone, but branches out into the many facets of movement. From single cells to invertebrate and vertebrate subjects, the study of movement encompasses methods in molecular neurobiology, electrophysiology, neuroimaging, neuroethology, and ethology [including anthropology and human evolution]. Such studies have led to revelations - *'[t]hat which we call thinking is the evolutionary internalization of movement'* [Llinás, 2002] - that contribute greatly in deepening our understanding of how we exist. At first glance, skilled reaching seems simple and unremarkable. Yet, the value of examining the movements that constitute reaching is rich:

> *'…the gestures of harvesting, which dictate the height of trees (and perhaps even the choice of certain fruits); and the gestures of manual capture, which determine the shape of the objects we choose to grasp, throw, and catch…[R]egularity* [i.e., form in geometry, rhythm, or sound], *chance, and movement - are what make nature appear as it does. They are also the elements that constitute perception.'* [Berthoz, 2000].

Epilogue

‘*The central generation of movement and the generation of mindness are deeply related; they are in fact different parts of the same process…* [F]*rom its evolutionary inception mindness is the internalization of movement.*’ [Llinás, 2002].

I move, I sense my movement, I sense my movement and how it interacts with the world, I create images of my movement and my self in the world, I make predictions, I remember, I control, I plan, I think, I have a mind. Emerging from a sessile life, where movement occurs by chance - randomly, to cells genetically driven to electrical coupling [Llinás, 2002], into navigating in a world outside of the self, introducing new experiences into the self through the tango between movement, its impact, and the nervous system, bequeathing increasingly complex movements and growing behavioural repertoires imparts foundations for a mind. With my mind, I reach out to the abstract world and grasp concept through embodiment.

REFERENCES

Adkins DL, Jones TA. [2005]. D-amphetamine enhances skilled reaching after ischemic cortical lesions in rats. *Neuroscience Letters, 380[3]:214-8.*

Ahmed A, Ruffman T. [2000].Why do infants make A not B errors in a search task, yet show memory for the location of hidden objects in a non-search task? In D Muir, A Slater [Eds.]. Infant Development: The Essential Readings. Blackwell Publishing.

Alveradashvili M, Foroud A, Lim D, Whishaw IQ. [2008]. “Learned baduse” as a critical factor limiting recovery of motor function: task specific practice and skilled reaching after forelimb motor cortex lesion in rats. *Behavioural Brain Research, 188[2]:281-90.*

Arbib MA, Bota M. [2003]. Language evolution: Neural homologies and neuroinformatics. *Neural Networks, 16:237-1260.*

Arbib MA, Mundhenk TN. [2005]. Schizophrenia and the mirror system: An essay. *Neuropsychologia, 43:265-280.*

Arbib MA. [2002]. The mirror system, imitation and the evolution of language. In C Nehani, K Dautenhahn [Eds.]. Imitation in Animals and Artifacts. MIT Press.

Arbib MA. [2005]. From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioural and Brain Sciences, 28[2]:105-24.*

Armbrüster C, Spijkers W. [2006]. Movement planning in prehension: Do intended actions influence the initial reach and grasp movement? *Motor Control, 10[4]:311-29.*

Aruin AS. [2005]. Support-specific modulation of grip force in individuals with hemiparesis. *Archives of Physical Medicine and Rehabilitation, 86[4]:768-75.*

Aziz-Zadeh L, Wilson SM, Rizzolatti G, Iacoboni M. [2006]. Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology, 16[18]:1818-23.*

Bainbridge Cohen B. [1993]. Sensing, Feeling, and Action: The Experiential Anatomy of Body-Mind Centering. Contact Editions: Northampton, MA.

Bartenieff I, Davis M. [1973]. Effort/Shape Analysis of Movement: The Unity of Expression and Function. Research Approaches to Movement and Personality. Arno Press: New York.

Bartenieff I. [1973]. A tool in dance therapy. *Proceedings of the American Dance Therapy Association Conference, New York.*

Bartenieff I. [1974]. Effort/Shape in teaching ethnic dance. In T Comstock, [Ed.]. New Dimensions in Dance Research: Anthropology of Dance. I. The American Indian. Committee on Research in Dance: New York.

Barternieff I, Lewis D. [1980]. Body Movement: Coping with the Environment. Gordon & Breach Science Publishers: USA.

Beach FA. [1945]. Current concepts of play in animals. *The American Naturalist, 79[785]:523-541.*

Beauchamp MS, Martin A. [2007]. Grounding object concepts in perceptin and action : Evidence from fMRI studies of tools. *Cortex, 43[3]:461-468.*

Berger SE. [2008]. A longitudinal study of the role of infants' locomotor expertise on the development of inhibition. *International Conference on Infant Studies, Vancouver, BC.*

Beritoff JS. [1965]. Neural Mechanisms of Higher Vertebrate Behavior. Brown: New York.

Bernstein NA. [1967]. The Coordination and Regulation of Movement. Pergamon Press: New York.

Berthoz A. [2000]. The Brain's Sense of Movement. Perspectives in Neuroscience. Harvard University Press: USA.

Bhat AN, Lee HM, Galloway JC. [2007]. Toy-oriented changes during early arm movements: II. Joint kinematics. *Infant Behavior and Development, 30:307-324.*

Bhat AN, Galloway JC. [2006]. Toy-oriented changes during early arm movements: Hand kinematics. *Infant Behavior and Development, 29:358-372.*

Bhat AN, Galloway JC. [2007]. Toy-oriented changes during early arm movements: III. Constraints on joint kinematics. *Infant Behavior and Development, 30:515-522.*

Bizzi E, Tresch MC, Saltiel P, d'Avella A. [2000]. New perspectives on spinal motor systems. *Nature Reviews. Neuroscience, 1:101-108.*

Bobath B. [1990]. Adult Hemiplegia: Evaluation and Treatment. Third Edition. Heinmann Medical: London.

Boissy P, Bourbonnais D, Carlotti MM, Gravel D, Arsenault BA. 1999]. Maximal grip force in chronic stroke subjects and its relationship to global upper extremity function. *Clinical Rehabilitation, 13[4]:354-62.*

Bortoff GA, Strick PL. [1993]. Corticospinal terminations in two new world primates: Further evidence that corticomotoneuronal connections provide part of the neural substrate for manual dexterity. *Journal of Neuroscience, 13:5105-5118.*

Bourbonnais D, Vanden Noven S. [1989]. Weakness in patients with hemiparesis. *American Journal of Occupational Therapy, 43[5]:313-19.*

Boyd LA, Vidoni ED, Daly JJ. [2007]. Answering the Call: The influence of neuroimaging and electrophysiological evidence on rehabilitation. *Physical Therapy, 87[6]:684-703.*

Bradshaw JL. [2001]. Developmental Disorders of the Frontostriatal System: Neuropsychological, Neuropsychiatric and Evolutionary Perspectives. Psychology Press: Canada.

Brodal A. [1973]. Self-observations and neuro-anatomical considerations after a stroke. *Brain, 96:675-694.*

Brown JL. [1975]. The Evolution of Behavior. W.W. Norton and Company: New York.

Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ. [2001]. *The European Journal of Neuroscience, 13[2]:400-4.*

Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund HJ, Rizzolatti G. [2004]. Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron, 42:323–334.*

Butefisch CM. [2004]. Plasticity in the human cerebral cortex: Lessons from the normal brain and from stroke. *The Neuroscientist, 10[2]:163-173.*

Butler AB, Hodos W. [1996]. Comparative Vertebrate Neuranatomy: Evolution and Adaptation. Wiley-Liss: New York.

Caminiti R, Johnson PB, Urbano A. [1990]. Making arm movements within different parts of space: Dynamic aspects in the primate motor cortex. *Journal of Neuroscience, 10:2039-2058.*

Caramia MD, Palmieri MG, Giacomini P, Iani C, Dally L, Silvestrini M. [2000]. Ipsilateral activation of the unaffected motor cortex in patients with hemiparetic stroke. *Clinical Neurophysiology, 111:1990-1996.*

Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL. [2003]. Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proceedings of the National Academy of Sciences of the United States of America, 100:5497–5502.*

Castro, A.J. [1990]. Plasticity in the motor system. In T.R.C. Kolb, B. [Ed.]. The Cerebral Cortex of the Rat, pp. 563-588. MIT Press: Cambridge.

Chen Y, Pellis SM, Sirkin DW, Potegal M, Teitelbaum, P. [1986]. Bandage backfall: Labyrinthine and non-labyrinthine components. *Physiology and Behavior, 37:805-814.*

Cirstea MC, Levin, MF. [2000]. Compensatory strategies for reaching in stroke. *Brain, 123:940-953.*

Cirstea MC, Mitnitski AB, Feldman AG, Levin MF. [2003]. Interjoint coordination dynamics during reaching in stroke. *Experimental Brain Research, 151[3]:289-300.*

Cirstea MC, Ptito A, Levin MF. [2003]. Arm reaching improvements with short-term practice depend on the severity of the motor deficit in stroke. *Experimental Brain Research, 152[4]:476-88.*

Clark A. [2006]. Language, embodiment, and the cognitive niche. *Trends in Cognitive Sciences, 10[8]:370-4.*

Clarke J, Ploughman M, Corbett D.A. [2007]. Qualitative and quantitative analysis of skilled forelimb reaching impairment following intracerebral hemorrhage in rats. *Brain Research, 145:204-212.*

Clearfield MW, Feng F, Thelen E, [2007]. The development of reaching across the first year in twins of known placental type. *Motor Control, 11[1]:29-53.*

Coghill GE. [1929]. Anatomy and the Problem of Behavior. Cambridge University Press: Cambridge.

Cramer SC, Chopp M. [2000]. Recovery recapitulates ontogeny. *Trends in Neuroscience, 23:265-271.*

Cramer SC, Nelles G, Benson RR, Kaplan JD, Parker RA, Kwong KK, Kennedy DN, Finklestein SP, Rosen BR. [1997]. A functional MRI study of subjects recovered from hemiparetic stroke. *Stroke, 26:2518-2527.*

Damasio, AR. [1994]. Descartes' Error: Emotion, Reason, and the Human Brain. GP Putnam's Sons: New York.

Dancause N. [2006]a. Neurophysiological and anatomical plasticity in the adult sensorimotor cortex. *Reviews in the Neurosciences, 17[6]:561-80.*

Dancause N. [2006]b. Vicarious function of remote cortex following stroke: recent evidence from human and animal studies. *Neuroscientist, 12[6]:489-99.*

Dapretto M, Davies MS, Pfeifer JH, Scott AA, Sigman M, Bookheimer SY, Iacoboni M. [2006]. Understanding emotions in others: mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience, 9[1]:28-30.*

Darwin C. [1887]. Origin of Certain Instincts. *Nature, 179:417-418.*

Dell C. [1966]. A language for movement. *Music Journal, XXIV, 50:56-57.*

Dell C. [1977]. A Primer for Movement Description. Dance Notation Bureau: New York.

