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Neural adaptations for social learning

Structural and functional investigations of action observation networks in macaques, chimpanzees, and humans

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An abstract of a dissertation submitted to the Faculty of the James T. Laney School of Graduate Studies of Emory University in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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Abstract

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Social learning is an important ability in primate life, and human specializations for social learning are part of what set us apart from the rest of the animal kingdom. In particular, humans' ability to copy not only the outcomes of observed actions but also their movement details has been linked to the emergence of cumulative culture. Social learning involves an action observation network that is distributed across frontal, parietal, and occipitotemporal cortex. This dissertation reports species differences in the structure and function of these networks that may underlie species differences in social learning. First, diffusion tensor imaging studies revealed progressively greater parietal and inferotemporal connectivity from macaques to chimpanzees to humans. These structural differences parallel, and may underlie, functional differences. FDG-PET neuroimaging studies in chimpanzees revealed that like humans and unlike macaques, chimpanzees have overlapping brain responses for performed action, observed transitive action, and observed intransitive action. Since chimpanzees and humans but not macaques are capable of copying movement details (imitating), this suggests that the ability to "mirror" not only action outcomes but also movement details is a correlate to the ability to copy those movement details. Furthermore, the chimpanzee neural response to observed action was situated mainly in prefrontal cortex, which may reflect top-down processing related to a conceptual, abstract representation of the observed action, while humans had greater parietal and occipitotemporal activation, which may reflect greater bottom-up processing on the details of movements, body parts, and objects. This may explain why humans tend to copy movement details while chimpanzees tend to copy action outcomes. Finally, chimpanzees with greater activation in ventral premotor cortex and lateral occipital cortex performed better in a separate behavioral test on copying action outcomes/movements and tool use, suggesting that selection pressure for social learning behavior could act on brain responses to observed action. These results are relevant to the evolution of action observation, social learning, and possibly culture.

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[1] *A portion of Section 1.1 is reproduced with minor edits from Hecht, E. E., L. E. Murphy, D. A. Gutman, T. M. Preuss and L. A. Parr (Under revision). "Functional neuroimaging of the chimpanzee mirror system reveals human specializations for social learning." J Neurosci.*

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Chapter 1:

Introduction

1.1. Why study the evolution of social learning?

Consider the exponential growth in technology over just the past few decades that landed our species on the moon, built CERN, and let us genetically engineer our own food. We are able to accomplish these feats because each generation builds on the expertise of the last – because human culture is *cumulative*, or adds successive modifications and improvements to socially transmitted behaviors over time (Tennie, Call et al. 2009, Whiten, McGuigan et al. 2009). In contrast, consider our closest living primate relatives, chimpanzees. The stone tools they use to crack nuts have remained essentially unchanged since about the time humans invented the first alphabets (Mercader, Barton et al. 2007). [6]

Why is chimpanzee culture so static, while human culture is so dynamic? At least part of the answer lies in *social learning*, the ability of one individual to observe and then intentionally replicate another's behavior. Differences in the way in which one individual acquires behaviors from another, when viewed in aggregate at a population level, add up to differences in culture. The existence of cumulative culture in humans has been linked to a specific, unique aspect of our social learning abilities: we copy not only actions' overall end results, but also their specific component movements (Dean, Kendal et al. 2012). Our species' drive to copy specific methods extends even to the point of reproducing steps which do not contribute to the action's end result, termed "over-imitation" (Whiten, McGuigan et al. 2009). In contrast, chimpanzee social learning use is strongly goal-oriented. Chimpanzees are more likely to copy an observed action's end

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result than its specific methods. Furthermore, chimpanzees have marked difficulty copying actions that do *not* involve objects and consist only of movements "without results" (Hayes and Hayes 1952, Custance, Whiten et al. 1995).

What *part* of an observed action is socially learned (the methods or the end result) has relevance for what *types* of actions can be socially learned. Humans' ability to focus on component movements allows individuals to quickly acquire and improve on complex chains of actions that are beyond their ability to personally invent (Tennie, Call et al. 2009). Because chimpanzees focus mainly on observed actions' results and not the movements that achieve them, each animal must re-discover for itself exactly how to achieve those results. Each animal's independent discovery is necessarily limited by its own intellect, so chimpanzee culture remains fixed at the inventive capacity of a single individual, while the frontier of human culture continues to expand (Tennie, Call et al. 2009).

If we can understand what in the human brain makes our brand of social learning unique – why it is that we copy not only the product but also the *process* of an observed action – we will have a mechanistic explanation for a defining characteristic of our species. This dissertation aims to move us closer to such an explanation.

1.2. What can other animals tell us about human social learning?[7]

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While some aspects of human social learning are unique, human social learning is built on underlying processes that are partially shared with other species. In the search to identify the defining characteristics of the human brain, it is necessary to consider brain evolution in a broader context.

Students of evolutionary neuroscience may be familiar with the metaphor of an old apartment building for brain evolution. At first, the building is heated by a series of wood-burning fireplaces. Later, a coal-fueled steam system is added in the chimneys and hearths. Later still, an HVAC system is installed, with electrical wiring grafted to the old hot water pipes. Every time something goes wrong with the heat, someone has to determine whether the problem is due to a wiring problem in the HVAC system, damage to the old hot water pipes along which those wires run, or a structural problem in the old chimneys that house the whole apparatus. Like the addition of new heating systems to the apartment building, evolution adds new functions to the brain by building on the pre-existing architecture, but these old systems don't disappear. The new functions are integrated with their pre-existing ones, and the continued function of the new systems relies on the soundness of the old ones.

A prominent instantiation of this idea was MacLean's triune brain theory (MacLean 1990), which posited that instinctual behavior is controlled by the brain's "reptilian complex" (basal ganglia), basic social behavior by the "paleomammalian complex" (limbic system), and higher cognitive function by the "neomammalian complex" (cerebral neocortex). Later anatomical work showed this model to be overly simplistic, but the basic concept of hierarchical processing is echoed by the recent proliferation in dual process models in neuroscience and psychology. Current models tend to make a linear distinction. One system is described as unconscious or preconscious, implicit,

automatic, low effort, rapid, perceptually driven, while another is described as conscious, explicit, controlled, high effort, slow, and analytic or reflective (reviewed in (Evans 2008)). For the sake of simplicity, we will refer to the first system as "reflexive" and the second as "reflective," although this linear distinction is likely also overly simplistic.

For some time, it was assumed that reflective social cognitive processes were evolutionary "upgrades" unique to humans, or perhaps humans and our closest living relatives, and much behavioral research focused on identifying which skills are "uniquely human" (Evans 2008, de Waal and Ferrari 2010). However, there are reasons not to assume that humans' most advanced forms of social cognition lack correlates in other species. Like the upgrades to the apartment heating system, human social cognitive "upgrades" must achieve the same basic purpose as their simpler predecessors – interacting with other individuals in the environment in an adaptive way. Evolution modifies previously existing forms to create new ones (for example, wings are modifications of limbs), and the new forms retain some features of the old ones (bone structure). These adaptations must arise in the context of a previously working social cognitive system, and as such, must incorporate with it. New neural mechanisms must function within the organism's existing social cognitive framework, or else the organism's social behavior will be impaired and its chances of survival will be reduced. Therefore, neural adaptations for new social cognitive functions are likely to involve some of the same neural architecture as preexisting systems.

Furthermore, functions that were once attributed only to humans are increasingly being identified in other species. Thus, reflective social cognition is probably uniquely *developed* in humans, but not unique *to* us (Evans 2008). It is important to remember that all life on earth has been evolving for the same amount of time and the phylogenic

tree has no "top." Differences in function represent adaptation to different niches, not higher or lower position in a *scala naturae*. A growing number of researchers in the field of comparative behavior stress the explanatory utility of viewing behavior as phylogenically continuous (de Waal and Ferrari 2010), a position that was espoused by Darwin (Darwin 1872).

All of this argues that studying animals can tell us something about human social cognition. Human neuroscience is currently very interested in the brain's "most modern upgrades" – reflective processes like theory of mind, or thinking about what another person is thinking (Premack and Woodruff 1978), as well as related processes like imitation, perspective-taking, and empathy. Understanding these functions is relevant for understanding and treating disorders of social cognition like autism in which they are impaired. But like the old apartment building, these functions aren't stand-alone systems. Deficits in the higher level functions may even be due to underlying, less obvious deficits in the lower level functions, so understanding the interplay between higher- and lower-level functions is essential for understanding and treating disease.

1.2.1. The big picture: Self-other matching phenomena across the animal kingdom

In this review, we explore this concept, as well as the question of what in particular the study of animals can tell us about human social cognition. We do so in the context of *self-other matching*, defined as any phenomenon in which the observation of another's behavior or state causes the observer's behavior or state to become congruent with it. We have chosen this broad operational definition for several reasons. First, it allows phenomena to be categorized by easily observable output. In many species, comparable behavioral data is available but data about underlying physiology or neural substrates is

not (or is available but contentious, as in the question of whether human imitation involves or relies on the mirror system). Grouping results by behavioral output allows for cross-species comparisons without any *a priori* perspective about underlying physiological processes. We will, however, draw connections to underlying physiological and neural substrates when possible. Second, self-other matching can occur in a reflexive manner, but this reflexive processing can have measurable effects on reflective processes. Third, self-other matching phenomena are present in varying degrees of complexity across a wide range of phyla.

In this review, we limit our scope to vertebrates. We focus heavily on non-hum,an primates, since they are most closely related to humans and also the subject of a large body of comparative research (including this dissertation), but we also discuss some research in canids, rodents, birds, and reptiles. In humans, self-other matching encompasses phenomena like motor resonance, mimicry, imitation, emulation, empathy, and perspective taking (defined in **Table 1-2.1**), which likely rely on partially discrete and partially overlapping neural and psychological mechanisms. Comparing which of these functions are present in which other species can help us to structure our thinking about the organization of these processes within our own species.

Self-other matching in the motor domain is of the most relevance to the topic of this dissertation, so we consider this topic first. We then consider self-other matching in two comparison domains, the perceptual domain and the emotional domain. The purpose of this broad perspective is to identify general patterns and principles in order to generate an overarching theoretical framework that can be applied to social learning.

1.2.2. Self-other matching in the motor domain: somatic movements

Somatomotor self-other matching can occur at a reflexive level via motor resonance. Motor resonance is a general idea implicating the activation of common neural or psychological substrates for observed and executed action – e.g., observing another's action causes my motor system to "resonate" with theirs. When motor resonance causes the overt output of an observed action, this is termed motor contagion. A well-known example of motor contagion occurs during infancy. For a brief period in development, neonatal macaques, humans, and chimpanzees copy observed orofacial movements (Meltzoff and Moore 1977, Meltzoff and Moore 1983, Heimann, Nelson et al. 1989, Myowa-Yamakoshi, Tomonaga et al. 2004, Ferrari, Visalberghi et al. 2006, Bard 2007, Ferrari, Paukner et al. 2009, Ferrari, Paukner et al. 2009, Paukner, Ferrari et al. 2011). Human infants also copy observed finger movements (Nagy, Compagne et al. 2005). This effect disappears sometime around age 2 weeks in macaques, 2 months in chimpanzees, and 3 months in humans (Meltzoff and Moore 1977, Meltzoff and Moore 1983, Heimann, Nelson et al. 1989, Myowa-Yamakoshi, Tomonaga et al. 2004, Ferrari, Visalberghi et al. 2006). The fact that this period lasts longer in humans may be relevant to species differences in adult social cognition, although this idea awaits exploration. In adult humans, motor contagion in everyday social interactions is sometimes called the "chameleon effect." This is the tendency to mimic others' postures, mannerisms, facial expressions, and behaviors. It increases liking, smoothes social interactions, and is more common in empathic people (Chartrand and Bargh 1999). Orangutans spontaneously and rapidly mimic facial expressions during play (Davila Ross, Menzler et al. 2008), chimpanzees experience contagion for aggressive and affliative social interactions (Videan, Fritz et al. 2005), and macaques are more likely to eat when seeing or hearing another monkey eat (Ferrari, Maiolini et al. 2005). In one study, human experimenters imitated capuchin monkey's actions on a ball, such as poking or mouthing it (Paukner,

Ferrari et al. 2011). The monkeys later preferred to spend more time in proximity to imititator versus non-imitator humans, and also preferred to interact with them in a task where tokens could be exchanged for food. This suggests that motor contagion may play a role in their naturalistic social interactions and may be important for establishing affiliative relationships and prosocial behavior.

In addition to facilitating the production of actions congruent to others', motor resonance can interfere with the production of non-congruent actions. This is termed "motor interference" and is measured by a reduction in movement accuracy while observing a non-congruent movement. In humans, motor interference appears around age 4-5, is influenced by prior knowledge or experience of the individual performing the observed action, is weakened by self-focus, and is stronger when the subject has practiced the observed action and when the demonstrator is similar to the subject (Marshall, Bouquet et al. 2010, Saby, Marshall et al. 2011). Observing a sinusoidal arm movement interferes with the observer's own movement more if the observed movement is directed towards a goal, suggesting that goal directed actions are more contagious than non-goal-directed actions (Bouquet, Shipley et al. 2010). To our knowledge, motor interference has not been studied in other species, although like motor resonance, it seems like an easily addressable topic. For example, in a paradigm used to study reach-to-grasp movements, macaque monkeys grasp a bar in an apparatus that measures the force, velocity, and direction of their arm movements (e.g., (Kalaska, Cohen et al. 1989)). This could be used to measure perturbations to a monkey's movements while watching congruent versus incongruent movements by another monkey.

In humans, evidence for a shared physiological basis of action execution and observation at a low level comes from electrophysiological experiments. Transcranial magnetic

stimulation to motor cortex can be used to produce motor-evoked potentials (MEPs) in the periphery – e.g., stimulation to the thumb area of primary motor cortex evokes a measurable electrophysiological effect in the thumb muscles. MEPs are greater during observation of movements involving those muscles; this effect occurs for both goal-directed and non-goal directed movements (Fadiga, Fogassi et al. 1995, Maeda, Kleiner-Fisman et al. 2002). Furthermore, the timecourse of MEPs follows the timecourse of the observed action, showing that the human motor system matches the individual, component movements of an observed action (Gangitano, Mottaghy et al. 2001). Additionally, electrical stimulation to a nerve produces activation (twitching) in monosynaptically-connected muscle fibers, called the H-reflex. Baldissera et al. (Baldissera, Cavallari et al. 2001) elicited H-reflexes from flexor finger muscles while subjects viewed a hand either opening or closing. Activation of the flexor muscles was greater when subjects observed a hand *opening*, which is opposite of what occurs during actual hand-opening execution (flexors close the hand) and also opposite of the resonant excitability that occurs stimulation at the level of the cortex (i.e., the TMS experiments above). This implies that motor resonance in the brain is somehow inhibited in the periphery. Because the H-reflex is known to be monosynaptic, this indicates that this inhibition occurs at or above the level of the spinal cord. Human electrophysiology experiments have also found a shared basis for action execution and observation. Humans have suppression of sensorimotor cortical rhythms during both action observation and execution, measurable with either EEG (electroencephalography) or MEG (magnetoencephalography) (Pineda 2005, Hari 2006). This occurs during observation of facial expressions as well as both transitive and intransitive limb movements and is distributed somatotopically over sensorimotor cortex according to the body part being observed (Muthukumaraswamy and Johnson 2004, Muthukumaraswamy, Johnson et al. 2004, Oberman, Hubbard et al.

2005, Muthukumaraswamy, Johnson et al. 2006, Moore, Gorodnitsky et al. 2011). The effect is stronger for reach-to-grasp actions that are directed towards an object than those that are not (Muthukumaraswamy and Johnson 2004, Muthukumaraswamy, Johnson et al. 2004).

These types of TMS, EEG, and MEG experiments have not been performed in macaques, but single-cell recordings show that mirror neurons in ventral premotor area F5 and inferior parietal areas PF/PFG are sensitive to both the execution and observation of similar movements, including both manual actions and orofacial movements (Gallese et al., 1996; Rizzolatti et al., 1996; Ferrari et al., 2003). However, macaque mirror neurons only respond to observed manual actions which are object- or goal-directed; they do not respond to observed mimed (intransitive) actions (Gallese, Fadiga et al. 1996, Rizzolatti, Fadiga et al. 1996, Ferrari, Gallese et al. 2003). The human homologues of macaque F5 and PF/PFG are thought to be Brodman areas 44 and 40, respectively (Rizzolatti and Craighero 2004). In human neuroimaging experiments, these regions are active during observation and execution of similar actions in a somatotopic manner (Buccino, Binkofski et al. 2001). Motor contagion in humans has been proposed to rely on a mirror system homologous to that in macaques (Blakemore and Frith 2005). If this is true, then motor contagion and motor interference should occur in macaques (as well as any other species that have a mirror system), although to our knowledge this has not been tested.

In addition to the reflexive phenomena described above, individuals can also copy each other's behavior in a less automatic, more controlled manner. Many species are capable of using observational learning to copy another's goal-directed action. Rats can learn to run a maze by observing another rat (Zentall and Levine 1972). Some birds socially learn each other's songs (Zentall 2004). Guppy fish can socially learn foraging innovations

(Laland and Reader 1999). Wild macaques learn to wash sand off sweet potatoes by watching other macaques (Kawamura 1959). Both capuchin monkeys and chimpanzees learn to use tools by watching conspecifics (Fragaszy and Visalberghi 1989, Inoue-Nakamura and Matsuzawa 1997).

Undoubtably, not all of these phenomena involve reflective processing. When considering the impressive variety of social learning across species, it is important to recognize that the same general function – copying another's behavior – can result from different psychological and neurophysiological mechanisms in different species. Various schemas exist for categorizing different types of social learning behavior (e.g., (Whiten, Horner et al. 2004, Zentall 2006)). In general, the types of social learning behavior that are most widespread across species do not involve a representational understanding of the goal behind an observed action; for example, observers' attention may be drawn to particular objects or locations in the environment, facilitating their own independent discovery of how to produce the action (stimulus enhancement); they may learn about the positive or negative value of an object or event (valence learning); or they may reflexively copy aspects of the observed action's movements without reflective understanding of its goal (mimicry). Many of these phenomena may occur reflexively, without representational understanding of the observed action's goal.

Forms of controlled social learning that involve an understanding of the observed goal are more rare, but are well-studied in primates. Most non-human primate social learning is classed as emulation (copying an action's goal or result but not specific movements or methods) rather than imitation (copying both the goal and methods) (Whiten, McGuigan et al. 2009) While some studies report imitation in non-human species (e.g., chimpanzees: (Hayes and Hayes 1952, Custance, Whiten et al. 1995, Horner

and Whiten 2005); marmosets:(Voelkl and Huber 2000)), none of these species use it so profusely and complexly as humans. In particular, a decades-long body of behavioral research describes a bias towards emulation in chimpanzees, and a bias towards imitation in humans (Whiten, McGuigan et al. 2009). For example, in one task (Horner and Whiten 2005), the experimenter demonstrates a complex series of actions that open a puzzle box (pulling levers, pressing buttons, etc.). When the puzzle box is opaque and the relationship between these maneuverings and the opening of the box is not perceptible, both chimpanzees and human children copy these actions with high fidelity. However, if a transparent box is used, it becomes obvious that some of the demonstrator's actions do not contribute to opening the box. Chimpanzees dispense with these useless actions and use the most efficient method to open the box. Human children, on the other hand, persist with these actions, even when instructed not to reproduce any "useless" or "silly" actions, and even when they verbally report that they understand that they are useless (Lyons, Young et al. 2007). This is termed "overimitation," and it is even stronger in adults than in children (McGuigan, Makinson et al. 2010).

Developmentally, copying of goal directed actions emerges over the first two years of life in humans, and in chimpanzees during the first four years (Inoue-Nakamura and Matsuzawa 1997, Elsner 2007, Elsner, Hauf et al. 2007). Human infants are more likely to reproduce actions that have goals than those that do not (Elsner 2007), and when preschool children copy a goal-directed movement, they tend to use movements that are less congruent with the demonstrator's than if there is no goal (Bekkering, Wohlschlager et al. 2000). It is interesting to note that motor interference effects are not observable until the age of four to five years (Marshall, Bouquet et al. 2010, Saby, Marshall et al. 2011), suggesting that motor resonance, which would otherwise cause interference, may

be somehow damped during the time that goal-directed copying is developing. However, children show electrophysiological correlates of motor resonance (mu suppression) as early as 6 months and seem to do so throughout development (Lepage and Theoret 2006, Nystrom 2008, van Elk, van Schie et al. 2008). An important area of future research will be the developmental relationship of reflexive motor resonance phenomena with more controlled social learning phenomena.

To date, the neural correlates of goal-directed behavioral copying have only been studied in humans. In humans, two recent meta-analyses of functional neuroimaging studies on imitation found that it involves the homologues of the macaque mirror regions (Brodman areas 44 and 40), as well as broader regions of superior parietal lobe, inferior parietal lobe, dorsolateral prefrontal cortex, and both dorsal and ventral premotor cortex which includes the homolog of macaque F5 (Caspers, Zilles et al. 2010, Molenberghs, Cunnington et al. 2011). Lesions to either frontal or parietal regions can cause apraxia, a neuropsychological disorder which can involve deficits in imitation (Goldenberg 2009). While the macaque mirror system is activated by the observation of goal-directed actions, notably, monkeys do not imitate according to the definition above (Fragaszy and Visalberghi 2004). However, macaques do recognize when their goal-directed actions are being imitated by a human experimenter (Paukner, Anderson et al. 2005). Even accepting a looser definition of imitation, it is obvious that macaques' social learning is less profuse and less complex than humans'. Furthermore, the macaque mirror system does not respond to meaningless actions not directed at an object, e.g. mimed grasping, while the human mirror system does (Rizzolatti and Craighero 2004). This suggests that species differences in the mirror system could be related to species differences in social learning.

We recently examined the white matter connectivity of the mirror system in macaques, chimps, and humans (Hecht, Gutman et al. 2012). These results are described fully in Chapter 2 of this volume. In macaques and chimps, the bulk of the white matter within the mirror system connects temporal perceptual areas directly to the frontal mirror region and surrounding frontal areas. Since the frontal mirror region is thought to contain a "vocabulary of motor acts" where actions are coded according to their goals or results (Rizzolatti, Camarda et al. 1988, Bonini, Rozzi et al. 2009), this pathway might underlie macaques' and chimps' bias towards copying an action's results over its movements. In humans, relatively more white matter in the mirror system passes through parietal cortex. Since the parietal mirror region is thought to perform sensorimotor mapping of the spatial and temporal details of observed and executed movements (Rozzi, Ferrari et al. 2008, Bonini, Rozzi et al. 2009), this increased connectivity might allow humans to map observed actions onto their own motor systems with greater kinematic detail, and could be related to our propensity for "overimitation."

Taken together, research on phylogeny, development, and neural activation suggests that self-other mapping in the somatomotor domain can occur via both reflexive and reflective processes. A reflexive mechanism is in place very early whereby observed movements are automatically reproduced. After a short period – days, weeks, or months depending on the species (with unknown implications of this difference) – an inhibitory process (or a decrease in excitation) comes online and this automatic mimicry disappears. In human adults, this inhibition seems to be mediated by the spinal cord, perhaps leaving the brain free to mirror observed action uninhibitedly (Rizzolatti and Craighero 2004). This direct, low level self-other matching mechanism is thought to result from simple Hebbian synaptic potentiation during development: an individual's own action causes motor and visual neurons to "fire together," increasing the chances

that they will eventually "wire together," so that after repeated co-activation, activation in one neuron alone can cause activation in the other, creating neurons that activate in response to observed, unexecuted action (Keysers and Perrett 2004, Brass and Heyes 2005). Such a mechanism should be widespread across phylogeny, might account for the development of premotor/parietal mirror neurons as well as other, heterogeneous cell types in other parts of the brain, and might account for motor contagion and mimicry across various species.

On the other hand, a reflective mechanism allowing the reproduction of goal-directed actions emerges later in development and is more limited across phylogeny. In humans, it involves some of the same neural substrates as reflexive motor resonance, as well as other regions more commonly associated with reflective processing, like dorsolateral prefrontal cortex and superior parietal cortex (Caspers, Zilles et al. 2010, Molenberghs, Cunnington et al. 2011). A distinction can be made between copying actions' results versus movements; humans focus on copying movements, while chimpanzees and other primates focus on copying goals. This difference in behavior may be the result of an underlying difference in neural responsivity (whether the mirror system can respond to intransitive action), which itself may be a result of a difference in the amount of connectivity with parietal cortex (Hecht, Gutman et al. 2012). The idea that copying results and copying movements are semi-dissociable processes is supported by clinical evidence. Goldenberg (Goldenberg 2009) argues that lesions to frontal cortex in humans impair imitation of goal-directed actions, while lesions to parietal cortex impair imitation of non-goal-directed, meaningless actions. Furthermore, non-goal-directed imitation may be specifically impaired in autism (Gowen, Stanley et al. 2008). Paulus et al. (20011) suggest that developmentally, motor resonance is necessary but not sufficient for social learning of goal directed actions. This holds across phylogeny: reflexive motor

resonance and mimicry are seen across a wide variety of species, and seem to be necessary but not sufficient for the development of social learning involving a reflective understanding of observed goals, which is more rare across phylogeny.