Denny-Brown D, Botterall EH. [1947]. The motor function of the agranular frontal cortex. *Research publications - Association for Research in Nervous and Mental Disease, 27:235-345.*

Denny-Brown D, Chamber RA. [1958]. The parietal lobe and behavior. *Research Publications - Association for Research in Nervous and Mental Disease, 36:35-117.*

Denny-Brown D. [1958]. The nature of apraxia. *The Journal of Nervous and Mental Disease, 126:9-32.*

Descartes, R. [1664]. Traité de l'Homme. Angot: Paris.

di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G. [1992]. Understanding motor events: A neurophysiological study. *Experimental Brain Research, 91[1]:176-80.*

Diamond A. [1985]. Development of the ability to use recall to guide action, as indicated by infants' performance on AB. *Child Development, 56:868-883.*

Diamond A. [1988]. Abilities and neural mechanisms underlying AB performance. *Child Development, 59:523-527.*

Diamond A. [1990]. Developmental time course in human infants and infant monkeys, and the neural bases of, inhibitory control in reaching a. *Annals of the New York Academy of Sciences 608[1]:637–676.*

Diamond A. [2000]. Close interrelation of motor development and cognitive development and of the cerebellum and prefrontal cortex. *Child Development, 71[1]:44-56.*

Diamond A. [2007]. Interrelated and interdependent. *Developmental Science, 10[1]:152-158.*

Dijkstra K, Misirlisov M. [2006]. Event components in autobiographical memories. *Memory, 14[7]:846-52.*

Dove ME, Eskes G, Klein RM, Shore D. [2007]. A left attentional bias in chronic neglect: A case study using temporal order judgments. *Neurocase, 13[1]:37-49.*

Dow RS. [1942]. The evolution and anatomy of the cerebellum. *Biological Reviews of the Cambridge Philosophical Society, 17:179-220.*

Eilam D, Golani I. [1988]. The ontogeny of exploratory behavior in the house rat [*Rattus rattus*]: The mobility gradient. *Developmental Psychobiology, 21[7]:679-710.*

Eilam D, Golani I. [1989]. Home base behavior of rats [*Rattus norvegicus*] exploring a novel environment. *Behavioural Brain Research, 34[3]:199-211.*

Eshkol N, Wachman A. [1958]. Movement Notation. Weidenfeld & Nicholson: London.

Fadiga L, Fogassi L, Pavesi G, Rizzolatti G. [1995]. Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology, 73:2608 –2611.*

Fagen R, Conitz J, Kunibe E. [1997]. Observing behavioural qualities. *International Journal of Comparative Psychology, 10[4]:167-79.*

Farnè A, Serino A, Làdavas E. [2007]. Dynamic size-change of peri-hand space following tool-use: Determinants and spatial characteristics revealed through cross-modal extinction. *Cortex, 43[3]:436-443.*

Farr TD, Whishaw IQ. [2002]. Quantitative and qualitative impairments in skilled reaching in the mouse [*Mus musculus*] after a focal motor cortex stroke. *Stroke, 33[7]:1869-75.*

Fellows S, Schwarz M, Schaffrath C, Dömges F, Noth J. [1997]. Disturbances of precision grip in Huntington's disease. *Neuroscience Letters, 226[2]:103-6.*

Fentress JC. [1973]. Development of grooming in mice with amputated forelimbs. *Science, 179:704-705.*

Ferrari PF, Gallese V, Rizzolatti G, Fogassi L. [2003]. Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *The European Journal of Neuroscience, 17:1703–1714.*

Ferrari PF, Rozzi S, Fogassi L. [2005]. Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience, 17:212–226.*

Ferrier D. [1876]. The Function of the Brain. Smith, Elder & Company: London.

Field AP, Hole GJ. [2003]. How to Design and Report Experiments. London: Sage.

Finger S. [1994]. Origins of Neuroscience: A History of Explorations into Brain Function. Oxford University Press: New York.

Flash T, Handzel AA. [2007]. Affine differential geometry analysis of human arm movements. *Biological Cybernetics, 96[6]:577-601.*

Flash T, Hochner B. [2005]. Motor primitives in vertebrates and invertebrates. *Current Opinion in Neurobiology, 15:660–666.*

Flourens M-J-P. [1824]. Researches Expérimental sur les Propriétés et les Fonctions du Systeme Nerveux dans les Animeaux Vertebrés. Crévot: Paris.

Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G. [2005]. Parietal lobe: From action organization to intention understanding. *Science, 308:662– 667.*

Fogassi L, Ferrari PF. [2007]. Mirror Neurons and the Evolution of Embodied Language. *Current Directions in Psychological Science, 16[3]:136-141.*

Fogassi, Gallese, Fadiga, Lupinno, Matelli, Rizzolatti. [1997]. The space around us. *Science, 277:190-191.*

Fonagy P, Target M. [2007]. The rooting of the mind in the body: New links between attachment theory and psychoanalytic thought. *Journal of the American Psychoanalytic Association, 55[2]:411-56.*

Foroud A, Pellis SM. [2002]. Development of "anchoring" in the play fighting of rats: Evidence for an adaptive age-reversal in the juvenile phase. *International Journal of Comparative Psychology, 15:11-20.*

Foroud A, Pellis SM. [2003]. The development of "roughness" in the play fighting of rats: A Laban Movement Analysis perspective. *Developmental Psychobiology, 42:35–43.*

Foroud A, Whishaw IQ, Pellis SM. [2004]. Experience and cortical control over the pubertal transition to rougher play fighting in rats. *Behavioural Brain Research, 149:69–76.*

Foroud A, Whishaw IQ. [2006]. Changes in the kinematic structure and non-kinematic features of movements during skilled reaching after stroke: A Laban Movement Analysis in two case studies. *Journal of Neuroscience Methods, 158:137–149.*

Foroud A. [2002]. Playing with Play: Movement and Experience in the Development of Play Fighting in Rats. MSc. Thesis, University of Lethbridge.

Fritsch G, Hitzig E. [1870]. Uber die elektrische Erregbarkeit des Grosshirns. *Arch. F. Anat., Physiol und Wissenchaftl Mediz., Leipzip. 300-332.* [On the electrical excitability of the cerebrum.] Translated by G von Borin [1960]. In Some Papers on the Cerebral Cortex. WW Nowinski [Ed.], p.73-96. Thomas: Springfield IL.

Frey SH. [2008]. Tool use, communicative gesture and cerebral asymmetries in the modern human brain. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences, in press.*

Fugl Meyer, AR. [1980]. Post-stroke hemiplegia assessment of physical properties. *Scandinavian Journal of Rehabilitation Medicine. Supplement, 7:85-93.*

Gallese V, Fadiga L, Fogassi L, Rizzolatti G. [1996]. Action recognition in the premotor cortex. *Brain, 119[pt 2]:593– 609.*

Gallese V, Keysers C, Rizzolatti G. [2004]. A unifying view of the basis of social cognition. *Trends in Cognitive Neuroscience, 8[9]:396-403.*

Gallese V. [2003]. The roots of empathy: The shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology, 36[4]:171-80.*

Gallese V. [2006]. Intentional attunement: A neurophysiological perspective on social cognition and its disruption in autism. *Brain Research, 1079[1]:15-24.*

Gallese V. [2007]a. Embodied simulation: From mirror neuron systems to interpersonal relations. *Novartis Foundation Symposium, 278:3-12.*

Gallese V. [2007]b. Before and below 'theory of mind': Embodied simulation and the neural correlates of social cognition. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 362[1480]:659-69.*

Garbarini F, Adenzato M. [2004]. At the root of embodied cognition: Cognitive science meets neurophysiology. *Brain Cognition, 56[1]:100-6.*

Gentilucci M, Corballis MC. [2006]. From manual gesture to speech: A gradual transition. *Neuroscience and Biobehavioral Reviews, 30[7]:949-60.*

Georgopoulos AP. [1986]. On reaching. *Annual Reviews of Neuroscience, 9:147-170.*

Georgopoulos AP. [1988]. Neural integration of movement: Role of motor cortex in reaching. *The FASEB Journal, 2:2849-2857.*

Georgopoulos AP. [1994]. Behavioural neurophysiology of the motor cortex. *The Journal of Laboratory and Clinical Medicine, 124[6]:766-774.*

Georgopoulos AP. [1996]. Arm movements in monkeys: Behavior and neurophysiology. *Journal of Comparative Physiology, 179:603-612.*

Golani I, Bronchti G, Moualem D, Teitelbaum, P. [1981]. "Warm-up" along dimensions of movement in the ontogeny of exploration in rats and other infant mammals. *Proceedings to the National Academy of Science USA, 78[11]:7226-7229.*

Golani I, Fentress JC. [1985]. Early ontogeny of face grooming in mice. *Developmental Psychobiology, 18[6]:529-544.*

Golani, I. [1976]. Homeostatic motor processes in mammalian interactions: A choreography of display. In PPG Bateson and PH Klopfer [Eds.]. Perspectives in Ethology, Volume 2, p. 69-134. New York: Plenum Press.

Goldberg, Dineva, Feng J, Gregor, Thelen E, Spencer JP. [2008]. Action tendencies from feet to hands: Kicking and button-pressing in an A-not-B task. *International Conference on Infant Studies, Vancouver, BC.*

Goldman A. [2006]. Simulating Minds: The Philosophy, Psychology, and Neuroscience of Mindreading. Oxford University Press: New York.

Goodale MA, Milner D. [2004]. Sight Unseen: An Exploration of Conscious and Unconscious Vision. Oxford University Press: New York.

Goodale MA, Westwood DA, Milner AD. [2004]. Two distinct modes of control for object-directed action. *Progress in Brain Research, 144:131-144.*

Goodale MA. [2001]. Different spaces and different times for perception and action. *Progress in Brain Research, 134:313-331.*

Goodman D, Kelso JA. [1983]. Exploring the functional significance of physiological tremor: A biospectroscopic approach. *Experimental Brain Research, 49:419-431.*

Goodman LS, Gilman A. [1970]. The Pharmacological basis of therapeutics. Fourth Edition. MacMillan: New York.

Grafton ST, Arbib MA, Fadiga L, Rizzolatti G. [1996]. Localization of grasp representations in humans by positron emission tomography. Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Experimental Brain Research, 112[1]:103-11.*

Gray JA. [1985]. A whole and its parts: Behaviour, the brain, cognition and emotion. *Bulletin of the British Psychological Society, 38:99-112.*

Gray LA, O'Reilly JC, Nishikawa KC. [1997]. Evolution of forelimb movement patterns for prey manipulation in Anurans. *Journal of Experimental Zoology, 277:417-24.*

Graziano MSA, Aflalo TN, Cooke DF. [2005]. Arm movements evoked by electrical stimulation in the motor cortex of monkeys. *Journal of Neurophysiology, 94[6]:4209-4223.*

Graziano MSA, Aflalo TN. [2007]a. Rethinking cortical organization: Moving away from discrete areas arranged in hierarchies. *The Neuroscientist, 13[2]:138-147.*

Graziano MSA, Aflalo TN. [2007]b. Mapping behavioral repertoire onto the cortex. *Neuron, 56:239-251.*

Graziano MSA, Cooke DF, Taylor CSR, Moore T. [2003]. Distribution of hand location in monkeys during spontaneous behavior. *Experimental Brain Research, 155:30-36.*

Graziano MSA, Cooke DF, Taylor CSR. [2000]. Coding the location of the arm by sight. *Science,* 290:1782-1786.