1.2.4. Self-other matching in the perceptual domain: eye movements and cognition about perception

An individual can match their own visual perception or attention to another's by following gaze direction (Emery, Lorincz et al. 1997). It is easy to see how gaze following is a broadly adaptive trait -- if something has drawn my conspecific's attention, it likely deserves my attention as well, since we share food sources, predators, prey, and potential mating partners. Bringing one's own perception into congruence with another individual's is a first step towards bringing behavior into congruence. Therefore, it is not surprising that this basic behavior occurs automatically across the animal kingdom, in various species of reptiles, birds, and mammals.

In its simplest form, gaze following is tested by having the subject view a conspecific or human experimenter looking up, down, or to the side, and measuring whether the subject performs a congruent adjustment in visual attention. This test is passed by tortoises, a variety of birds, domestic goats, dogs and wolves, and a variety of primates (Bugnyar, Stowe et al. 2004, Schloegl, Kotrschal et al. 2008, Loretto, Schloegl et al. 2009, Rosati and Hare 2009, Wilkinson, Mandl et al. 2010, Kehmeier, Schloegl et al. 2011, Range and Viranyi 2011, Teglas, Gergely et al. 2012). Some species, such as macaques (Emery, Lorincz et al. 1997), only follow shifts in head or whole body orientation, while others, such as chimpanzees (Tomasello, Hare et al. 2007), can follow shifts in eye gaze alone. Humans' white sclera make our eye movements more apparent

than other species', who have darker sclera; this is thought to be a contributing factor in our ability to follow eye movements (Tomasello, Hare et al. 2007, Rosati and Hare 2009).

In a more complex version of this task, the demonstrator individual looks toward an object that is occluded from the subject's view by a barrier. Animals that can pass this task are said to follow gaze "geometrically" and are inferred to have some referential understanding of the content of the demonstrator's perception – i.e., that the demonstrator is "looking *at*" a particular thing. Species that fail this task are taken to lack the ability to take the visual perspective of others (Rosati and Hare 2009). Species currently known to follow gaze geometrically include a subset of those above: spider monkeys and capuchins (Amici, Aureli et al. 2009), chimpanzees, bonobos, and gorillas (Okamoto-Barth, Call et al. 2007), dogs (Teglas, Gergely et al. 2012), wolves (Range and Viranyi 2011), rooks (Schloegl, Kotrschal et al. 2008), and ravens (Bugnyar, Stowe et al. 2004).

In a yet more complex task, perspective-taking is studied in humans and great apes using tasks that test the subject's ability to know that another individual does not know something that the subject does. For example, in the Sally-Anne test (Baron-Cohen, Leslie et al. 1985), Sally places a toy in her basket and then leaves the room. Anne then enters the room and moves the toy. The subject is asked where Sally will look for her toy when she returns. This measures whether the subject has "theory of mind," or the ability to attribute mental states or perspectives to others which are separate from one's own (Premack and Woodruff 1978). Thus it is an explicit measure of a reflective process. However, there is evidence that implicit processing is also involved in this task. Both human adults and children are less accurate at judgments about their own visual

perspective when there is another person present with a different physical perspective, suggesting that we reflexively map what others can see and that this uses the same cognitive machinery as awareness of what we can see (Samson, Apperly et al. 2010, Surtees and Apperly 2012). Human infants look longer at the correct answer in a Sally-Anne test before they can produce a correct explicit verbal response, suggesting that they have implicit awareness of others' perceptual knowledge (Clements and Perner 1994). Various experiments suggest that chimpanzees are able to take the perspective of others (Povinelli, Nelson et al. 1990, Hare, Call et al. 2001, Brauer, Call et al. 2007, Krachun and Call 2009, Krachun, Carpenter et al. 2009). For example, in one study (Hare, Call et al. 2001), subordinate chimpanzees preferred to approach food behind a barrier, so that a dominant chimpanzee could not see.

The complexity of gaze following behavior changes across development, and this differs between species. In humans, gaze following emerges between 3-18 months (Scaife and Bruner 1975, Carpenter, Nagell et al. 1998, Corkum and Moore 1998). In rhesus macaques, it begins to emerge around 5.5 months; in chimpanzees, between 3-4 years (Rosati and Hare 2009). At first, infants follow head movements but not eye movements, and continue to follow a demonstrator's repeated gazes toward an information-less target (such as a blank ceiling). This suggests a lack of understanding that eyes are the mechanism of perception, and that gaze following behavior is relatively inflexible, automatic, and not affected by learning. Later, infants begin to follow eye movements alone, and later still they can inhibit repeated gaze-follows to a meaningless target. The ability to follow gaze geometrically emerges around this time. This pattern of development is similar in wolves, macaques, chimpanzees, and humans (Scaife and Bruner 1975, Carpenter, Nagell et al. 1998, Corkum and Moore 1998, Ferrari, Kohler et al. 2000, Rosati and Hare 2009, Range and Viranyi 2011).

The neural basis of gaze following has been studied in humans and macaques. In humans, neuroimaging experiments have implicated the superior temporal sulcus, cuneus, inferior parietal lobule, and intraparietal sulcus in perceiving others' looking direction (Puce, Allison et al. 1998, Wicker, Michel et al. 1998, Hoffman and Haxby 2000, Pelphrey, Singerman et al. 2003, Pelphrey, Viola et al. 2004, Materna, Dicke et al. 2008). Superior temporal sulcus is involved in encoding intentions related to gaze (Pelphrey, Singerman et al. 2003), while intraparietal sulcus may be related to shifts in one's own visual attention regardless of social context (Materna, Dicke et al. 2008). In macaques, cells in superior temporal sulcus respond to different angles of head orientation (Perrett, Oram et al. 1991). Cells in area LIP of the intraparietal sulcus fire both when the monkey looks in the cell's preferred direction and when another monkey looks in the same direction (Shepherd, Klein et al. 2009). A second population of cells in this area was suppressed by the observation of other monkeys' gaze. Interestingly, most of F5 mirror neurons are tuned to a particular visual perspective for observed grasping movements, suggesting a role for perspective in the somatomotor self-other matching system (Caggiano, Fogassi et al. 2011).

Considering the neural and behavioral research together across phylogeny, some patterns emerge. There are no species that are capable of following eye movements alone but not head movements, or head movements but not whole body movements. Developmentally, across species, the ability to follow eye movements alone emerges after the ability to follow head or body movements. Additionally, there are no species that follow gaze behind a barrier but not into empty space, and following gaze into empty space always emerges in development before following gaze around a barrier. The ability to follow gaze geometrically co-emerges with the ability to *not* follow repeated gazes

towards an informationless target, such as a blank ceiling. Thus it appears that there are two fairly discrete components to gaze following: an early-developing, automatic one, and a later-developing, controlled one that takes into account the referential information in the gaze.

It seems likely that these components might rely on at least partially separable neural substrates. Shepherd et al (Shepherd, Klein et al. 2009) suggest that LIP cells are involved in the reflexive mode of gaze following. Similarly, Pelphrey et al (Pelphrey, Singerman et al. 2003) suggest that human intraparietal sulcus is concerned with egocentric mapping of spatial attention. This suggests the hypothesis that the automatic, implicit mode of gaze following can be mapped to parietal cortex. We wonder whether Shepherd et al.'s (Shepherd, Klein et al. 2009) second population of cells that were suppressed by observed gaze changes might serve to override this automatic "mirroring" of attention, and whether the onset of their inhibition during development might coincide with the onset of the ability to habituate to meaningless gazes. Conversely, Pelphrey et al. (Pelphrey, Singerman et al. 2003) suggest that in humans, the superior temporal sulcus may be more involved with judging the intentionality of others' actions, and has been implicated more broadly in reflective social cognitive processes like theory of mind. Thus we can hypothesize that this region might underlie the referential understanding of the content of others' gaze.

1.2.5. Self-other matching in the emotional domain

In addition to the somatomotor and oculomotor domains, self-other matching also occurs in the autonomic domain. This can extend to very low-level functions, such as pupil size (Harrison, Singer et al. 2006, Harrison, Wilson et al. 2007, Harrison, Gray et

al. 2009) and respiration (Jeannerod and Frak 1999, Paccalin and Jeannerod 2000, Mulder, de Vries et al. 2005, Kuroda, Masaoka et al. 2011). "Contagion" of autonomic states has been well studied across species in the domain of pain, fear, and anxiety. For example, geese have heart rate increases after viewing their mate in conflict (Wascher, Fraser et al. 2010). Mice have stronger responses to pain after viewing another mouse in pain (Langford, Crager et al. 2006, Jeon, Kim et al. 2010, Jeon and Shin 2011). Monkeys exhibit behavioral signs of fear when watching another monkey in fear, even when the observer cannot see the item that is feared (Mineka and Cook 1993). Crying is contagious in human infants (Geangu, Benga et al. 2010). In adult humans, photographs of others in danger or pain induces a freezing postural response (Azevedo, Volchan et al. 2005, Facchinetti, Imbiriba et al. 2006).

Beyond simply "catching" the emotion of fear non-referentially, various species can learn *what* to fear by watching others through observational learning. For example, in an experiment with crows, adult crows were captured, banded, and released by human experimenters wearing distinctive masks. The offspring of these adult crows, who observed the masked experimenters' actions, later produced alarm calls to humans wearing the same masks, even though they had had no interaction with the humans personally (Cornell, Marzluff et al. 2011). Similarly, monkeys can acquire fear of snakes after watching other monkeys' fearful interactions with snakes, without any personal experience with snakes (Cook and Mineka 1989, Cook and Mineka 1990). When human adults observe others undergoing a panic attack after a conditioned stimulus, they show greater electrodermal responses and report more fear and anxiety for that stimulus (Kelly and Forsyth 2007). In humans, observational learning of fear, like Pavlovian conditioning, produces increased skin conductance measurements in response to a masked (nonconsciously viewed) image, while simple verbal instruction that an item is

dangerous does not (Olsson and Phelps 2004). This suggests that observational learning of fear acts via a reflexive, implicit mechanism rather than a controlled, explicit mechanism.

Individuals of various species can also learn what *not* to fear by watching others. Attenuation of fear by observational learning has been reported in mice (Guzman, Tronson et al. 2009), and extinction of avoidance behavior is facilitated by observational learning in rats (Uno, Greer et al. 1973). Monkeys that observe other monkeys behaving non-fearfully with snakes are less likely to acquire fear of snakes themselves, and overshadowing can also be achieved through observational learning in monkeys (Mineka and Cook 1986, Cook and Mineka 1987). Human children who see their mothers responding positively to a fear-inducing stimulus are less fearful of the stimulus (Gerull and Rapee 2002, Egliston and Rapee 2007). For human children learning to overcome a fear of swimming, swimming lessons are more effective when paired with observation of a non-fearful child swimming (Weiss, McCullagh et al. 1998).

Self-other matching for autonomic states seems to rely on the same neural structures that produce those states in the observer. In mice, observational fear learning is blocked by inactivation of the anterior cingulate or the parafascicular and mediodorsal thalamic nuclei, which relay the affective dimension of pain to cortex, but not by inactivation of the ventral posterolateral or posteromedial thalamic nuclei, which relay the sensory dimension of pain to cortex(Jeon, Kim et al. 2010). In humans, felt and seen pain activate anterior cingulate and anterior insula (Lamm, Decety et al. 2010). Felt and seen disgust also activate the insula (Wicker, Keysers et al. 2003, Wright, He et al. 2004, Jabbi, Bastiaansen et al. 2008). The amygdala seems to be necessary for the perception of fear in others – Adolph's famous patient SM, who suffered bilateral

calcification of the amygdala, is both unable to experience fear personally and has difficulty attributing it to others (Adolphs, Tranel et al. 1994, Feinstein, Adolphs et al. 2010).

Another example of automatic, reflexive self-other matching in this domain is facial expressions. As mentioned previously, orofacial movements are automatically imitated for a brief postnatal period in macaques, chimpanzees, and humans (Meltzoff and Moore 1977, Meltzoff and Moore 1983, Heimann, Nelson et al. 1989, Myowa-Yamakoshi, Tomonaga et al. 2004, Ferrari, Visalberghi et al. 2006, Ferrari, Paukner et al. 2009, Ferrari, Paukner et al. 2009, Paukner, Ferrari et al. 2011), and adult orangutans rapidly mimic facial expressions during play (Davila Ross, Menzler et al. 2008), but no other studies have assessed involuntary facial mimicry in adult animals. In adult humans, viewing another individual's facial expression causes rapid facial reactions, or brief, reflexive, low-intensity mimicry of the expression on one's own face, measureable with EMG (Dimberg and Thunberg 1998). This occurs even when stimuli are presented to the blind hemisphere of patients with unilateral visual cortex lesions, so it does not require cortical processing, or, presumably, awareness (Tamietto, Castelli et al. 2009). Interfering with this ability reduces emotion detection accuracy – subjects are less accurate at naming happy facial expressions when holding a pencil in their mouth (Oberman, Winkielman et al. 2007), lesions to somatosensory cortex impair facial expression recognition (Adolphs, Damasio et al. 2000), and botulinum toxin injections decrease emotion recognition across multiple expressions (Neal and Chartrand 2011). Furthermore, the application of a restricting gel to facial skin, which increases feedback signals, increases emotion perception accuracy (Neal and Chartrand 2011). This suggests that some part of this implicit, automatic mimicry is informational – i.e., facial feedback from the mimicked expression activates neural representations about the

meaning of the expression. However, facial expressions, face-voice combinations, and body expressions all evoke similar EMG responses in the face, suggesting that humans also resonate with the affective meaning of expressions and not just the motor pattern (Magnee, Stekelenburg et al. 2007).

Motor resonance and contagion for facial expressions seem to rely on some of the same mechanisms as motor resonance and contagion for somatic movements. While viewing facial expressions, neonatal macaques show mu suppression, thought to be an EEG index of mirror neuron activity (Ferrari, Vanderwert et al. In press). Adult macaques activate frontal mirror neurons during the observation of facial expressions (Ferrari, Gallese et al. 2003). Human children (Dapretto, Davies et al. 2006) and adults (Molenberghs, Cunnington et al. 2011) activate inferior frontal gyrus, the homologue of macaque F5, during the observation of facial expressions, and also show mu suppression during facial expression observation (Oberman, Hubbard et al. 2005, Moore, Gorodnitsky et al. 2011). Interestingly, infant macaques who imitate facial gestures have more developed reaching-grasping behavior and fine motor control in the hand than their conspecifics who do not, providing further evidence that this phenomenon is linked to motor resonance in the somatomotor domain (Ferrari, Paukner et al. 2009).

Yawns are a specific example of a facial expression that is contagious in several species. In addition to humans, macaques (Paukner and Anderson 2006), gelada baboons (Palagi, Leone et al. 2009), chimpanzees (Anderson, Myowa-Yamakoshi et al. 2004, Campbell, Carter et al. 2009, Campbell and de Waal 2011), and dogs (Joly-Mascheroni, Senju et al. 2008, Harr, Gilbert et al. 2009) also experience contagious yawning. In humans, viewing others' yawns activates precuneus, posterior cingulate, and superior temporal sulcus, all regions that have been associated with "higher-level"

forms of social cognition (Platek, Mohamed et al. 2005, Schurmann, Hesse et al. 2005). Platek (Platek 2010) notes that individual humans who are more susceptible to contagious yawning tend to be better at higher-order social cognitive measures like theory of mind processing and self-face recognition, and suggests that yawn contagion may involve evolutionarily old processes that became the basis for these more complex forms of social cognition.

In addition to self-other matching of autonomic states and facial expressions, others' emotions can also be matched in a more explicit, reflective manner. Preston and de Waal (2002) use the term "cognitive empathy" to describe a referential understanding of another's emotional state. Several studies show a link between reflective and reflexive self-other matching of emotion. Subjects who score high on emotional empathy scales have stronger facial mimicry for observed emotions, while low-empathy subjects activate facial muscles incongruent with the observed expression – e.g., "smiling" when seeing an angry face (Sonnby-Borgstrom 2002). Similarly, high-empathy subjects show greater contagion for pupil size (Harrison, Wilson et al. 2007). Autism and schizophrenia, both disorders which impair higher-order measures of empathizing, involve abnormal facial mimicry of observed facial expressions (McIntosh, Reichmann-Decker et al. 2006, Oberman, Winkielman et al. 2009, Varcin, Bailey et al. 2010) and a reduction in yawn contagion (Haker and Rossler 2009, Helt, Eigsti et al. 2010). A better understanding of the interaction between reflexive and reflective forms of emotional self-other matching may provide new directions for treatment in disorders of social cognition.

Another broad area of inquiry for future research is the interaction between self-other matching in the emotional domain with self-other matching in other domains. These

interactions undoubtedly exist. For example, in the motor domain, as noted earlier, mimicry of postures, mannerisms, facial expressions, and behaviors increases liking, smoothes social interactions, and is more common in empathic people (the chameleon effect (Chartrand and Bargh 1999)). This brings up the interesting question of whether targeting or training self-other matching in the somatomotor domain (or another domain) might improve self-other matching in the emotional domain. Given that something like the chameleon effect seems to occur in capuchin monkeys, since monkeys prefer to interact with humans who imitate them (Paukner, Suomi et al. 2009), research on this topic in other species might be useful for understanding it in our own.

1.2.6. General patterns and principles of self-other matching

In this review, we have aimed to provide specific examples of how reflective processes are related to reflexive processes in self-other matching across species in three specific domains – in the motor domain (somatic movements), in the perceptual domain (eye movements and cognition about visual perception), and in the emotional domain. Many unanswered questions remain; we have highlighted a few specific questions, with some potential ways to address them, in **Table 1.2-2**. This dissertation is focused on one of these questions, which is highlighted in yellow. Despite these unanswered questions, taking a broader perspective and considering these domains together, several patterns emerge.

First, in each of these domains, there are early-developing, automatic processes that rapidly match the observer's state to others'. These could emerge based on a simple Hebbian mechanism, as individuals learn associations between observable effects and internal states within the context of their own behavior. As these associations are

solidified, observation of only the process's effect (a fearful expression or the perception of an arm movement) can activate representations of the internal state that causes it (the emotion of fear or the motor representation of the arm movement). Since Hebbian learning is a common feature of nervous systems, seen even in mollusks, this type of self-other matching is likely widespread across the animal kingdom. An important caveat for this idea is that some early-developing self-other matching behaviors – such as facial mimicry and following the direction of a turned head – might appear too early to rely on Hebbian learning outside the womb and may be instinctive. The possible interplay between instinct and learning in self-other matching would be an interesting topic for future research.

Second, more complex forms of self-other matching in each domain emerge later in development and are less prevalent across phylogeny. They involve some of the same neural substrates as their related lower-level processes, as well as other neural systems associated with representational thought. The function of the lower-level processes can impact higher-level processes. For example, paralysis of one's own facial muscles impairs recognitions of others' facial expressions (Neal and Chartrand 2011). In general, these higher-level functions seem not to be present in species that lack the underlying lower-level functions – e.g., to date there are no species that are capable of geometric gaze following but not the simpler form of automatic gaze following into empty space. Many of these higher-level functions are uniquely developed in humans, and some may even be completely unique to humans. However, the longer that comparative psychology investigates which behaviors are uniquely human, the more once-unique functions are found in other species.

Third, the proper function and development of the lower-level systems is often critical for the proper function and later development of the higher-level systems. Because these higher-level functions like imitation, perspective taking, and empathy are more immediately observable and salient, social cognitive deficits are often attributed to dysfunctions in these higher-level functions, but it is important to also address whether there may be a less obvious deficit in an underlying lower-level function. For example, autism was once accepted as primarily a disorder of theory of mind (Baron-Cohen, Leslie et al. 1985). More recent research, though, has shown that high-functioning autistic individuals can pass tests of theory of mind, albeit using different mechanisms. Current research is increasingly pointing toward cascade effects where early disruptions in lower-level social processes cause derailments of later-developing, higher-level processes. For example, early abnormalities in gaze following may underlie later deficits in perspective taking (Elsabbagh, Mercure et al. 2012); abnormalities in motor resonance for body movements may lead to deficits in imitation (Gowen, Stanley et al. 2008); and abnormalities in facial expression mimicry may be related to difficulties with empathy (McIntosh, Reichmann-Decker et al. 2006, Oberman, Winkielman et al. 2009).

A comparative, evolutionary approach highlights the role of these underlying, lower-level processes because it frames neural and psychological systems in a way that emphasizes continuity. As organisms evolve increasing complexity, new functions must be integrated into the framework of pre-existing, simpler functions, like new heating systems being grafted onto old ones in an apartment building. An understanding of the normal or disordered function of the new systems would be incomplete without an understanding of the underlying, older ones. Thus, our understanding of the psychological and neural mechanisms of self-other mapping, other forms of social

cognition, and other functions in general in our own species can be informed by considering these functions in others.

Of course, it is obvious that there are some things about human behavior and the human brain that are special. Some human behaviors or neural features may not have easily identifiable correlates in other species (although we argue that most probably do, to some extent). A comparative perspective can also inform understanding of behavioral abilities that only humans have: they must rely on aspects of neural organization that are unique to humans. Unique neural features can only be mapped to unique behavioral features if we have a firm understanding of which neural and behavioral features are shared with other species.

1.3. Theoretical framework and hypotheses for studying the evolution of human social learning

Applying the patterns and principles above to the topic of social learning, we generate the following theoretical framework and general hypothesis:

1) Complex behaviors are the aggregate result of underlying, component processes.
    - ➔ In social learning, the measured behavioral output – e.g., whether or not an observed action's specific movements are copied – is the "tip of the iceberg." Underlying this is an array of component processes which may include biological motion perception, object identification, reflexive motor resonance, and/or conceptual understanding about action means and ends.

2) Some complex behaviors are unique to humans, but some of the underlying processes are shared with our animal relatives.

   ➔ Although even our closest primate relatives, chimpanzees, do not copy specific movements in the same way that we do, they almost certainly share many of the underlying, component processes. Given that these processes have homologous neural bases in humans and macaques, these neural bases are almost certainly also shared by chimpanzees.

3) Differences in these underlying processes can translate to differences in the complex behaviors to which they contribute.

   ➔ General hypothesis: Differences in the component processes that occur when a chimpanzee versus a human views another individual's action translate to differences in the way in which chimpanzees versus humans replicate that observed action. In other words, species differences in social learning are due to species differences in the neural networks that process observed actions.

In order to generate more specific hypotheses about human neural adaptations for social learning, it is necessary to consider the neural networks that are involved in action observation and what is known and not known about how they differ between humans and other primates.

1.3.1. Neural networks involved in action observation

In both humans and macaques, observing a simple object-directed grasping action activates a distributed network of frontal, parietal, and temporal regions. However, studies suggest a greater component of frontal activation in macaques. In an fMRI

study, macaques had more prefrontal activation than humans when viewing objects, assessed by both spatial extent and magnitude (Denys, Vanduffel et al. 2004). In a set of macaque 2-deoxyglucose studies, object-directed grasp perception caused more activation in ventral premotor than inferior parietal cortex (Raos, Evangeliou et al. 2004, Raos, Evangeliou et al. 2007).

In addition, both humans and macaques have a frontoparietal mirror system which activates both during the observation of action, and during actual execution of similar actions. In macaques, mirror neurons exist in area F5 of ventral premotor cortex and in areas PF/PFG of inferior parietal cortex. In humans, the homologues of these regions are Brodmann area 44 and Brodmann area 40. Both show region-level mirror responses during executed and observed actions, although single cell mirror responses in these regions have not been investigated in humans. In both humans and macaques, the superior temporal sulcus is thought to provide perceptual input to the frontal and parietal mirror regions (Rizzolatti and Craighero 2004). Superior temporal sulcus processes the visual perception of biological motion, including complex action like grasping and locomotion (Puce and Perrett 2003). In humans, imitation involves these three mirror system regions – Brodmann area 44, Brodmann area 40, and superior temporal sulcus – in addition to other regions including surrounding regions of inferior prefrontal cortex, ventral premotor cortex, and inferior parietal cortex, as well as dorsal premotor cortex, and superior parietal cortex (Iacoboni, Woods et al. 1999, Iacoboni, Koski et al. 2001, Molenberghs, Cunnington et al. 2009).

The existence of mirror systems in both macaques and humans raises a critical question: *If the human mirror system supports imitation, and macaques have mirror neurons, then why don't macaques imitate?* Or, on a more global level, how are neural systems

for action observation and action observation-execution matching different across species? An answer to this question would have broad relevance for understanding social behavior across the animal kingdom, because neural systems for self-other matching are proposed to support not only complex behaviors like imitation but also more phylogenetically widespread processes which are common to many species, like emotional contagion (Preston and de Waal 2002).