Graziano MSA, Hu XT, Gross CG. [1997]. Coding the locations of objects in the dark. *Science, 277:239-241.*

Graziano MSA, Taylor CSR, Moore T, Cooke DF. [2002]. The cortical control of movement revisited. *Neuron, 30:349-362.*

Graziano MSA, Taylor CSR, Moore T. [2002]. Complex movements evoked by microstimulation of precentral cortex. *Neuron, 34:841-851.*

Graziano MSA. [1999]. Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings to the National Academy of Science USA, 96:10418-10421.*

Graziano MSA. [2006]. The organization of behavioural repertoire in motor cortex. *Annual Review of Neuroscience, 29:105-134.*

Green PH. [1972]. Problems of organization of motor systems. In R Rosen, FM Snell [Eds.]. Progress in Theoretical Biology, Volume 2, p. 303-338. Academic: New York.

Hadar U, Wenkert-Olenik D, Krauss R, Soroker N. [1998]. Gesture and the processing of speech: Neuropsychological evidence. *Brain and Language, 62[1]:107-26.*

Halsband U, Freund H. [1993]. Motor learning. *Current Opinion in Neurobiology, 3:940-9.*

Harris-Love ML, McCombe Waller S, Whitall J. [2005]. Exploiting interlimb coupling to improve paretic arm reaching performance in people with chronic stroke. *Archives of Physical Medicine and Rehabilitation, 86[11]:2131-7.*

Hartshorn K, Olds L, Field T, Delage J, Cullen C, Escalona A. [2001]. Creative movement therapy benefits children with autism. *Early Child Development and Care, 166:1-5.*

Heiser M, Iacoboni M, Maeda F, Marcus J, Mazziotta JC. [2003]. The essential role of Broca's area in imitation. *The European Journal of Neuroscience, 17:1123–1128.*

Held R, Hein A. [1963]. Movement-produced stimulation in the development of visually guided behavior. *Journal of Comparative Physiology and Psychology, 56:872-876.*

Hines MO. [1942]. The development and regression of reflexes, postures, and progression in the young macaque. *Contributions to Embryology: Carnegie Institute, 30:153-209.*

Hlustik P, Solodkin A, Gullapalli RP, Noll DC, Small SL. [2001]. Somatotopy in human primary motor and somatosensory hand representations revisited. *Cerebral Cortex, 11:312-321.*

Holdefer RN, Miller LE. [2002]. Primary motor cortical neurons encode functional muscle synergies. *Experimental Brain Research, 146:233-243.*

Holstege, G. [1996]. The somatic motor system. *Progress in Brain Research, 107:9-26.*

Hsu JE, Jones TA. [2005]. Time-sensitive enhancement of motor learning with the less-affected forelimb after unilateral sensorimotor cortex lesions in rats. *The European Journal of Neuroscience*, 22[8]:2069-80.

Hughes C. [1996]. Brief report: Planning problems in autism at the level of motor control. *Journal of Autism and Developmental Disorders, 26:99-107.*

Hutchinson A. [1977]. Labanotation: The system of analyzing and recording movement. Third edition. Theatre Arts Books: New York.

Iacoboni M, Mazziotta JC. [2007]. Mirror neuron system: Basic findings and clinical applications. *Annals of Neurology, 62[3]:213-218.*

Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. [2005]. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology, 3:e79.*

Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G. [1999]. Cortical mechanisms of human imitation. *Science, 286:2526 –2528.*

Ingles JL, Eskes GA, Phillips SJ. [1990]. Fatigue after stroke. *Archives of Physical Medicine and Rehabilitation, 80[2]:173-8.*

Iverson JM, Thelen E. [1999]. Hand, Mouth and Brain. *Journal of Consciousness Studies, 6[11-12]:19-40.*

Iwaniuk AN, Whishaw IQ. [2000]. On the origin of skilled forelimb movements. *Trends in Neuroscience, 23[8]:372-76.*

Jackson JH. [1889]. On the comparative study of diseases in the nervous system. *British Medical Journal, 2:355.*

Jackson, JH. [1932]. Selected Writings of John Hughlings Jackson, Volume 2. J Taylor [Ed.] Hodder and Stoughton: London.

Jang SH. [2007]. A review of motor recovery mechanisms in patients with stroke. *NeuroRehabilitation, 22[4]:253-9.*

Jankowska E, Hammar I. [2002]. Spinal interneurons: How can studies in animals contribute to the understanding of spinal interneuronal systems in man? *Brain Research Reviews, 40:19-28.*

Jeanerrod M. [1988]. The Neural and Behavioural Organization of Goal-Directed Movements. Oxford University Press: Oxford.

Jeannerod M, Arbib MA, Rizzolatti G, Sakata H. [1995]. Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends in Neuroscience, 18:314-329.*

Kakei S, Hoffman D, Strick P. [1999]. Muscle and movement representations in the primary motor cortex. *Science, 285:2136-2139.*

Kandel ER, Schwartz JH, Jessell TM. [2000]. Principles of Neural Science. Fourth Edition. McGraw-Hill.

Keysers C, Kohler E, Umiltà MA, Nanetti L, Fogassi L, Gallese V. [2003]. Audiovisual mirror neurons and action recognition. *Experimental Brain Research, 153:628–636.*

Kleim JA, Barbay S, Cooper NR, Hogg TM, Reidel CN, Remple MS, Nudo RJ. [2002]. Motor learning-dependent synaptogenesis is localized to functionally reorganized motor cortex. *Neurobiology of Learning and Memory, 77[1]:63-77.*

Klein C. [2005]. Movement disorders: Classifications. *Journal of Inherited Metabolic Disease, 28[3]:425-39.*

Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G. [2002]. Hearing sounds, understanding actions: Action representation in mirror neurons. *Science, 297[5582]:846-8.*

Kolb B, Whishaw IQ. [1996]. Fundamentals of Human Neurophsychology. Fourth Edition. WH Freeman and Company: USA.

Konczak J, Jansen-Osmann P, Kalveram KT. [2003]. Development of force adaptation during childhood. *Journal of Motor Behavior, 35[1]:41-52.*

Koski L, Wohlschläger A, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Iacoboni M. [2002]. Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex, 12:847– 855.*

Krakauer JW. 2005 Arm function after stroke: From physiology to recovery. *Seminars in Neurology, 25[4]:384-95.*

Krauss RM. [1998]. Why do we gesture when we speak? *Current Directions in Psychological Science, 7:54-60.*

Laban R. [1960]. The Mastery of Movement. Revised third edition by L Ullman. Macdonald & Evans: London

Lakke JPFWF. [1985]. Axial apraxia in Parkinson's disease. *Journal of Neurological Sciences, 69:37-46.*

Lamontagne A, Stephenson JL, Fung J. [2007]. Physiological evaluation of gait disturbances post stroke. *Clinical Neurophysiology, 118[4]:717-29.*

Landgren S, Phillips CG, Porter R. [1962]. Cortical fields of origin of the monosynaptic pyramidal pathways to some alpha motoneurons of the baboon's hand and forearm. *Journal of Physiology, 161:112-125.*

Lang CE, Schieber MH. [2004]. Reduced muscle selectivity during individuated finger movements in humans after damage to the motor cortex or corticospinal tract. *Journal of Neurophysiology, 91:1722-1733.*

Lang CE, Wagner JM, Bastian AJ, Hu Q, Edwards DF, Sahrmann SA, Dromerick AW. [2005]. Deficits in grasp versus reach during acute hemiparesis. *Experimental Brain Research, 166[1]:126-36.*

Lang CE, Wagner JM, Edwards DF, Sahrmann SA, Dromerick AW. [2006]. Recovery of grasp versus reach in people with hemiparesis poststroke. *Neurorehabilitation and Neural Repair, 20[4]:444-54.*

Lang EJ, Llinás R, Sugihara I. [2006]. Isochrony in the olivocerebellar system underlies complex spike synchrony. *Journal of Physiology, 573[1]:277-9.*

Lang EJ, Sugihara I, Llinás R. [2006]. Olivocerebellar modulation of motor cortex ability to generate vibrissal movements in rat. *Journal of Physiology, 571[1]:101-20.*

Lawrence DG, Kuypers HGJM. [1968]a. The functional organization of the motor system in the monkey. I. The effects of bilateral pyramidal lesions. *Brain, 91:1-14.*

Lawrence DG, Kuypers HGJM. [1968]b. The functional organization of the motor system in the monkey. II. The effects of lesions of the descending brain stem. *Brain, 91:15-36.*

Lawrence DG. [1994]. Central neural mechanisms of prehension. *Canadian Journal of Physiological Pharmacology, 72:580-582.*

Leary MR, Hill DA. [1996]. Moving on: Autism and movement disturbance. *Mental Retardation, 34:39-53.*

Lee HM, Bhat A, Scholz JP, Galloway JC. [2008]. Toy-oriented changes during early arm movements: IV. Shoulder-elbow coordination. *Infant Behavior and Development, in press.*

Leiguardia R. [2001]. Limb apraxia: Cortical or subcortical. *Neuroimage, 14 [1pt2]:137-141.*

Leiguardia RC, Marsden CD. [2000]. Limb apraxis: Higher order disorders of sensorimotor integration. *Brain, 123:860-879.*

Lemon RN, Baker SN, Davis JA. Kirkwood PA, Maier MA, Yang HS. [1998]. The importance of the cortico-motoneuronal system for control of grasp. *Novartis Foundation Symposium, 218:202-215.*

Lemon RN, Griffiths J. [2005]. Comparing the function of the corticospinal system in different species: Organizational differences for motor specialization? *Muscle Nerve, 32:261-279.*

Lemon RN, Johansson RS, Westling G. [1995]. Corticospinal control during reach, gras, and precision lift in man. *Journal of Neuroscience, 15:6145-6156.*

Levin MF, Desrosiers J, Beauchemis D, Bergeron N, Rochette, A. [2004]. Development and validation of a scale for rating motor compensations used for reaching in patients with hemiparesis: The reaching performance scale. *Physical Therapy, 84:8-22.*

Levin MF. [1996]a. Interjoint coordination during pointing movements is disrupted in spastic hemiparesis. *Brain, 119[1]:281-293.*

Levin MF. [1996]b. Should stereotypic movement synergies in hemiparetic patients be considered adaptive? *Behavioural Brain Sciences, 19:79-80.*

Li CS, Padoa-Schioppa C, Bizzi E. [2001]. Neuronal correlates of motor performance and motor learning in the primary motor cortex of monkeys adapting to an external force field. *Neuron, 30:593-607.*

Llinás RR. [2002]. I of the Vortex: From Neurons to Self. MIT Press: USA.

Lockman JJ, Ashmead DH, Bushnell EW. [1984]. The development of anticipatory hand orientation during infancy. *Journal of Experimental Child Psychology, 37:176-86.*

Lough S, Wing AM, Fraser C, Jenner JR. [1984]. Measurements of recovery of function in the hemiparetic upper limb following stroke: A preliminary report. *Human Movement Science, 3:247-56.*

Maclellan CL, Grams J, Adams K, Colbourne F. [2005]. Combined use of a cytoprotectant and rehabilitation therapy after severe intracerebral hemorrhage in rats. *Brain Research, 1063[1]:40-7.*

Magnus R. [1926]. Animal posture. *Proceedings of the Royal Society, 980:339-353.*

Maletic V. [1987]. Body, Space, Expression: The Development of Rudolf Laban's Movement and Dance Concepts. Mouton de Gnoyter: New York.