One clue to an answer may come from an already-identified difference between the human and macaque mirror systems. Macaque mirror neurons do not respond to intransitive actions (those that lack an object, such as a mimed grasping movement) (Rizzolatti, Fadiga et al. 1996); in contrast, human mirror regions do (Buccino, Binkofski et al. 2001). This functional difference implies underlying anatomical and/or physiological differences. We hypothesize that at least one such underlying difference could concern the organization of connections within the distributed mirror system network. Because each node of this network performs a different type of information processing, species differences in the connectivity between these nodes could produce species differences in which aspects of observed actions are "mirrored" onto the observer's own motor system, and thus copied. In other words, species differences in connectivity could translate to species differences in brain activation, which in turn could translate to species differences in social learning. This leads to the following specific hypotheses.

1.3.2. Specific hypotheses to be investigated

- ➔ Hypothesis 1: The structural connectivity of the action observation network differs between macaques, chimpanzees, and humans. This hypothesis is

investigated in Chapter 2, which compares macaque, chimpanzee, and human connectivity between the frontoparietal mirror system and the temporal regions that provide its perceptual input.

➔ Hypothesis 2: Neural responses to observed action differ between macaques, chimpanzees, and humans. This hypothesis is investigated in Chapter 3.

- Part A: The aspects of an observed action that are "mirrored" determine which aspects can be behaviorally copied. If this is true, whether or not a species is capable of copying action movements apart from results should align with whether or not its mirror system responds to actions which consist of movement without results. Chapter 3.1 measures overlapping activations between chimpanzee action execution and transitive and intransitive action observation, and compares this with published macaque and human findings.

- Part B: Behavioral differences in social learning are the result of underlying neural differences in the component processes involved in action observation. If this is true, the distributed pattern of activation during action observation should differ between species. Chimpanzee and human activations in frontal, parietal, and temporal cortex during transitive action observation are compared in Chapter 3.2.

➔ Hypothesis 3: Individual variation in behavior is correlated with individual variation in brain activation when viewing actions. This hypothesis is investigated in Chapter 4.

Table 1.2-1. Self-other matching terms and definitions.

General terms	Mimicry	In this review, used as a general, non-specific umbrella term for any kind of reflexive, non-intentional, overt self-other matching
	Copying	In this review, used as a general, non-specific umbrella term to refer to any kind of intentional, reflective, overt self-other matching
Motor domain	Motor resonance	Activation of common neural or psychological substrates for observed and executed action – e.g., observing another's action causes my motor system to "resonate" with theirs
	Motor contagion	The overt, reflexive mimicry of an observed action via motor resonance
	The "chameleon effect"	Humans' tendency to reflexively mimic others' postures, mannerisms, facial expressions, and behaviors, which plays a functional role in human social interactions
	Motor interference	A reduction in movement accuracy when observing a non-congruent movement, caused by reflexive motor resonance
	Social learning or observational learning	Family of mechanisms by which an individual can copy an observed goal-directed behavior
	Emulation	Copying an action's goal or end result, but not its component movements or methods
	Imitation	Copying both an action's end result and the component movements
	Overimitation	Copying component movements which do not contribute to reaching the action's goal
Perceptual domain	Gaze following	A shift in eye gaze direction in order to match one's own visual perception to another individual's
	Following gaze geometrically	Following another individual's gaze behind a barrier; inferred to imply the ability for perspective-taking
	Perspective taking	The understanding that another's perceptual knowledge can differ from one's own (not always used to connote a reflective process)
	Theory of mind	The understanding that another's representational mental states can differ from one's own (a type of perspective taking; generally connotes a reflective, controlled process)

Table 1.1-1 (continued). Self-other matching terms and definitions.

Emotional domain	Contagion	The reflexive instantiation of an observed emotional or autonomic state in one's self (non-referential)
	Observational fear learning	Acquiring a fear response to a particular stimulus based on observation of another individual's experience with that stimulus (referential)
	Rapid facial reactions	Brief, reflexive, low-intensity mimicry of observed facial expressions, measurable by increased EMG activity in congruent facial muscles
	Cognitive empathy	A referential, reflective, explicit understanding of another individual's emotional state

Table 1-2.2. Unanswered questions in self-other matching research.

General questions	To what degree does self-other matching across domains rely on a common or shared mechanism?
	Is Hebbian learning during early development a general mechanism for self-other matching across domains? If so, can we find some sort of reflexive self-other matching in any organism that has Hebbian learning and a basic ability to perceive the behavior of conspecifics?
	Are there any experience-independent (hardwired) mechanisms for self-other matching?
Motor domain	The period of automatic mimicry of facial expressions lasts longer in humans than chimps, and longer in chimps than macaques. Is this relevant to adult species differences in social cognition? To address this question, we will first need to understand how neonatal mimicry impacts behavioral and neural development within these species
	Does automatic mimicry of facial expressions occur in non-primate mammals, reptiles, and birds? This might be studied with high-resolution video analysis of naturalistic social interactions
	Does the "chameleon effect" play a role in naturalistic social interactions in non-human species? Following Paulkner et al. (2011), this might be tested by experimentally manipulating whether an animal's behavior is copied
	Does motor resonance occur at low level, below the threshold for overt mimicry, in nonhuman animals? This might be studied with motor interference tasks, mu suppression of the EEG during observed movement, or the spinal H-reflex
	Mirror neurons have been found in macaques, rodents, and birds. This suggests that they likely exist in phylogenetically intermediate species. What other animals have mirror neurons, where are they, and how do they function?
	In humans, is motor resonance selectively damped during the time that children are learning to copy the goals of actions? This could be addressed with longitudinal studies mapping the time course of neonatal mimicry, motor contagion, goal-directed imitation, and motor interference within individual children
	Do humans have unique neuroanatomy or neural responses underlying our unique capacity for imitation and overimitation? This can be accomplished with comparative neuroscience research. → *This dissertation investigates this question.*

Table 1-2.2 (continued). Unanswered questions in self-other matching research.

Perceptual domain	What is the role of perspective-taking in self-other matching in the somatomotor domain?
	How is the developmental stage of automatic gaze-following overridden? Does it coincide with the physiological development of inhibitory mirror neurons for gaze direction (Shepherd et al., 2009)?
	Are separate neural systems involved in automatic, reflexive gaze following and reflective, referential understanding of the content of others' visual perception?
Emotional domain	What emotions are "contagious" in other species? Does this differ across species? This could be tested through naturalistic observation or laboratory-contrived situations that ensure that the observer's reactions can not be attributed solely to own emotional response to the stimulus
	Do adult nonhuman animals show rapid facial reactions for observed facial expressions, or for bodily expressions of emotion? This could be measured with facial (or body) EMG
	If so, does self-other matching for facial/bodily expressions of emotion contribute to emotion understanding in these other species? This could be measured by training animals to do an explicit task on emotion identification (e.g., match to sample), interfering with mimicry similar to Oberman et al. (2007), and measuring changes in accuracy
	Following Platek (2010), why are human individuals who are more susceptible to contagious yawning better at measures of higher-order social cognition? More broadly, what is the relationship between low-level emotion/autonomic contagion and these more reflective functions?
	Can we treat dysfunctions in these more reflective functions by targeting underlying, reflexive functions?
	How does self-other matching in the emotional domain interact with self-other matching in other domains? Can we treat dysfunctions in emotional self-other matching by targeting self-other matching in other domains?

Chapter 2:

Connectivity[8]

[8] *Chapter 2 is reproduced with minor edits from Hecht, E. E., D. A. Gutman, T. M. Preuss, M. M. Sanchez, L. A. Parr and J. K. Rilling (2012). "Process Versus Product in Social Learning: Comparative Diffusion Tensor Imaging of Neural Systems for Action Execution-Observation Matching in Macaques, Chimpanzees, and Humans." Cereb Cortex.*

2.1. Comparative diffusion tensor imaging of neural systems for action execution-observation matching in macaques, chimpanzees, and humans

2.1.1 Summary

This chapter tests Hypothesis 1:

➔ Species differences in social learning are related to species differences in the structural connectivity of the action observation network.

This was accomplished using diffusion tensor imaging, a structural neuroimaging method that reconstructs white matter tracts. We analyzed DTI scans in macaques, chimpanzees, and humans, and compared connectivity between the inferior frontal and inferior parietal mirror system regions, as well as the lateral temporal cortical regions that provide perceptual input to these mirror regions. Three major results emerged:

1) In macaques and chimpanzees, the preponderance of this circuitry consists of frontal-temporal connections via the extreme/external capsules. In contrast, humans have more substantial temporal-parietal and frontal-parietal connections via the middle/inferior longitudinal fasciculi and the third branch of the superior longitudinal fasciculus.

2) In chimpanzees and humans but not macaques, this circuitry includes connections with inferior temporal cortex.

3) In humans alone, connections with superior parietal cortex were also detected.

Based on these results, we suggest a model linking species differences in mirror system connectivity and responsivity with species differences in behavior, including adaptations for imitation and social learning of tool use.

2.1.2. Materials and methods

Subjects

Subjects included: one post mortem rhesus macaque (*Macaca mulatta*, female, age 11 years, perfused with formalin and scanned immediately after death); a set of 5 in vivo rhesus macaques (*Macaca mulatta*, 3 female, all age 6 years); one post-mortem chimpanzee (*Pan troglodytes*, female, age 28 years, scanned 14 hours after death); a set of 5 *in vivo* chimpanzees (*Pan troglodytes*, 5 female, mean age 14.8 years); and a set of 30 in vivo humans (*Homo sapiens*, male, mean age 20.2 years), all right-handed, with no history of neurologic or psychiatric illness. In vivo macaque and chimpanzee subjects were scanned under anesthesia. Post mortem brains were fixed with formalin. Procedures complied with the IRB and IACUC regulations of Emory University. 60-direction diffusion tensor imaging scans were acquired for each subject. T1-weighted structural MRI scans were also acquired for in vivo subjects; B_0 images were used as structural images for post mortem subjects because no T1 images were available for these subjects.

Image acquisition and scan parameters

Details for each subject group's scans are listed in **Table 2-1**.

Structural templates

We generated nonlinear T1 macaque and chimpanzee templates using FSL (*http://www.fmrib.ox.ac.uk/fsl/*). First, all subjects' images were rigidly rotated into AC-PC position. The images then underwent brain extraction, bias correction, noise reduction, and contrast enhancement. Next, the images were registered to pre-existing linear templates (Rilling, Barks et al. 2007, Parr, Hecht et al. 2009) using affine registration. The linearly aligned images were then summed and averaged to produce a study-specific linear template. Each subject's scan was then nonlinearly aligned to this initial linear template. Finally, the nonlinearly aligned images were summed and averaged to produce nonlinear templates.

Region of interest definition

Regions of interest (ROIs) were used to seed tractography analyses of control areas and the mirror system, and were drawn manually and bilaterally based on published macaque (Paxinos, Huang et al. 2000) and chimpanzee(Bailey, Bonin et al. 1950) maps and the human atlases implemented in FSL. The ROIs for each analysis are shown in the figure for that analysis.

For the mirror system analyses, macaque ROIs were placed in areas F5c and PF/PFG; chimpanzee ROIs were placed in areas FCBm (BA 44) and PF/PFG; and human ROIs were placed in the pars opercularis of the inferior frontal gyrus (BA 44) and the supramarginal gyrus (BA 40). These regions were chosen in order to include the regions

that contain macaque mirror neurons (F5 and PF/PFG) and their putative chimpanzee and human homologues (chimpanzee FCBm and PF/PFG and human BA 44 and BA 40, respectively). For all subjects, the superior temporal sulcus included both the dorsal and ventral banks and the fundus, extending along the entire extent of the sulcus. Superior temporal sulcus was included because it is typically considered as a major visual input for the mirror system (i.e., processing of biological motion (Iacoboni and Dapretto 2006)). The inferior temporal cortex ROI included all cortex ventral to the superior temporal sulcus ROI, terminating at the border with the parahippocampal gyrus. Thus this ROI included the inferior temporal and fusiform gyri in macaques, and the middle temporal, inferior temporal, and fusiform gyri in chimpanzees and humans. This ROI was included because we hypothesized that connections between inferotemporal cortex and frontal and parietal mirror regions might be important for social learning of object and/or tool use.

The geniculostriate and corticospinal tracts were chosen for control tractography because we hypothesized that that they might not differ substantially between the species studied. Because the lateral geniculate nucleus is rather small, the mapping of a template-space ROI to individual brains could be problematic. Therefore, for the geniculostriate control tractography, ROIs were placed in coronal sections of the optic chiasm and occipital white matter. The corticospinal tract runs from primary motor cortex to the brainstem and spinal cord. For the corticospinal control tractography, ROIs were placed in axial sections of the internal capsule and white matter deep to sensorimotor cortex.