Marativa A, Iriki A. [2004]. Tools for the body [schema]. *Trends in Cognitive Science, 8[2]:79-86.*

Martin JH, Engber D, Meng Z. [1982]. Effect of forelimb use on postnatal development of the forelimb motor representation in primary motor cortex of the cat. *Journal of Neurophysiology, 93:2822-2831.*

McCrea PH, Eng JJ, Hodgson AJ. [2002]. Biomechanics of reaching: Clinical implications for individuals with acquired brain injury. *Disability and Rehabilitation, 24[10]:534-41.*

McCrea PH, Eng JJ, Hodgson AJ. [2005]. Saturated muscle activation contributes to compensatory reaching strategies after stroke. *Journal of Neurophysiology, 94[5]:2999-3008.*

McDonnell, M.N., Hillier, S.L., Ridding, M.C., Miles, T.S. [2006]. Impairments in precision grip correlate with functional measures in adult hemiplegia. *Clinical Neurophysiology, 117:1474–1480.*

McNeill D. [1992]. Hand and Mind: What Gestures Reveal About Thought. University Chicago Press.

Melillo R, Leisman G. [2004]. Neurobehavioural Disorders of Childhood: An Evolutionary Perspective. Springer-Science, USA.

Micera S, Carpaneto J, Posteraro F, Cenciotti L, Popovic M, Dario P. [2005]. Characterization of upper arm synergies during reaching tasks in able-bodied and hemiparetic subjects. *Clinical Biomechanics, 20[9]:939-46.*

Michaelsen SM, Jacobs S, Roby-Brami A, Levin MF. [2004]. Compensation for distal impairments of grasping in adults with hemiparesis. *Experimental Brain Research, 157[2]:162-73.*

Michaelsen SM, Levin MF. [2004]. Short-term effects of practice with trunk restraint on reaching movements in patients with chronic stroke: A controlled trial. *Stroke, 35[8]:1914-9.*

Montessori M. [1964]. The Montessori Method. Schokem Books: New York.

Montessori M. [1967]. The Absorbent Mind. Dell Publishing: New York.

Morecraft RJ, Herrick JL, Stilwell-Morecraft KS, Louie JL, Schroeder CM, Ottenbacher JG, Schoolfield MW. [2002]. Localization of arm representation in the corona radiata and internal capsule in the non-human primate. *Brain, 125: 176-198.*

Mountcastle VB, Lynch JC, Georgopoulos AP, Sakata H, Acuna C. [1975]. Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology, 38:871-907.*

Muller R-A, Watson CE, Muzik O, Chugani HT. [1998]. Motor organization after early middle cerebral artery stroke: A PET study. *Pediatric Neurology, 19:294-298.*

Newman-Norlund RD, van Schie HT, van Zuijlen AM, Bekkering H. [2007]. The mirror neuron system is more active during complementary compared with imitative action. *Nature Neuroscience, 10:817– 818.*

Niedenthal PM. [2007]. Embodying emotion. *Science, 316[5827]:1002-5.*

Nudo RJ, Milliken GW. [1996]. Reorganization of movement representations in primary motor cortex following focal ischemic infarcts in adult squirrel monkeys. *Journal of Neurophysiology, 75[5]:2144-2149.*

Oberman LM, Hubbard EM, McCleery JP, Altschuler EL, Pineda JA, Ramachandran VS. [2005]. EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Cognitive Brain Research, 24:190-198.*

Olivier I, Hay L, Bard C, Fleury M. [2007]. Age-related differences in the reaching and grasping coordination in children: Unimanual and bimanual tasks. *Experimental Brain Research, 179[1]:17-27.*

Paillard J, Jordan P, Brouchon M. [1981]. Visual motion cues in prismatic adaptation: Evidence of two separate and additive processes. *Acta Psychologica, 48:253-270.*

Panksepp J. [1981]. The ontogeny of play in rats. *Developmental Psychobiology, 14:327-332.*

Pasztor TJ, Smith LK, MacDonald NK, Michener GR, Pellis SM. [2001]. Sexual and aggressive play fighting of sibling Richardson's ground squirrels. *Aggressive Behavior, 27: 323-337.*

Paulson G, Gottlieb G. [1968]. Development reflexes: The reappearance of foetal and neonatal reflexes in aged patients. *Brain, 91:37-52.*

Pavlov IP [1927]. Conditioned Reflexes: An investigation of the Physiological Activity of the Cerebral Cortex. Translated by GV Anvep. Oxford University Press: London.

Pellis SM, Officer RCE. [1987]. An analysis of some predatory behaviour patterns in four species of carnivorous marsupials [Dasyuridae], with comparative notes on the eutherian cat *Felis catus*. *Ethology, 75:177-96.*

Pellis SM, Pellis VC, Chen Y, Barzci S, Teitelbaum P. [1989]. Recovery from axial apraxia in the lateral hypothalamic labryinthectomized rat reveals three elements of contact-righting: Cephalocaudal dominance, axial rotation, and distal limb action. *Behavioural Brain Research, 35:241-251.*

Pellis SM, Pellis VC, Foroud A. [2005]. Play Fighting: Aggression, Affiliation, and the Development of Nuanced Social Skills. In RE Tremblay WW Hartup J Archer [Eds.]. Developmental Origins of Aggression. Guilford Press: New York.

Pellis SM, Pellis VC. [1987]. Play-fighting differs from serious fighting in both target of attack and tactics of fighting in the laboratory rat *Rattus norvegicus*. *Aggressive Behavior, 13:227-42.*

Pellis SM. [1996]. Righting and the modular organization of motor programs. In K-P Ossenkopp, M Kavaliers, PR Sanberg [Eds]. Measuring Movement and Locomotion: From Invertebrates to Humans. R.G. Landes Company: New York.

Pellis, S.M. [1981]. A description of social play in the Australian magpie *Gymnorhina tibicen* based on Eshkol-Wachman movement notation. *Bird Behaviour,* 3:61-79.

Pellis, S.M. [1982]. An analysis of courtship and mating in the Cape Barren goose *Cereopsis novahollandiae* Latham based on the Eshkol-Wachman movement notation. *Bird Behaviour*, *4:30-41.*

Pellis, S.M. [1983]. Development of head and foot coordination in the Australian magpie *Gymnorhina tibicen*, and the function of play. *Bird Behaviour, 4:57-62.*

Pellis, S.M. [1989]. Fighting: the problem of selecting approporiate behavior patterns. In RJ Blanchard, PF Brain, DC Blanchard, S Parmigiani [Eds.], Ethoexperimental Approaches to the Study of Behavior, p. 361-374. Kluwer Academic Publishers: Dordrecht.

Pellis VC, Pellis SM, Teitelbaum P. [1991]. A descriptive analysis of the postnatal development of contact-righting in rats [*Rattus norvegicus*]. *Developmental Psychobiology, 24[4]: 237-263.*

Petrides M, Cadoret G, Mackey S. [2005]. Orofacial somatomotor responses in the macaque monkey homologue of Broca's area. *Nature, 435:1235-1238.*

Pfeifer JH, Iacoboni M, Mazziotta JC, Dapretto M. [2008]. Mirroring others' emotions relates to empathy and interpersonal competence in children. *Neuroimage, 39[4]:2076-85.*

Piaget J. [1954]. The Construction of Reality in the Child. Routledge: New York.

Piecharka DM, Kleim JA, Whishaw IQ. [2005] Limits on recovery in the corticospinal tract of the rat: Partial lesions impair skilled reaching and the topographic representation of the forelimb in motor cortex. *Brain Research Bulletin, 66[3]:203-11.*

Plato [Trans., Saunders TJ. 1975]. The Laws. Penguin: Harmondsworth Middlesex, UK.

Platz T, Bock S, Prass K. Reduced skilfulness of arm motor behaviour among motor stroke patients with good clinical recovery: Does it indicate reduced automaticity? Can it be improved by unilateral or bilateral training? A kinematic motion analysis study. *Neuropsychologia, 2001, 397:687-98.*

Ramachandran VS, Oberman LM. [2006]. Broken Mirrors: A Theory of Autism. *Scientific American, 295[5]:63-69.*

Rauschecker JP. [2001]. Cortical map plasticity in animals and humans. *Progress in Brain Research, 138:73-88.*

Reina GA, Moran DW, Schwartz AB. [2001]. On the relationship between joint angular velocity and motor cortical discharge during reaching. *Journal of Neurophysiology, 85:2576-2589.*

Rizzolatti G, Arbib MA. [1998]. Language within our grasp. *Trends in Neurosiences, 21:188-194.*

Rizzolatti G, Craighero L. [2004]. The mirror-neuron system. *Annual Review of Neuroscience, 27:169 –192.*

Rizzolatti G, Fadiga L, Gallese V, Fogassi L. [1996]. Premotor cortex and the recognition of motor actions. *Brain Research. Cognitive Brain Research, 3:131–141.*

Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, Fazio F. [1996]. Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research, 111:246 –252.*

Roby-Brami A, Feydy A, Combeaud M, Biryukova EV, Bussel B, Levin MF. [2003]. Motor compensation and recovery for reaching in stroke patients. *Acta Neurologica Scandinavica, 107[5]:369-81.*

Roby-Brami A, Jacobs S, Bennis N, Levin MF. [2003]. Hand orientation for grasping and arm joint rotation patterns in healthy subjects and hemiparetic stroke patients. *Brain Research, 969[1-2]:217-29.*

Rosander K, von Hofsten C. [2002]. Development of gaze tracking of small and large objects. *Experimental Brain Research, 146:257-64.*

Rumi MJ. [Trans., Coleman B. 1995]. The Essential Rumi. Haper Collins: New York.

Sanes JN, Donaghue JP. [2000]. Plasticity and primary motor cortex. *Annual Reviews of Neuroscience, 23:393-415.*

Sanes JN, Wang J, Donaghue JP. [1992]. Immediate and delayed changes of rat cortical output representations with new forelimb configurations. *Cerebral Cortex, 2:141-152.*

Sanford J, Moreland J, Swanson LR, Stratford PW, Gowland C. [1993]. Reliability of the Fugl-Meyer assessment for testing motor performance in patients following stroke. *Physical Therapy, 73[7]:447-454.*

Schallert T, Teitelbaum, P. [1981]. Haloperidol, catalepsy and equilibrium functions in the rat: Antagonistic interaction of clinging and labyrinthine righting reactions. *Physiology and Behavior, 27:1077-1083.*

Schendel K, Robertson LC. [2004]. Reaching out to see: Arm position can attenuate human visual loss. *Journal of Cognitive Neuroscience, 16[6]:935-43.*

Schieber MH, Santello M. [2004]. Hand function: Peripheral and central constraints on performance. *Journal of Applied Physiology, 96:2293-2300.*

Schieber MH. [2004]. Motor control: Basic units of cortical output? *Current Biology, 14:R353-R354.*

Schneiberg S, Sveistrup H, McFadyen B, McKinley P, Levin MF. [2002]. The development of coordination for reach-to-grasp movements in children. *Experimental Brain Research, 146[2]:142-54.*

Scott SH, Kalaska JF. [1995]. Changes in motor cortex activity during reaching movements with similar hand paths but different arm postures. *Journal of Neurophysiology, 73:2563-2567.*

Scott SH, Kalaska JF. [1997]. Reaching movements with similar hand paths but different arm orientations. I. Activity of individual cells in motor cortex. *Journal of Neurophysiology. 77:826-852.*

Scott SH. [2004]. Optimal feedback control and the neural basis of volitional motor control. *Nature Review. Neuroscience. 5:532-546.*

Sergio LE, Kalaska JF. [2003]. Systematic changes in motor cortex cell activity with arm posture during directional isometric force generation. *Journal of Neurophysiology, 89:212-228.*

Sherrington CS. [1906]. The Integrative Action of the Nervous System. Yale University Press: New Haven.