For post mortem subjects, ROIs were placed directly in diffusion space, since only one post mortem subject for each species was used. For in vivo subjects, ROIs were placed

on the template brain and then registered to each subject's diffusion space. We then created expanded diffusion space white matter skeletons for each in vivo subject and used these to mask ROIs. This ensured that all tractography streamlines would be started in gray matter, to avoid picking up tracts that might pass under a cortical area but not into it.

Probabilistic tractography

FSL's software package was used to reconstruct diffusion information for all subjects. We used a probabilistic tractography algorithm designed to track through crossing fibers and into cortex (Behrens, Berg et al. 2007). This algorithm starts 25,000 "streamlines" in each voxel of the ROIs used in that analysis, and tracks these streamlines through the brain, voxel by voxel, based on the orientation and size of the first and second diffusion directions in the current voxel and the surrounding voxels. We used "networks mode" tractography, which restricts results only to those streamlines which pass through all ROIs used in a given analysis. We also used a distance correction algorithm, because connectivity probability values decrease with distance, and distance between homologous nodes of the mirror system depends on a species' brain size. These methods were used to examine the connectivity between the following sets of ROIs: (a) frontal-parietal-superior temporal sulcus; (b) frontal-parietal; (c) frontal-superior temporal sulcus; (d) frontal-inferior temporal cortex; (e) parietal-superior temporal sulcus; (f) parietal-inferior temporal.

Each analysis produced an image in which intensity corresponded to the probability of connectivity between all ROIs used in that analysis. However, raw values may not be directly comparable across brains due to differences in scan quality, voxel size, etc.

Therefore, we used the following novel, conservative normalization procedure. Each image was thresholded to include only the voxels with the top 1% of the robust range of probability values for that image, where the robust range is calculated using all but the top and bottom 2% of values. For in vivo subjects, these images were then affinely registered to template space, binarized, and summed to create a composite image. In these composite images, the intensity of each voxel corresponds to the number of subjects who have a high probability of connectivity between the ROIs used in that analysis (higher than 99% of the other probability values for that image). Composite images were again thresholded to show only those voxels that were common to at least 50% of subjects. Thus, in the final composite images, all colored voxels denote areas of the brain where at least 50% of subjects had very high probability of connectivity between the ROIs for that analysis; red denotes connectivity shared by 50% of subjects, and yellow denotes connectivity shared by 100% of subjects. We identified the fiber tracts carrying the observed connections (e.g., medial longitudinal fasciulus, extreme capsule, etc.) by consulting DTI atlases (Schmahmann, Pandya et al. 2007, Oishi, Faria et al. 2010) alongside individual subjects' tractography results overlaid on their color-weighted diffusion maps.

We also quantitatively compared tractography results across species. There is no single accepted method for quantification of DTI results that relates differences in streamline counts to differences in actual axonal connections, especially when comparing across species. Therefore, we used the following conservative normalization procedure. Streamline counts were corrected for distance to reduce the confound of varying brain sizes. Streamline counts were also normalized by the number of voxels in the seed ROIs, since larger seed ROIs initiate more streamlines. Finally, we used the geniculostriate tract as a control pathway to normalize streamline counts in the mirror system across

brains. Distance- and ROI-size-corrected streamline counts for our geniculostriate tracts also did not differ significantly between species (Independent Samples Kruskall-Wallis test, p=.377). Therefore, we divided all streamline counts for mirror system connections by that subject's geniculostriate streamline total. Thus quantitative comparisons between brains are controlled for individual and species differences in brain size, ROI size, and scan quality. For between-species comparisons, nonparametric statistics were used since sample sizes differed and normality tests failed. For within-species comparison, normality assumptions held and parametric statistics were used.

2.1.3. Results

Control tractography

In order to assess the reliability of our method and make certain that our results would not be confounded by variations in scan parameters or image resolution between species (**Table 2-1**), we performed control tractography in a pathway that is unlikely to differ substantially between primate species, the geniculostriate pathway (**Figure 2-2,** item A). Statistical comparisons revealed no significant difference in streamline numbers in the geniculostriate tract across species (**Table 2-3,** item A). Comparison of tractography images also revealed qualitative similarity across species in both the geniculostriate pathway and an additional control pathway, the corticospinal tract (**Figure 2-2**, item B). Importantly, the geniculostriate tractography results are consistent with a well-known species difference in the location of primary visual cortex. In humans, primary visual cortex is located on the medial face of occipital cortex, while in nonhuman primates, it extends around the occipital pole to cover a large part of the lateral occipital lobe. The geniculostriate tractography reflects this, with the human

pathway curving towards the medial face of the occipital lobe and the macaque and chimpanzee pathways terminating at the occipital poles. Thus our methods can detect species differences in features known to vary across species, but do not produce species differences in features known to be similar across species. This indicates that our analysis avoids both false positive and false negative results. Because differences in spatial resolution and other scanning parameters did not produce tractography differences in these control tracts, differences in scanning procedures are unlikely to result in tractography differences in mirror system connections.

It is important to note that our method is able to track connections across synapses (e.g., from optic chiasm to lateral geniculate nucleus to primary visual cortex). In the tractography images presented here, each colored voxel shares above-threshold connectivity, although not necessarily monosynaptically, with every seed ROI used in that analysis (see 2.1.2. Materials and methods). Thus, these analyses investigate the connectivity of distributed, semi-discrete networks, on a more global level than is typical of studies using injected tracers.

Mirror system tractography

We compared mirror system connectivity across species both qualitatively and quantitatively. Qualitative results are presented first and are summarized in **Figure 2-4**. **Figure 2-4-1** shows extensive larger, additional views of tractography.

Qualitative results

The mirror system as a whole: Connections between the frontal mirror region, parietal mirror region, and superior temporal sulcus. First, we simultaneously seeded each species' frontal mirror region, parietal mirror region, and superior temporal sulcus. This "big picture" analysis allowed us to compare across species the connections within the mirror system as a whole (summarized in **Figure 2-4**; more detailed views shown in **Figure 2-4-1**). Qualitative comparisons are based on tracts' spatial extent and intensity (indicated by the color map representing number of subjects sharing overlapping connections). We identified three major species differences. First, there was variation across species in the relative size of this circuit's dorsal versus ventral components (inferior/middle longitudinal fasciculi, third branch of superior longitudinal fasciculus, and arcuate fasciculus versus extreme/external capsules; pink versus green arrows in **Figure 2-4**). In macaques, the ventral connection between the frontal and superior temporal nodes was much larger than the dorsal connection between the frontal and parietal nodes; in chimpanzees, the discrepancy was smaller; and in humans, these connections were more nearly equal. Second, in humans and chimpanzees, but not macaques, this connectivity analysis yielded a projection to inferior temporal object processing regions (blue arrows in **Figure 2-4**). Third, in humans but not chimpanzees or macaques, this analysis yielded a considerable projection to superior parietal cortex (purple arrow in **Figure 2-4**).

To more specifically investigate which connections accounted for these species differences in anatomy, and how they might relate to species differences in social learning behavior, we then separately investigated the connectivity between individual pairs of regions.

Connections between the frontal and parietal mirror regions. In all three species, connections between the frontal and parietal mirror regions followed the third branch of the inferior longitudinal fasciculus (summarized in **Figure 2-5**; more detailed views shown in **Figure 2-5-1**). This pathway appeared similar across species. However, in humans, these connections included a sizeable projection into superior parietal cortex (purple arrow in **Figure 2-5**) that was not present in macaques or chimps.

Connections between the superior temporal sulcus and the frontal mirror region. We found connections between the superior temporal sulcus and the frontal mirror region via similar ventral routes in all three species (summarized in **Figure 2-6**; more detailed views shown in **Figure 2-6-1)**. These connections course through the extreme/external capsules (green arrows in **Figure 2-6**). Our results indicate that the superior temporal sulcus in macaques is connected with the ventral frontal cortex, a region that includes area 45 as well as the frontal mirror region. As macaque tract-tracing studies do not identify direct connections between F5 and temporal cortex (Petrides and Pandya 2009), our results probably reflect multi-synaptic connections between superior temporal sulcus and area 45, which in turn connects to F5, the frontal mirror region. In humans but not chimpanzees or macaques, this analysis also detected a second, dorsal pathway (pink arrow in **Figure 2-6**). One component of this pathway passed through the parietal opercular white matter directly adjacent to the anterior supramarginal gyrus. These connections travel through the inferior/middle longitudinal fasciculi to the third branch of the superior longitudinal fasciculus. Connections through the arcuate fasciculus were also detected, but this tract travels deeper in the white matter beneath parietal cortex and does not reach parietal gray matter (Rilling, Glasser et al. 2008).

Connections between inferior temporal cortex and the frontal mirror region. Tractography between inferior temporal cortex and the frontal mirror region yielded similar results to tractography between the superior temporal sulcus and the frontal mirror region (summarized in **Figure 2-7**; more detailed views shown in **Figure 2-7-1**). All three species showed a ventral connection via the extreme/external capsules, which reached more anterior frontal regions *en route* to the frontal mirror region (green arrows in **Figure 2-7**). However, in humans but not chimpanzees or macaques, this analysis also yielded a second, dorsal pathway which passed through the parietal opercular white matter directly adjacent to the anterior supramarginal gyrus (pink arrow in **Figure 2-7**). Paralleling the results of the previous section, these connections followed the inferior/middle longitudinal fasciculi and third branch of the superior longitudinal fasciculus. Again, connections through the arcuate fasciculus were also detected, but this tract travels deeper in the white matter beneath parietal cortex and does not reach parietal gray matter (Rilling, Glasser et al. 2008).

Connections between the superior temporal sulcus and parietal mirror region. In all three species, the superior temporal sulcus and parietal mirror region were linked by the inferior/middle longitudinal fasciculi (summarized in **Figure 2-8**; more detailed views in **Figure 2-8-1**). However, this pathway showed three major species differences. First, the anterior extent of this pathway into the temporal lobe varied across species, being smallest in macaques, intermediate in chimpanzees, and greatest in humans. Second, in humans and chimpanzees but not macaques, this analysis also detected connections to the middle and inferior temporal gyri; these connections appeared more robust in humans than chimpanzees (blue arrows in **Figure 2-8**). Third, in humans but not chimpanzees or macaques, this analysis additionally detected a sizeable connection to superior parietal cortex (purple arrow in **Figure 2-8**).

Connections between inferior temporal cortex and the parietal mirror region. Inferior temporal cortex and the parietal mirror region were connected by tracts similar to those connecting the superior temporal sulcus and the parietal mirror region (summarized in **Figure 2-9**; more detailed views shown in **Figure 2-9-1**). They were very sparse in macaques, were stronger and extended more rostrally into the temporal lobes in chimpanzees, and were strongest and extended most rostrally in humans (blue arrows in **Figure 2-9**). These connections follow the inferior/middle longitudinal fasciculi. Additionally, in humans only, this analysis yielded a sizeable connection with superior parietal cortex (purple arrow in **Figure 2-9**).

Quantitative results

We performed several statistical analyses on mirror system connectivity using streamline count as a dependent variable. A previous study used a similar approach in macaques and humans (Croxson, Johansen-Berg et al. 2005). Because streamline counts vary between *in vivo* and post mortem datasets, we used only in vivo datasets for our quantitative analyses. We controlled for brain size, ROI size, and differences in scan quality. We first quantitatively compared the number of streamlines in each sub-connection across species (**Table 2-3**, item B). For each sub-connection, humans had significantly more streamlines than either chimpanzees or macaques. Chimpanzees and macaques did not differ significantly from each other.

We also wondered whether one species' mirror system might have relatively more or fewer streamlines connecting to a particular node. Therefore, we compared the ratio of total mirror system streamlines that reached each ROI across species (**Table 2-3**, item

C). Humans have a significantly greater portion of mirror system streamlines devoted to the frontal ROI than chimpanzees, and a greater portion of streamlines devoted to the inferior temporal ROI than macaques. Macaques have a greater portion of streamlines devoted to the superior temporal sulcus than humans. These differences are qualitatively appreciable in **Figure 2-4** (pink versus green arrows). There was no significant difference for any ROI between macaques and chimps.