Sherrington CS. [1939]. On the motor area of the cerebral cortex. In D Denny-Brown [Ed.]. Selected Writings of Sir Charles Sherrington, p. 397-439. Hamish Hamilton Medical Books: London.

Singer T. [2007]. The neuronal basis of empathy and fairness. *Novartis Foundation Symposium, 278:20-30.*

Smith L, Gasser M. [2005]. The development of embodied cognition: Six lessons from babies. *Artificial Life, 11[1-2]:13-29.*

Smith LB, Thelen E. [2003]. Development as a dynamic system. *Trends in Cognitive Sciences, 7[8]:343-348.*

Smith LK, Metz GA. Dietary restriction alters fine motor function in rats. [2005]. *Physiology and Behavior, 85[5]:581-92.*

Solaro C, Brichetto G, Casadio M, Roccatagliata L, Ruggiu P, Mancardi GL, Morasso PG, Tanganelli P, Sanguineti V. [2007]. Subtle upper limb impairment in asymptomatic multiple sclerosis subjects. *Multiple Sclerosis, 13[3]:428-32.*

Stavness C. [2006]. The effect of positioning for children with cerebral palsy on upper-extremity function: A review of the evidence. *Physical and Occupation Therapy in Pediatrics, 26[3]:39-53.*

Teitelbaum O, Benton T, Shah PK, Prince A, Kelly JL, Teitelbaum P, [2004]. Eshkol-Wachman movement notation in diagnosis: The early detection of Asperger's syndrome. *Proceedings to the National Academy of Science USA, 101[32]:11909-14.*

Teitelbaum P, Cheng MF, Rozin P. [1969]. Development of feeding parallels its recovery after hypothalamic damage. *Journal of Comparative and Physiological Psychology, 67[4]:430-41.*

Teitelbaum P, Cheng MF, Rozin P. [1969]. Stages of recovery and development of lateral hypothalamic control of food and water intake. *Annals of the New York Academy of Science, 157[2]:849-60.*

Teitelbaum P, Teitelbaum O, Nye J, Fryman J, Maurer RG. [1998]. Movement analysis in infancy may be useful for early diagnosis of autism. *Proceedings of the National Academy of Sciences of the USA, 95:13982-13987.*

Teitelbaum P, Wolgin DL, DeRyck M, Marin OSM. [1976]. Bandage-backfall reaction: Occurs in infancy hypothalamic damage, and catalepsy. *Proceedings of the National Academy of Science USA, 73[9]:3311-3314.*

Teitelbaum P. [1967]. Physiological Psychology: Fundamental Principles. Prentice Hall: New Jersey.

Teitelbaum, P. [1971]. The encephalization of hunger. In E Stellar, JM Sprague [Eds.]. Progress in Physiological Psychology, Volume 4, p. 319-350. Academic Press: New York.

Teitelbaum P, Teitelbaum O, Fryman J, Maurer RG. [2002]. Infantile reflexes gone astray in austim. *Journal of Developmental and Learning Disorders, 6:15–22.*

Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, Perani D. [2005]. Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience, 17[2]:273-81.*

Thelen E, Corbetta D, Spencer JP. [1996]. Development of reaching during the first year: Role of movement speed. *Journal of Experimental Psychology Human Perception and Performance,* 22[5]:1059-76.

Thelen E, Fisher DM. [1982]. Newborn stepping: An explanation for a ‘disappearing’ reflex. *Developmental Psychobiology, 18 [5]:760-775.*

Thelen E, Spencer JP. [1998]. Postural control during reaching in young infants: A dynamic systems approach. *Neuroscience and Biobehavior Reviews, 22[4]:507-14.*

Tibben A. [2007]. Predictive testing for Huntington's disease. *Brain Research Bulletin, 72[2-3]:165-71.*

Tinbergen N. [1973]. Ethology and Stress Disease. *Nobel Lecture, 113-130.*

Todorov E, Jordon MI. [2002]. Optimal feedback control as a theory of motor coordination. *Nature Neuroscience, 5:1226-1235.*

Tomasello M, Carpenter M. [2007]. Shared intentionality. *Developmental Science, 10[1]:121-125.*

Trevarthen CB. [1968]. Two mechanisms of vision in primates. *Psychologische Forschung, 31:299-337.*

Trombly CA. Deficits of reaching in subjects with left hemiparesis: A pilot study. [1992]. *American Journal of Occupational Therapy, 46[10]:887-97.*

Trombly CA. Observations of improvement of reaching in five subjects with left hemiparesis. [1993]. *Journal of Neurology, Neurosurgery, and Psychiatry, 56[1]:40-5.*

Twitchell TE. [1957]. The restoration of motor function following hemiplegia in man. *Brain, 74:443-480.*

Twitchell TE. [1969]. Early development of avoiding and grasping in man. In KJ Connolly [Ed.]. Mechanism of Motor Skill Development. Academic Press: London.

Twitchell TE. [1970]. Reflex mechanisms and the development of prehension. In KJ Connolly [Ed.]. Mechanism of Motor Skill Development. Academic Press: London.

Umiltà MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, Rizzolatti G. [2001]. I know what you are doing. A neurophysiological study. *Neuron, 31:155–165.*

Ungerleider LG, Mishkin, M. [1982]. Two cortical visual systems. In DJ Ingle, MA Goodale, RJW Mansfield [Eds.]. Analysis of Visual Behavior. MIT Press: Cambridge.

Utley A, Steenbergen B. [2006]. Discrete bimanual co-ordination in children and young adolescents with hemiparetic cerebral palsy: Recent findings, implications and future research directions. *Pediatric Rehabilitation, 9[2]:127-36.*

van der Meer ALH. [1997]. Keeping the arm in the limelight: Advanced visual control of arm movements in neonates. *European Journal of Paediatric Neurology, 4:103-8.*

van Dijk H, Jannink MJ, Hermens HJ. [2005]. Effect of augmented feedback on motor function of the affected upper extremity in rehabilitation patients: A systematic review of randomized controlled trials. *Journal of Rehabilitative Medicine, 37[4]:202-11.*

Van Harreveld A, Kok dJH. [1935]. A propos de la nature de la catalepsie experimentale. *Archives Néerlandaises de Physiologie de l'Homme et des Animaux, 10:411-429.*

Vasey PL, Foroud A, Duckworth N, Kovacovsky SD. [2006]. Male–Female and Female–Female Mounting in Japanese Macaques: A Comparative Study of Posture and Movement: *Archives of Sexual Behavior, 35[2]:117–129.*

Viviani P, Flash T. [1995]. Minimum-jerk, two-thirds power law, and isochrony: Converging approaches to movement planning. *Journal of Experimental Psychology. Human Perception and Performance, 21[1]:32-53.*

von Hofsten C, Lindhagen K. [1979]. Observations on the development of reaching for moving objects. *Journal of Experimental Child Psychology, 28:158-173.*

von Hofsten C, Rőnnqvist L. [1988]. Preparation for grasping an object: A developmental study. *Journal of Experimental Psychology: Human Perception and Performance, 14:610-21.*

von Hofsten C. [1979]. Development of visually directed reaching: The approach phase. *Journal of Human Movement Studies, 5:160-178.*

von Hofsten C. [1980]. Predictive reaching for moving objects by human infants. *Journal of Experimental Child Psychology, 30:369-382.*

von Hofsten C. [1982]. Eye-hand coordination in newborns. *Developmental Psychology, 18:450-61.*

von Hofsten C. [2007]. Action in Development. *Developmental Science, 10[1]:54-60.*

Vouloumanos A, Werker JF. [2007]. Listening to language at birth: Evidence for a bias for speech in neonates. *Developmental Science, 10[2]:159-64.*

Wagner JM, Dromerick AW, Sahrmann SA, Lang CE. [2007]. Upper extremity muscle activation during recovery of reaching in subjects with post-stroke hemiparesis. *Clinical Neurophysiology, 118[1]:164-76.*

Wallace DG, Hamilton DA, Whishaw IQ. [2006]. Movement characteristics support a role for dead reckoning in organizing exploratory behavior. *Animal Cognition, 9[3]:219-28.*

Wallace PS, Whishaw IQ. [2003]. Independent digit movements and precision grip patterns in 1-5-month-old human infants: Hand-babbling, including vacuous then self-directed hand and digit movements, precedes targeted reaching. *Neuropsychologia, 41[14]:1912-8.*

Wapner S, Cirillo L. [1968]. Imitation of a model's hand movement: Age changes in transposition of left-right relations. *Child Development, 39:887– 894.*

Webb AA, Muir GD. [2005]. Sensorimotor behaviour following incomplete cervical spinal cord injury in the rat. *Behaviour Brain Research, 165[2]:147-59.*

Weiller C, Ramsay SC, Wise RJ, Friston KJ, Frackowiak RS. [1993]. Individual patterns of functional reorganization in the human cerebral cortex after capsular infarction. *Annals of Neurology, 33:181-189.*

Werker JF. [2003]. Baby steps to learning language. *The Journal of Pediatrics. 143[4]:S62-9.*

Werker JF, Tees RC. [1992]. The organization and reorganization of human speech perception. *Annual Review of Neuroscience, 15:377-402.*

Werker JF, Tees RC. [1999]. Influences on infant speech processing: Toward a new synthesis. *Annual Review of Psychology, 50:509-535.*

Whishaw IQ, Dringenberg, Pellis SM. [1992]. Spontaneous forelimb grasping in free feeding by rats: Motor cortex aids limb and digit positioning. *Behavioural Brain Research, 48[2]:113-125.*

Whishaw IQ, Gorny B, Foroud A, Kleim JA. [2003]. Long–Evans and Sprague–Dawley rats have similar skilled reaching success and limb representations in motor cortex but different movements: Some cautionary insights into the selection of rat strains for neurobiological motor research. *Behavioural Brain Research, 145:221–232.*

Whishaw IQ, Pellis SM, Gorny BP, Pellis VC. [1991]. The impairments in reaching and the movements of compensation in rats with motor cortex lesions: An endpoint, videorecording, and movement notation analysis. *Behavioural Brain Research* 42:77-91.

Whishaw IQ, Pellis SM, Gorny BP. [1992]a. Skilled reaching in rats and humans: Evidence for parallel development or homology. *Behavioural Brain Research, 47[1]:59-70.*

Whishaw IQ, Pellis SM, Gorny BP. [1992]b. Medial frontal cortex lesions impair the aiming component of rat reaching. *Behavioural Brain Research, 50[1-2]:93-104.*

Whishaw IQ, Pellis SM. [1990]. The structure of skilled forelimb reaching in the rat: A proximally driven movement with a single distal rotatory component. *Behavioural Brain Research, 41:49-59.*

Whishaw IQ, Suchowersky O, Davis L, Sarna J, Metz GA, Pellis SM. [2002]. Impairment of pronation, supination, and body co-ordination in reach-to-grasp tasks in human Parkinson's disease [PD] reveals homology to deficits in animal models. *Behavioural Brain Research, 133[2]:165-76.*

Whishaw IQ. [2003]. Did a change in sensory control of skilled movements stimulate the evolution of the primate frontal cortex? *Behavioural Brain Research, 146[1-2]:31-41.*

Wilson, FR. [1998]. The Hand: How its Use Shapes the Brain, Language, and Human Culture. Pantheon Books: USA.

Windle V, Corbett D. [2005]. Fluoxetine and recovery of motor function after focal ischemia in rats. *Brain Research, 1044[1]:25-32.*

Windle WF. [1940]. Physiology of the Fetus. W.B. Saunders: Philadelphia.

Wolgin DL, Hein A, Teitelbaum P. [1980]. Recovery of forelimb placing after lateral hypothalamic lesions in the cat: Parallels and contrasts with development. *Journal of Comparative and Physiological Psychology*, 94[5]:795-807.

Wong YJ, Whishaw IQ. [2004]. Precision grasps of children and young and old adults: Individual differences in digit contact strategy, purchase pattern, and digit posture. *Behavioural Brain Research, 154[1]:113-123.*

Yarosh CA, Hoffman DS, and Strick PL. [2004]. Deficits in movements of the wrist ipsilateral to a stroke in hemiparetic subjects. *Journal of Neurophysiology, 92[6]:3276-3285.*

APPENDIX 1

Detailed Descriptions of Notated Scores from the Two Case Studies in Chapter 2

A. Reaching with the Right Arm in One Control Subject. The control subject makes a gestural movement with his right arm using Light Weight and Direct Space Efforts. Shortly after he initiates the movement with his right arm, the subject makes postural movement with his torso, which ends shortly before the arm gesture. At the end of the arm gesture, he pauses briefly. He then makes a small gesture with his right hand with Light Weight Effort while his torso is still, but not unsupportive in posture. This gesture is followed by another gestural movement, with his right arm, that is made with Light Weight and Direct Space Efforts, which begins with, but does not end with, Quick Time Effort. At the same time, his torso makes another postural movement that begins at the same time as the gestural arm movement, but ends slightly before the gesture is complete. Finally, his right arm makes another gestural movement, this time with Light Weight and Indirect Space Efforts.

B. Subject PL Reaching with the Right Arm. PL engages in Shapeflow movements of the torso that are expressed throughout the behaviour. He begins with a long gestural movement with his right arm using Direct Space Effort. Then, after a brief pause, he makes a short gesture with the right arm followed by a long gestural movement with his right arm that begins with Strong Weight and Bound Flow Efforts and continues with Light Weight and Direct Space Efforts. Finally, after another brief pause, he makes another long gestural movement with his right arm using Direct Space Effort. The entire movement, from beginning to end, is performed with a Spokelike Directional Shaping.

C. Subject PL Reaching with the Left Arm. PL makes a movement with his torso in a simultaneously Forward and Sideways right direction while making a gestural movement with his left arm that begins with Light Weight and Bound Flow Efforts, continues with Indirect Space Effort, and finishes with Bound Flow Effort. He follows with a brief pause, then, makes a short gesture with his hand. He then initiates a gestural movement of the arm with Strong Weight and Bound Flow Efforts, that continues with Quick Time Effort, then follows through with Light Weight, Direct Space, and Bound Flow Efforts. After another brief pause, PL makes a movement with his torso in a simultaneously Backward and Sideways left direction while making a gestural movement with his left arm using Bound Flow and Direct Space Efforts.

D. Subject IC Reaching with the Right Arm. IC makes a gestural movement with his right arm using Strong Weight, Bound Flow, and Direct Space Efforts, while simultaneously making a movement with his torso. At the end of the gesture, he pauses briefly, then makes a short gestural movement with his hand using Strong Weight. This is followed by short gesture of the head and the arm using first Quick Time, then Strong Weight and Direct Space Efforts. He then makes a postural movement with his torso. During this movement of the torso, he makes a gestural movement with the arm using Strong Weight, Bound Flow, and Direct Space Efforts. Towards the end of the gestural movement, his arm movement merges with the postural movement of his torso – called posture-gesture merger. That is, the movement of the arm is no longer a simple gesture in that it becomes part of the postural movement. There is a brief pause followed by a short posture-gesture merger movement and, finally, another gestural movement with his arm, this time with Strong Weight and Indirect Space Efforts as well as Arclike Shaping.

E. Subject IC Reaching with the Left Arm. The Motif shows that, when reaching with the left arm, IC makes more movements, involves more of his body, and uses more types of expressive movements than all other subjects. The notation begins by describing IC making two, whole body postural movements sequentially. The first whole body movement, made with a Rising Shaping Quality, carries a Forward movement of his torso as he makes three small gestures, with his left arm, at the beginning of the body movement. The three gestures are made with Bound Flow and Indirect Space Efforts. However, the second gesture is made with an additional Effort of Quick Time. After the third gesture, his arm stops moving (unless it is carried by the torso). The second whole body movement continues to carry is torso Forward. Then, within the same whole body movement, his torso begins a series of Backward, then Forward, movements that are repeated. Thus far, the second whole body postural movement is made with Bound Flow Effort. However, during the repeated Forward and Backward movements, IC also begins to use Shapeflow. He continues by using Shapeflow, as well as moving his torso Backward, then simultaneously Forward, Downward, and Sideways left as he makes a gestural movement with his left arm with Light Weight, Indirect Space, and Bound Flow Efforts. During the Forward + Downward movement of the torso, IC also makes a gestural movement with his left hand. Then, IC makes a simultaneous Backward and Sideways right movement with his entire body using Bound Flow Effort. Towards the end of this torso movement, he makes a gestural movement with his head; this gesture ends when the movement of his torso is completed. He then makes another long whole body movement with Rising and Spreading Shaping Qualities, in a Backward movement of his torso. After initiating this postural movement, IC makes a gestural movement with his left arm with Light Weight and Bound Flow Efforts. After a pause in the movement of his arm, which is not moving but is being carried backwards with his torso, he makes another gestural movement with his arm using Strong Weight and Bound Flow Efforts. After the whole body postural movement is complete, his entire body contracts and twists, with a Sinking Shaping Quality, as well as with Light Weight and Bound Flow Efforts. Toward the end of the contraction and twisting, IC makes a short gestural movement with his left arm using Bound Flow Effort. Finally, he extends his torso while making a gestural movement with his left arm using Light Weight, Indirect Space, and Bound Flow Efforts. Towards the end of this movement, IC makes a short gestural movement with his head.

APPENDIX 2

Correlations between Overall Scores on the EW-DRS and ERS

A negative correlation between the EW-DRS and ERS rating scales was found in the stroke group. When subjects had low scores on the EW-DRS, they had high scores on the ERS, indicating a poor performance by both rating scales. This correlation provides one measure of reliability of the newly designed ERS as it produces the same end result as the previously established EW-DRS. That is, either rating scale will provide an endpoint measure on the severity of skilled reaching after stroke. However, the two rating scales are not redundant in the type of information they provide. The EW-DRS quantifies motor deficits in the kinematic aspects of movement, and the ERS quantifies abnormal extraneous movements in both kinematic and non-kinematic aspects of movement during skilled reaching.

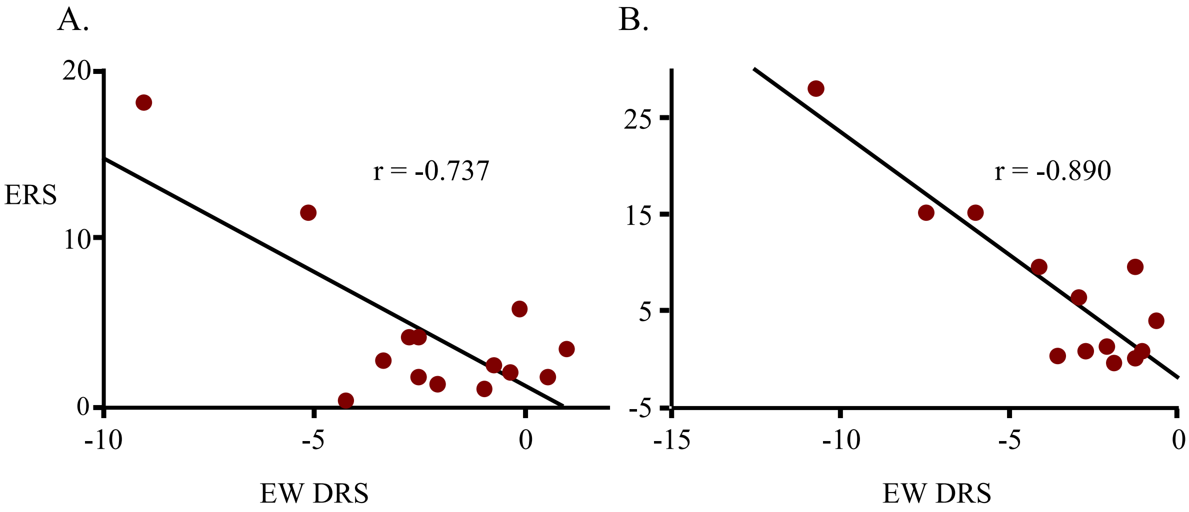


Figure A2. Correlations between Overall Scores on the EW-DRS and ERS when reaching with the A] Ipsilateral-to-Stroke Limb and B] Contralateral-to-Stroke Limb.

APPENDIX 3.1
Affected Subcomponents on the EW-DRS

Table A3.1 Affected Subcomponents on the EW-DRS. A] Reaching with the Ipsilateral-to-Stroke limb

	Orient		Lift		Aim				Pronate		Grasp				Supinate				Return		
Subject	Head fixate on target	Eyes fixate on target	Point at target	Opening of digits	Flexion of elbow	Hand carried directly to target	Hand ends above target	Trunk moves with hand on advance	Hand fully turned	Elbow opened	Thumb and index finger close to target	Uses pincer grasp	Independent movements of digits	Lift up on grasp	Supination I	Supination II	Head to meet hand	Trunk moves with hand on withdrawal	Hand pronate	Free digits from grasp	Hand open on lap
Right Hemisphere Lesions																					
Parietal Somatosensory					*		*	*	*				*	*	*			*		*	
Superior Posterior Parietal					*			*					*			*		*			
Parieto-Occipital				*						*			*								
Fronto-Parietal					*					*			*							*	*
Cerebral medially near falx				*		*	*		*	*		*	*	*		*				*	*
Posterior limb of Internal Capsule					*			*					*	*				*		*	
Thalamic								*		*		*	*				*	*	*	*	*
Subcortical					*			*		*			*	*	*	*		*		*	*
Left Hemisphere Lesions																					
Frontal + Anterior Parietal					*					*			*	*		*			*	*	*
Deep Parietal							*		*	*		*	*	*	*			*			
Bilateral Involvement																					
Bilateral Parieto-Occipital + Right Posterior Frontal + Cerebellum					*			*										*			
Cerebellar and Brainstem				*		*	*	*			*	*	*	*	*	*	*	*	*	*	*

* Indicates the subject received a score that is ≤ 0.75 on respective subcomponents.