We also investigated whether there were species differences in the connections of particular nodes to particular other nodes. To do this, we compared the portion of each ROI's total streamlines that reached each other ROI (**Table 2-3**, item D). Compared to chimps, humans have a lesser proportion of STS streamlines devoted to IFG (appreciable in **Figure 2-6**), a lesser proportion of IT streamlines devoted to IFG (appreciable in **Figure 2-7**), a greater proportion of STS streamlines devoted to SMG (appreciable in **Figure 2-8**), a greater proportion of SMG streamlines devoted to IT (appreciable in **Figure 2-9**), and a greater proportion of IT streamlines devoted to SMG (appreciable in **Figure 2-9**). Compared to macaques, humans have a greater proportion of IFG streamlines connecting to IT (appreciable in **Figure 2-7**). Compared to macaques, chimpanzees have a greater proportion of IFG streamlines devoted to IT (appreciable in **Figure 2-7**), a greater proportion of IT streamlines devoted to IFG (appreciable in **Figure 2-7**), and a lesser proportion of IT streamlines devoted to SMG (appreciable in **Figure 2-9**).

Finally, we investigated the quantitative distribution of streamlines within each species, to determine which node(s) accounted for most mirror system connectivity within each species (**Table 2-3**, item E). In humans, significantly more streamlines were connected to the parietal ROI than to either the superior temporal or inferior temporal ROIs. In

chimpanzees, there were no significant differences between nodes, indicating that all have about equal numbers of streamlines. In macaques, significantly more streamlines were connected to the superior temporal sulcus ROI than to either the frontal or inferior temporal ROIs. These differences are best appreciated in **Figure 2-4**.

2.1.4. Discussion

This is the first analysis enabling direct, cross-species comparison of the organization of mirror system circuitry in macaques, chimpanzees, and humans. Following de Waal and Ferrari's (2009) theoretical approach, it provides mechanistic information that can inform a bottom-up perspective on the evolution of social learning, illustrating how biological susbstrates of behavior can vary in continua across species. Our results for the different species are consistent with tract-tracing and diffusion tensor imaging studies in macaques, and with diffusion tensor imaging studies in chimpanzees and humans (Ramayya, Glasser et al. , Petrides and Pandya 1984, Croxson, Johansen-Berg et al. 2005, Makris, Kennedy et al. 2005, Rushworth, Behrens et al. 2006, Schmahmann, Pandya et al. 2007, Frey, Campbell et al. 2008, Glasser and Rilling 2008, Rilling, Glasser et al. 2008, Makris and Pandya 2009, Makris, Papadimitriou et al. 2009, Petrides and Pandya 2009). However, it is important to note potential limitations of this study. First, we are unable to examine tracts smaller than our largest voxel. Second, our algorithm tracks across synapses (**Figure 2-2**), rather than identifying cell-to-cell connections at the level of tract tracing; therefore, our results must be interpreted as region-to-region connections at the level of closely related distributed networks. Third, this method does not allow investigation of non-connectivity-related anatomical differences that may contribute to behavioral differences, such as differences in cell types or receptor distributions. Fourth, questions about laterality and sex differences must await studies

with larger sample sizes. Fifth, it is unclear how streamline counts align with actual axon counts even within a single brain, and there is no single widely accepted method for quantifying DTI data across species. While we have carefully normalized our cross-species comparisons, we suggest that readers take our quantitative comparisons as complementary to our qualitative results. Finally, there are multiple factors that can produce observed differences in the relative strength of pathways, such as path geometry, complexity, brain morphology, and data quality. However, we performed control analyses in the geniculostriate tract, which is likely to be quite evolutionarily conserved. This tract did not differ across species in our measures, suggesting that the observed species differences in mirror system tracts are reliable.

In our comparative analyses of the frontal, parietal, and temporal nodes of the mirror system, we identified three major species differences. Below, we consider the possible relevance of each of these differences to social learning. Our interpretation is framed around the functional roles that our ROIs may play in observation of others' actions. We suggest that because each node of the mirror system contributes a different type of information processing, differences in their connectivity may produce observational learning circuits weighted towards different aspects of observed actions. We propose a model (**Figure 2-10**) linking species differences in mirror system connectivity, mirror system functional responses, and social learning behavior.

The first major species difference we observed was in the relative weight of the dorsal versus ventral connections within each species' "core" imitation circuit. Qualitatively, this is indicated by the pink versus green arrows in **Figures 2-4**, **2-6**, and **2-7**, and EmC-ExC connections versus MLF-ILF/SLFIII connections in **Figure 2-10**. In macaques, extreme/external capsule connections far outweighed connections travelling

in the inferior/middle longitudinal fasciculi and the third branch of the superior longitudinal fasciculus. In chimpanzees, this discrepancy was less pronounced. In humans, extreme/external capsule connections are relatively smaller. Quantitatively, this is reflected in the statistical tests in Table 1 item E. The most-connected node of the human mirror system is the SMG ROI; there is no significant connectivity difference in chimpanzee mirror system nodes; and the most-connected node of the macaque mirror system is the STS ROI. The STS ROI is quite large, but importantly, streamline counts were controlled for ROI size.

The ventral extreme/external capsule connections offer a route of information transfer between temporal areas which process sensory input about others' actions (e.g., biological motion perception in the superior temporal sulcus (Puce and Perrett 2003) and objects and tool recognition in inferior temporal cortex (Beauchamp and Martin 2007) and frontal areas which process higher-level action goals or intentions (Johnson-Frey, Maloof et al. 2003, Goldenberg 2009) – but see (Huth, Nishimoto et al. 2012) for evidence for distributed representations. Thus these ventral connections may be useful for extracting mainly the physical end result and/or goal or intention of observed actions. The dorsal connections through the inferior/middle longitudinal fasciculi and the third branch of the inferior longitudinal fasciculus link temporal sensory areas and frontal areas, respectively, with inferior parietal cortex, which is involved in the spatial mapping of movement (Johnson-Frey, Maloof et al. 2003, Goldenberg 2009). These dorsal connections may be useful for extracting a finer level of kinematic detail from observed actions.

We propose that the functional relevance of this species difference may be related to biases towards emulation versus imitation, or towards copying the product versus the

process of an action. Macaques' social learning is strongly product-oriented: they emulate but do not imitate. Following Lyons et al. (Lyons, Santos et al. 2006), we suggest that the macaque mirror system is mainly tuned to environmental effects of observed actions – that it "mirrors" the ends of observed actions much more than the means, or the product more than the process, due to greater temporal-frontal than temporal-parietal connections in their mirror system. Thus perhaps macaque mirror neurons do not respond to intransitive manual actions because they lack a physical end result or effect on the environment: there is nothing for their goal-oriented mirror system to "mirror." Similarly, perhaps macaques do not imitate because imitation involves duplicating the process of an observed action, and their mirror systems compute mainly the product. In contrast to macaques, chimpanzees imitate under certain circumstances, but are biased towards emulation (Whiten, McGuigan et al. 2009). This may be related to chimpanzees' stronger connections between superior temporal sulcus and inferior parietal cortex, which may allow more processing of the finer details of the spatial/kinematic structure of observed actions. Chimpanzee imitation is still quite limited compared to human imitation, and humans are even more process-oriented than chimpanzees, duplicating even those movements in an action that do not contribute to the action's overall end result (Horner and Whiten 2005). This may be related to our further-increased temporal-parietal connections. We suggest that the human mirror system is configured to "mirror" not only the product but also the process of observed actions, which could explain why human mirror regions respond to intransitive (non-object-oriented) actions.

It is important to note that frontal-temporal-parietal circuits overlapping with those studied here are also implicated in other complex cognitive functions, including language, gesture, and tool use (Ramayya, Glasser et al. , Frey 2007, Glasser and Rilling

2008, Rilling, Glasser et al. 2008). All of these functions rely on social learning for cultural transmission. Several theories suggest that these functions may share a common neural substrate, which may or may not be the mirror system (Preuss 2007, Arbib, Liebal et al. 2008, Frey 2008, Corballis 2009). Motor mirroring, and self-other matching more broadly, is likely to offer other evolutionary advantages besides social learning of manual actions. More research is needed to fully elucidate the shared versus separate nature of these cognitive functions and the contribution that each white matter tract makes to each function.

The second major species difference we observed was in the connections of the parietal mirror region with inferior temporal cortex, where objects and tools are recognized. Qualitatively, this is indicated by the blue arrows in **Figure 2-4**, **2-8**, and **2-9**, and the blue connections in **Figure 2-10**. These connections were weak in macaques, stronger in chimpanzees, and strongest in humans. Quantitatively, this is supported by statistical comparisons in Table 1, item B: humans have more streamlines connecting SMG and IT than either macaques or chimps. These results are consistent with macaque tract-tracing studies that report a paucity of connections from area PF to inferior temporal object processing regions (Zhong and Rockland 2003, Rozzi, Calzavara et al. 2006).

We propose that these connections may support the observational learning of tool use by linking information processing about the identities of objects with information processing about the spatial/kinematic details of others' actions. The gradient in these connections from macaques to chimps to humans mirrors the gradient in social learning of tool use. Importantly, while wild macaques do not use tools, they do exhibit social learning of relatively spatially and kinematically unconstrained object-directed actions, such as potato washing and stone handling; we suggest that this is supported by

information transfer between temporal and frontal cortex via the extreme/external capsules.

Additionally, individual macaques can be trained to use tools in captivity. This causes the receptive field of bimodal visual/sensory neurons in caudal postcentral gyrus to expand to include the tool and/or space that can be reached with the tool (Iriki, Tanaka et al. 1996). Macaque tool use, compared with simple stick manipulation, activates intraparietal sulcus, as well as basal ganglia, presupplementary motor area, premotor cortex, and cerebellum (Obayashi, Suhara et al. 2001). Tool use training causes extension of afferents from ventrolateral prefrontal cortex and temporo-parietal junction into anterior intraparietal sulcus (Hihara, Notoya et al. 2006). The repeated appearance of inferior parietal cortex or intraparietal sulcus in these sets of results suggests that these regions are important for the acquisition of tool use. In another experiment with tool-trained macaques, Peeters et al. (Peeters, Simone et al. 2009) observed BOLD activation during tool use observation in the anterior supramarginal gyrus in humans but not in the corresponding area in either naive or tool-trained monkeys. These regions overlap with those used as parietal ROIs in this study. The authors propose that the anterior supramarginal gyrus contains a uniquely human tool use area that processes the cause-effect relationships between tools and actions. We suggest that an alternative or additional possible interpretation of these results is that the anterior supramarginal gyrus maps the kinematic details of observed actions onto the observer's own motor system, and that the lack of this mapping in macaques accounts for their lack of tool use in the wild.

The third major species difference we observed was that connections between the frontal and parietal mirror regions extended furthest into superior parietal cortex in humans.

Qualitatively, this is indicated by the purple arrows in **Figures 2-4**, **2-5**, **2-8**, and **2-9**, and the purple connections in Figure 2. These connections were not quantified since we did not have a superior parietal ROI in our analysis, but it is plainly evident that these connections are completely lacking in the macaque and chimpanzee tractography. Superior parietal cortex is associated with spatial awareness and attention (Husain and Nachev 2007); perhaps this connection supports increased attention to or awareness of the trajectories of others' actions through space. Interestingly, Hihara et al. (Hihara, Notoya et al. 2006) report axon extension from anterior inferior parietal cortex to superior parietal cortex in tool-trained macaques. Additionally, superior parietal regions are activated when modern humans make stone tools in the style of our earliest tool-making hominin ancestors (Oldowan tools) (Stout and Chaminade 2007, Stout, Toth et al. 2008). These superior parietal regions are reached by the uniquely human tract identified in our analyses (purple arrows in **Figures 2-4**, **2-5**, **2-8**, and **2-9**). Expansion of parietal cortex has been documented in hominin evolution (Bruner 2004), and modern human parietal cortex contains novel cortical areas (Orban, Claeys et al. 2006). Thus we speculate that the type of information processing carried out in superior parietal cortex while observing another's action supports the social learning of tool use. Together, the species differences in mirror system connectivity identified here offer a proximate, anatomical explanation for species differences in observational learning. An ultimate explanation must be evolutionary. Of course, each species must be well-adapted to the socioecological niche in which it evolved. Horner and Whiten (Horner and Whiten 2005) suggest that chimpanzees primarily emulate because this is the most adaptive observational learning strategy for them. Attending mainly to the product of an observed action, while mainly ignoring the motor process used to achieve it, may allow chimpanzees to infer rules about object affordances and means-ends relationships on a broad enough level to generalize this information to a new situation. Compared to

macaques, chimpanzees have alterations in the allocations of each ROI's connections that could support this: a greater proportion of IFG streamlines devoted to IT, a greater proportion of IT streamlines devoted to IFG, and a lesser proportion of IT streamlines devoted to SMG (**Table 2-3**, item D). We suggest that this reflects an adaptation that evolved after the macaque-chimpanzee phylogenic divergence that allows chimpanzees to mirror the product more than the process of observed actions. This may be particularly important for actions were means-ends relationships are tied to the success of the action, e.g., tool use – which are part of the behavioral repertoire of chimpanzees but not (untrained) macaques.