Table A3.1 [*continued*] B] Reaching with the Contralateral-to-Stroke limb

	Orient		Lift			Aim			Pronate			Grasp			Supinate				Return		
Subject	Head fixate on target	eyes fixate on target	Point at target	Opening of digits	Flexion of elbow	Hand carried directly to target	Hand ends above target	Trunk moves with hand on advance	Hand fully turned	Elbow opened	Thumb and index finger close to target	Uses pincer grasp	Independent movements of digits	Lift up on grasp	Supination I	Supination II	Head to meet hand	Trunk moves with hand on withdrawal	Hand pronate	Free digits from grasp	Hand open on lap
Right Hemisphere Lesions																					
Parietal Somatosensory				*	*		*	*	*	*			*		*			*		*	
Superior Posterior Parietal			*	*		*				*			*	*		*				*	
Parieto-Occipital				*						*			*					*		*	
Fronto-Parietal					*	*	*			*		*	*	*	*	*				*	*
Cerebral medially near falx				*	*											*				*	*
Posterior limb of Internal Capsule			*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Thalamic								*		*		*	*	*		*			*	*	*
Subcortical			*	*		*		*		*		*	*	*	*	*	*	*	*	*	*
Left Hemisphere Lesions																					
Frontal + Anterior Parietal							*	*	*				*	*	*		*	*		*	*
Deep Parietal							*		*	*			*			*	*	*			
Bilateral Involvement																					
Bilateral Parieto-Occipital + Right Posterior Frontal + Cerebellum				*	*	*	*	*		*			*			*		*		*	

* Indicates the subject received a score that is ≤ 0.75 on respective subcomponents.

APPENDIX 3.2

Affected Subcomponents on the ERS

Table A3.2 A] Reaching with the Ipsilateral-to-Stroke limb

	Advance							Grasp					Withdrawal						Release				
Subject	Uses more than one gesture	Limb moved by body/torso	Strong Weight Effort observed	Indirect Space Effort used at the end of the advance	Direct Space Effort not used at the end of the advance	Bound Flow Effort observed	Shaping Qualities Observed	Uses more than one gesture (I.e. makes multiple attempts)	Limb moved by body/torso (body is engaged)	Hand appears to be stuck on the pedestal	Use of or increased use of Bound Flow Effort	Shaping Qualities observed	Uses more than one gesture	Limb moved by body/torso	Strong Weight Effort observed	Indirect Space Effort used at the end of the withdrawal	Bound Flow Effort observed	Shaping Qualities Observed	Uses more than one gesture	Limb moved by body/torso	Strong Weight Effort observed	Bound Flow Effort observed	Shaping Qualities Observed
Right Hemisphere Lesions																							
Parietal Somatosensory						*					*												
Superior Posterior Parietal											*				*		*						
Parieto-Occipital			*								*					*					*		
Fronto-Parietal				*	*						*					*							
Cerebral medially near falx		*		*	*	*					*			*		*	*				*	*	
Internal Capsule			*			*				*	*		*		*				*		*		
Thalamic				*		*					*											*	
Subcortical		*												*									
Left Hemisphere Lesions																							
Frontal + Anterior Parietal						*					*						*					*	
Deep Parietal				*	*	*					*					*	*					*	
Bilateral Involvement																							
Bilateral Parieto-Occipital + Right Posterior Frontal + Cerebellum						*					*												
Cerebellar and Brainstem	*		*	*	*	*	*			*	*	*			*	*	*	*				*	*

* Indicates the subject received a score that is ≥ 0.21 on respective subcomponents.

Table A3.2 [*continued*] B] Reaching with the Contralateral-to-Stroke limb

	Advance							Grasp					Withdrawal						Release				
Subject	Uses more than one gesture	Limb moved by body/torso	Strong Weight Effort observed	Indirect Space Effort used at the end of the advance	Direct Space Effort not used at the end of the advance	Bound Flow Effort observed	Shaping Qualities Observed	Uses more than one gesture (I.e. makes multiple attempts)	Limb moved by body/torso (body is engaged)	Hand appears to be stuck on the pedestal	Use of or increased use of Bound Flow Effort	Shaping Qualities observed	Uses more than one gesture	Limb moved by body/torso	Strong Weight Effort observed	Indirect Space Effort used at the end of the withdrawal	Bound Flow Effort observed	Shaping Qualities Observed	Uses more than one gesture	Limb moved by body/torso	Strong Weight Effort observed	Bound Flow Effort observed	Shaping Qualities Observed
Right Hemisphere Lesions																							
Parietal Somatosensory						*					*											*	
Superior Posterior Parietal		*	*	*	*	*					*			*	*	*	*					*	
Parieto-Occipital				*							*										*		
Fronto-Parietal		*		*	*	*		*	*	*	*			*		*	*					*	
Cerebral medially near falx						*		*			*												
Posterior limb of Internal Capsule	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			*		
Thalamic				*	*	*		*									*					*	
Subcortical		*	*	*	*	*	*		*	*	*	*		*									
Left Hemisphere Lesions																							
Frontal + Anterior Parietal											*												
Deep Parietal				*				*															
Bilateral Involvement																							
Bilateral Parieto-Occipital + Right Posterior Frontal + Cerebellum	*	*		*	*	*					*			*	*	*	*					*	

* Indicates the subject received a score that is ≥ 0.21 on respective subcomponents.

APPENDIX 4

Examples of the Four Developmental Stages of Reaching in Infancy

The attached DVD has a video showing the developmental stages of reaching in one of the infants from the longitudinal study.

APPENDIX 5

Skilled Reaching Before and After Motor Cortex Stroke in Long Evans Rats

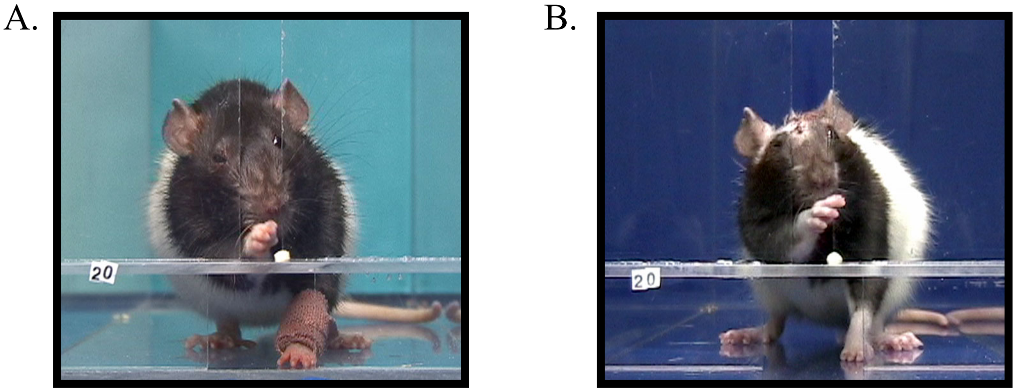
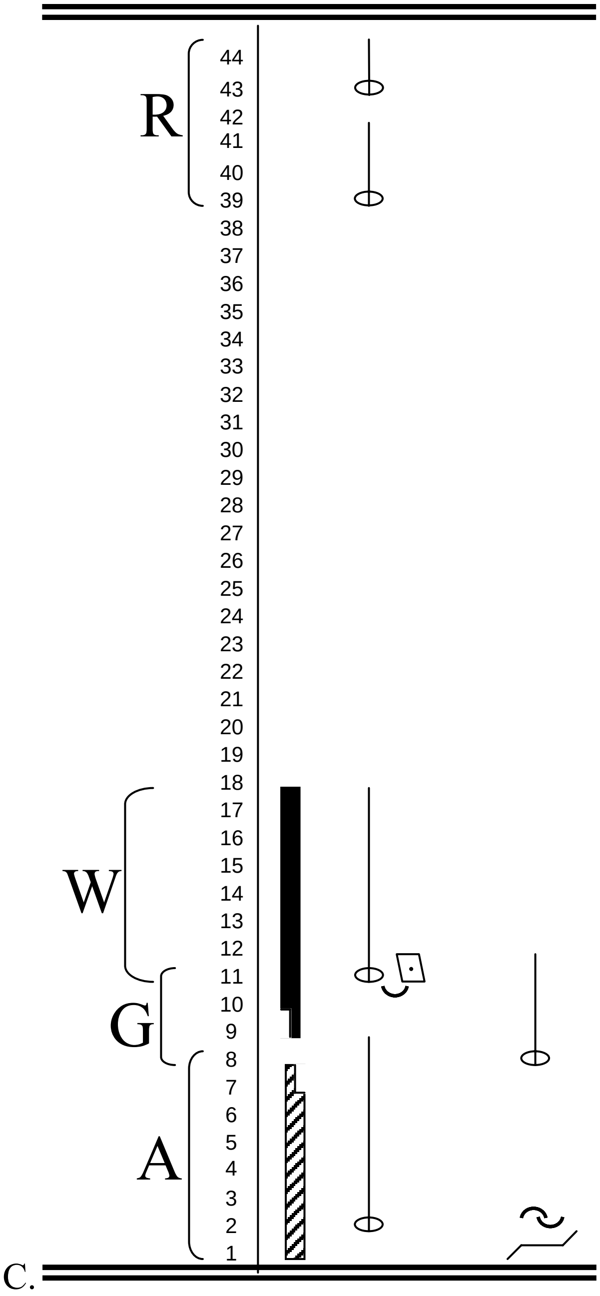
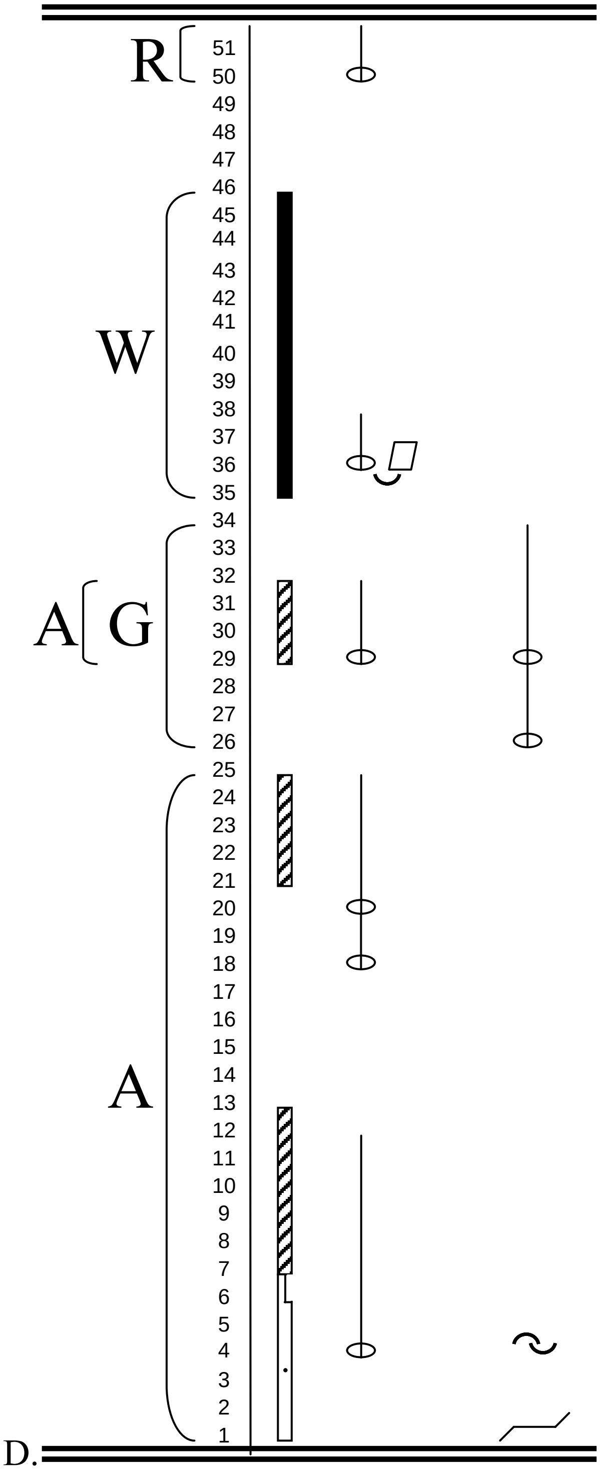


Figure A5. Skilled Reaching in A] Pre-Stroke, and B] Post-Stroke Rats.

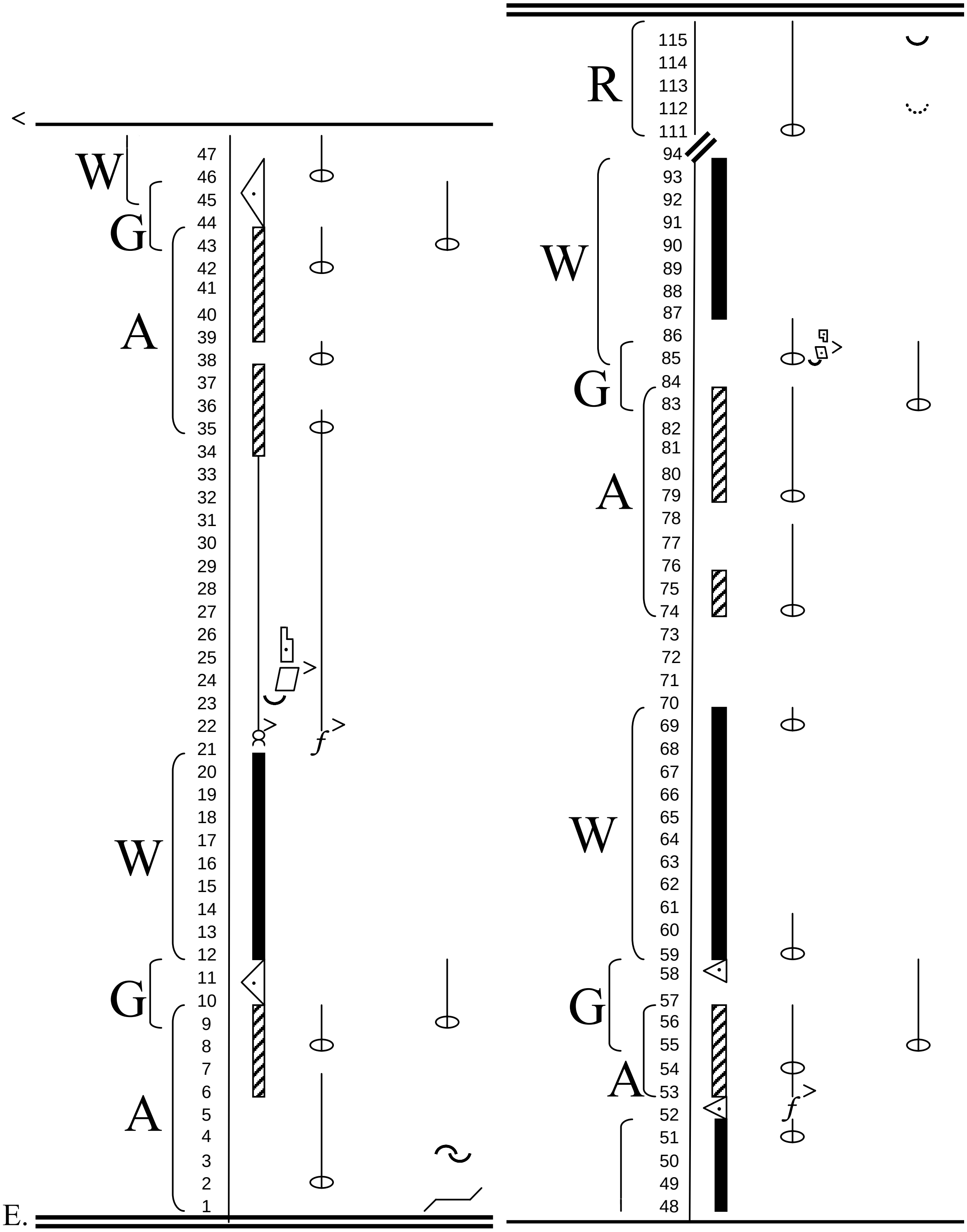
The following Motif scores are shorthand LMA notations of a rat reaching C] pre- and D] & E] post- motor cortex stroke. The notations are written, and read, from the bottom up. The double horizontal lines drawn at the bottom and top of the Motif indicate the beginning and end of the behaviour. In a case where the description for the behaviour is too long for one column, single bar lines are drawn at the top of the first column and at the bottom of the following column. Sub-columns within each Motif score from left to right are: Components [A = Advance, G = Grasp, W = Withdrawal, R = Release], Time [frame number at 30 frames/second], Body, Forelimb, and Forepaw. Thus the Motif is read horizontally as well as vertically. A person without LMA training can observe that the three Motifs differ from one another. A detailed description of the first Motif is provided below and is followed by a summary of how each of the following two Motifs differ. Adapted from Alveradashvili, Foroud, Lim and Whishaw, 2007.



C. Skilled Reaching Before Stroke. *Advance:* The rat begins by initiating a movement of the body in an upward + forward direction. At the beginning, its forepaw is weight bearing, and this is released as it begins to make a gesture with her forelimb. The forelimb gesture finishes briefly after the body movement. *Grasp:* As the forelimb gesture is ending, the rat begins to make a gesture with the forepaw, during this time. It begins to make another body movement in a downward + backward direction. *Withdrawal:* Still, during this time, as the forepaw gesture ends, she begins a new forelimb gesture, with a slight rotatory component, that finishes at the same time as the body movement. This is followed by a brief pause in movement as the rat consumes the pellet. *Release:* After the pause, the rat makes two short gestures, one after another. Note that the Advance component ends as the Grasp component begins and, as the Grasp component ends, the Withdrawal component begins.



D. Skilled Reaching Fourteen Days after Stroke. *Advance:* Instead of making an upward + forward directional body movement, the rat either moves the body forward, then upward, or upward. The forelimb gesture finishes slightly before the upward body movement finishes, rather than slightly after the body movement. There is a pause in movement. After the pause, the rat makes two additional consecutive short forelimb gestures. *Grasp:* The rat then makes two consecutive gestures with the forepaw, a new forelimb gesture begins at the same time as the second short forepaw gesture and finishes slightly beforehand. The rat also makes a body movement in an upward direction that begins and ends at the same time as the forelimb gesture. *Withdrawal:* Once the two consecutive forepaw gestures finish, the rat begins to make a body movement in a downward direction. During this time, it makes a short forelimb gesture that has a slight rotatory component. After a pause in movement, the rat makes one short forelimb gesture. *Release:* There is a shorter pause in movement as the rat consumes the pellet than in the previous notation. Note that the Advance component appears again during the Grasp component and that each of the components end before the next one begins, rather than one moving into the other as in the previous notation.



E. Skilled Reaching Twenty-Four Days after Stroke. *Advance:* The rat begins with a forelimb gesture, rather than a body movement, and makes an additional forelimb gesture. The body movement is in an upward direction. *Grasp:* The rat makes lateral body movement, in a direction opposite of the reaching limb. *Withdrawal:* The rat makes a downward, rather than a downward + backward, body movement. It then makes a postural movement, with its forebody only, that has a rotational + forward component. Throughout this postural movement, the rat's forelimb maintains a fixed position, in that it does not move with its body. *Advance:* The rat then makes two consecutive upward body movements and three consecutive forelimb gestures. *Grasp:* Towards the end of the second upward body movement and forelimb gesture, the rat initiates a forepaw gesture. It then makes another lateral body movement as the forepaw gesture finishes. *Withdrawal:* The rat initiates a forelimb gesture towards the end of the lateral body movement. When the gesture finishes, it makes a downward body movement. The rat makes a short forepaw gesture towards the end of downward body movement. It then makes another lateral body movement, while its forelimb maintains a fixed position as it transitions into another Advance component. *Advance:* The rat makes an upward body movement and initiates a forelimb gesture shortly after that finishes with the upward body movement. *Grasp:* Partway through the gesture and upward body movement, the rat initiates a forepaw gesture that finishes as the new, lateral body movement ends. *Withdrawal:* The rat initiates a forelimb gesture and downward body movement simultaneously; however, the body movement is longer than the gesture. Towards the end of the body movement, the rat makes another short forelimb gesture. There is a movement pause. *Advance:* The rat initiates a forelimb gesture and upward body movement simultaneously; however, the gesture is longer than the body movement. After the gesture finishes, the rat simultaneously begins and ends another forelimb gesture with an upward body movement. *Grasp:* Towards the end of the gesture and body movement, the rat makes a forepaw gesture that continues after the gesture and body movement finish. *Withdrawal:* Towards the end of the forepaw gesture, the rat makes a short forelimb gesture that has rotatory and backward components. Once this gesture is finished, it makes a downward body movement. There is a movement pause as it consumes the pellet. This pause is longer than in the other two notations. *Release:* The rat makes a forelimb gesture. Shortly after the beginning of the gesture, its paw makes light contact with the ground. Towards the end of the gesture its forepaw is in full contact with the ground though it is not yet weight-bearing.

APPENDIX 6

Skilled Reaching in Vervet Monkeys.

This scale is derived from combined EWMN and LMA notated scores of two female and two male vervet monkeys trained in a reaching task similar to the single pellet reaching task used for study in rats.

Table A6. Reaching Scale for Vervet Monkeys

Reaching Scale for Vervet Monkeys

Components	Subcomponents	Score
A. Orient	1. Head follows target	0, 0.5, 1
	2. Eyes follow target	0, 0.5, 1
	3. Body follows target	0, 0.5, 1
	4. Orientation is fixed until body turn to place food in mouth [#17]	0, 0.5, 1
B. Approach	5. Gait not interrupted for reach	0, 0.5, 1
	6. Body/torso expands on approach/advance	0, 0.5, 1
	7. Stays upright	0, 0.5, 1
	8. Stabilize [by bracing or planting one foot] part of the body while contralateral limbs keep in motion	0, 0.5, 1
C. Reach	9. Reach is part of swing phase of the forelimb	0, 0.5, 1
	10. Wrist is flexed prior to grasp	0, 0.5, 1
	11. Limb fully pronated prior to grasp	0, 0.5, 1
D. Grasp	12. Grasps target between digits 1 and 2	0, 0.5, 1
	13. Extra digits close during grasp	0, 0.5, 1
E. Withdraw	14. Lift upon grasping	0, 0.5, 1
	15. Supination before arm is out of slot	0, 0.5, 1
	16. Stabilize/mobilize relationship [similar to #8], either with ipsilateral support, or up/down body relationship, to prepare for #17 turn the body in order to bring head to hand	0, 0.5, 1
	17. Turns the body in order to bring head to hand	0, 0.5, 1
F. Release	18. Maintain stablize/mobilize relationship while performing #19	0, 0.5, 1
	19. Return to quadraped as turn body away from target	0, 0.5, 1
	20. Regain full gait	0, 0.5, 1
	21. Orient to back of the cage	0, 0.5, 1
		Total = 21