Extending Horner and Whiten's idea (Horner and Whiten 2005), we speculate that humans have a greater propensity to imitate, extending to over-imitation, because this is the most adaptive learning style for the set of selection pressures we experienced during our evolution. Humans' socially learned behaviors include actions that are much more kinematically constrained than those of chimpanzees and macaques – for example, consider bow hunting versus nut cracking and potato washing. Perhaps reproducing these more complex actions requires the capacity to copy not only observed actions' end or product but also their means or process. Compared to chimpanzees, humans have alterations in the allocation of each ROI's connections that could support this: a greater proportion of SMG streamlines devoted to IT, a lesser proportion of STS streamlines devoted to IFG, a greater proportion of STS streamlines devoted to SMG, a lesser proportion of IT streamlines devoted to IFG, and a greater proportion of IT streamlines devoted to SMG (**Table 2-3,** item D). We suggest that this reflects an adaptation that emerged after the chimpanzee-human phylogenic divergence that allows humans to mirror the process more than the product of observed actions. This may be particularly important for actions where "copy the demonstration exactly" is a more successful

strategy than “understand the means-ends relationship” – for example, actions where means-ends relationships are more or less comprehensible to most individuals, such as processes for preserving food or treating illness.

Table 2.1-1. Acquisition details for diffusion tensor imaging scans and corresponding structural scans.

Species	Status	Sex	Age	Scan details
Rhesus macaque	Post mortem	F	11 years	60-direction DTI images Scanner: 9.4 T Bruker; sequence: spin echo; B-value: 2000; voxel size: 0.55 mm isotropic (about 5.21 x 10^{-6} of total brain volume); 3 averages. No T1-weighted images acquired; ROI definition performed on B0 images (equivalent to high-resolution T2).
Rhesus macaque	In vivo	F	6 years	60-direction DTI images Scanner: 3T TRIO; Single-shot double spin-echo EPI (parallel imaging with GRAPPA, R=3); B-value: 1000; voxel size: 1.3 mm isotropic (about 1.06 x 10^{-5} of total brain volume); 12 averages. T1-weighted images used for ROI definition TR: 5000 msec; TE: 86 msec; matrix size: 64x64
	In vivo	M	6 years	
	In vivo	F	6 years	
	In vivo	M	6 years	
	In vivo	F	6 years	
Chimpanzee	Post mortem	F	28 years	60-direction DTI images Scanner: 4.7 T Bruker; sequence: spin echo; B-value: 4500; voxel size: 1.5 mm isotropic (about 3.72 x 10^{-6} of total brain volume); 2 averages. No T1-weighted images acquired; ROI definition performed on B0 images (equivalent to high-resolution T2).
Chimpanzee	In vivo	F	17 years	60-direction DTI images Scanner: 3T TRIO; sequence: single-shot double spin-echo; B value: 1000; voxel size: 1.8 mm isotropic (about 1.99 x 10^{-6} of total brain volume); 5 averages. T1-weighted images used for ROI definition TR: 5740 msec; TE: 84 msec; matrix size: 72x128
	In vivo	F	16 years	
	In vivo	F	13 years	
	In vivo	F	14 years	
	In vivo	F	14 years	

Table 2.1-1 (continued). Acquisition details for diffusion tensor imaging scans and corresponding structural scans.

Species	Status	Sex	Age	Scan details
Human	In vivo	M	20 years	64-direction DTI images Scanner: 3T Siemens TRIOTIM; Sequence: single-shot dual spin-echo EPI sequence with parallel imaging reconstruction; B-value: 1000; voxel size: 2.0 mm isotropic (about 1.09 x 10^{-6} of total brain volume); 2 averages. T1-weighted images used for ROI definition TR: 8700 msec; TE: 93 msec; matrix size: 128 x 128.
	In vivo	M	18 years	
	In vivo	M	19 years	
	In vivo	M	20 years	
	In vivo	M	22 years	
	In vivo	M	20 years	
	In vivo	M	20 years	
	In vivo	M	22 years	
	In vivo	M	20 years	
	In vivo	M	20 years	
	In vivo	M	20 years	
	In vivo	M	19 years	
	In vivo	M	21 years	
	In vivo	M	22 years	
	In vivo	M	19 years	
	In vivo	M	21 years	
	In vivo	M	21 years	
	In vivo	M	19 years	
	In vivo	M	21 years	
	In vivo	M	19 years	
	In vivo	M	18 years	
	In vivo	M	22 years	
	In vivo	M	20 years	
	In vivo	M	20 years	
	In vivo	M	21 years	
	In vivo	M	19 years	
	In vivo	M	19 years	
	In vivo	M	21 years	
	In vivo	M	22 years	
	In vivo	M	21 years	

Table 2.1-2. Quantification and statistical tests. Only significant results are listed. Results where significance does not survive Bonferroni correction for multiple comparisons are marked with an asterisk. All streamline counts were corrected for distance and ROI size. All mirror system streamline counts were normalized by that brain's geniculostriate streamline count.

Question	Statistical test	Dependent variable	p value	Conclusion
A) Do scan qualities differ between species?	Independent Samples Kruskall-Wallis test	Number of streamlines in geniculostriate tract	p=.377	No species differences in geniculostriate streamlines, which suggests no species differences in scan quality
B) Does the overall amount of mirror system connectivity differ between species?	Independent Samples Kruskall-Wallis test	Number of streamlines connecting IFG to SMG	p=.000	Streamlines differ across species in each mirror system sub-connection.
		Number of streamlines connecting IFG to STS	p=.000	
		Number of streamlines connecting SMG to STS	p=.000	
		Number of streamlines connecting IFG to IT	p=.001	
		Number of streamlines connecting SMG to IT	p=.000	
	Step-down Mann-Whitney U test (humans vs. chimps)	Number of streamlines connecting IFG to SMG	p=.001	Humans have more streamlines in each mirror system sub-connection than chimps.
		Number of streamlines connecting IFG to STS	p=.008	
		Number of streamlines connecting SMG to STS	p=.000	
		Number of streamlines connecting IFG to IT	p=.040*	
		Number of streamlines connecting SMG to IT	p=.000	
	Step-down Mann-Whitney U test (humans vs. macaques)	Number of streamlines connecting IFG to SMG	p=.000	Humans have more streamlines in each mirror system sub-connection than macaques.
		Number of streamlines connecting IFG to STS	p=.001	
		Number of streamlines connecting SMG to STS	p=.000	
		Number of streamlines connecting IFG to IT	p=.000	
		Number of streamlines connecting SMG to IT	p=.000	
	Step-down Mann-Whitney U test (chimps vs. macaques)	No comparisons with p<.05		Macaques and chimps do not differ in streamlines in any mirror system sub-connection.

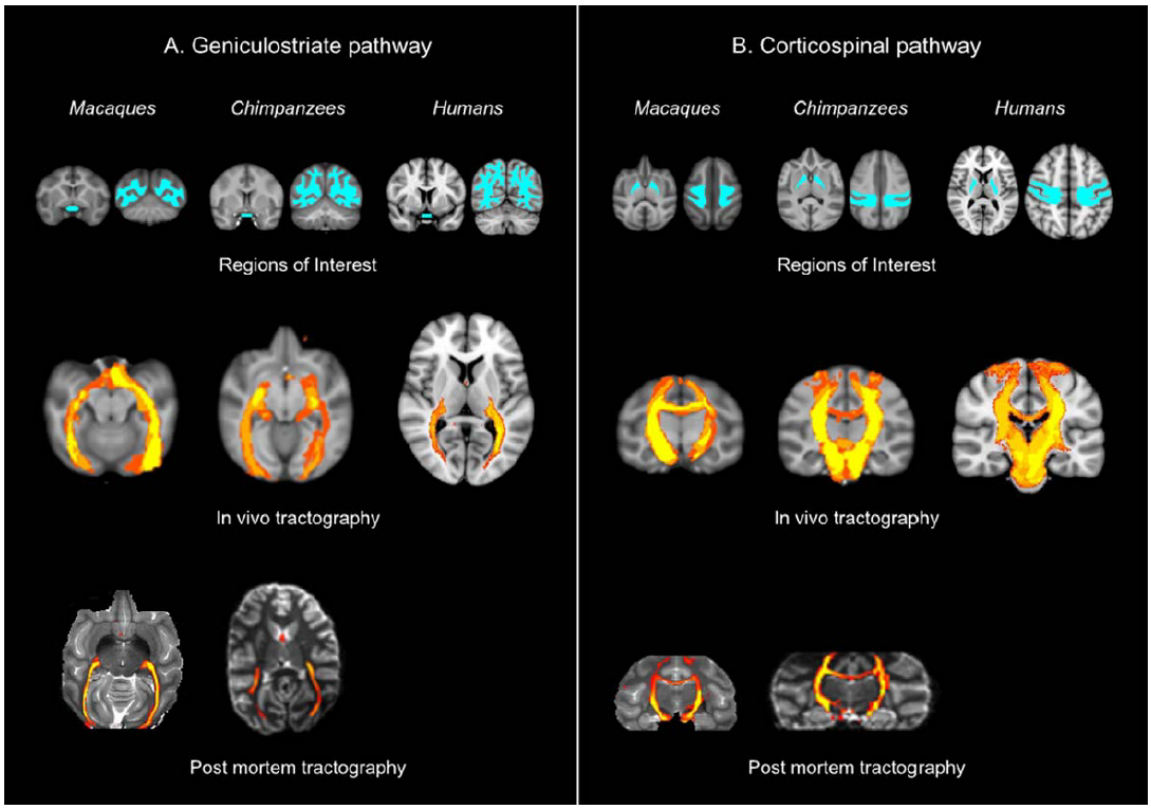
Table 2.1-2 (continued). Quantification and statistical tests. Only significant results are listed. Results where significance does not survive correction for multiple comparisons are marked with an asterisk. All streamline counts were corrected for distance and ROI size. All mirror system streamline counts were normalized by that brain's geniculostriate streamline count.

Question	Statistical test	Dependent variable	p value	Conclusion
C) Are there between-species differences in the proportional allocation of mirror system connections between nodes?	Mann-Whitney U test (humans vs. chimps)	Ratio of mirror system streamlines connecting to IFG	p=.036*	Humans have a greater proportion of mirror system streamlines devoted to the IFG node than chimps.
	Mann-Whitney U test (humans vs. macaques)	Ratio of mirror system streamlines connecting to STS	p=.018*	Humans have a greater proportion of mirror system streamlines devoted to IT than macaques. Macaques have a greater proportion devoted to STS.
		Ratio of mirror system streamlines connecting to IT	p=.000	
	Mann-Whitney U test (chimps vs. macaques)	No comparisons with p<.05		The proportion of mirror system streamlines devoted to any node does not differ between macaques and chimps.
D) Are there between-species differences in the proportional allocation of connectivity from individual mirror system ROIs to others?	Mann-Whitney U test (humans vs. chimps)	Ratio of SMG streamlines connecting to IT	p=.001	Compared to chimps, humans have a greater proportion of SMG streamlines devoted to IT, a lesser proportion of STS streamlines devoted to IFG, a greater proportion of STS streamlines devoted to SMG, a lesser proportion of IT streamlines devoted to IFG, and a greater proportion of IT streamlines devoted to SMG.
		Ratio of STS streamlines connecting to IFG	p=.046*	
		Ratio of STS streamlines connecting to SMG	p=.046*	
		Ratio of IT streamlines connecting to IFG	p=.024*	
		Ratio of IT streamlines connecting to SMG	p=.024*	
	Mann-Whitney U test (humans vs. macaques)	Ratio of IT streamlines connecting to IFG	p=.001	Compared to macaques, humans have a greater proportion of IFG streamlines connecting to IT.
	Mann-Whitney U test (chimps vs. macaques)	Ratio of IFG streamlines connecting to IT	p=.028*	Compared to macaques, chimpanzees have a greater proportion of IFG streamlines devoted to IT, a greater proportion of IT streamlines devoted to IFG, and a lesser proportion of IT streamlines devoted to SMG.
		Ratio of IT streamlines connecting to IFG	p=.047*	
		Ratio of IT streamlines connecting to SMG	p=.047*	

Table 2.1-2 (continued). Quantification and statistical tests. Only significant results are listed. Results where significance does not survive correction for multiple comparisons are marked with an asterisk. All streamline counts were corrected for distance and ROI size. All mirror system streamline counts were normalized by that brain's geniculostriate streamline count.

Question	Statistical test	Dependent variable	p value	Conclusion
E) Within a particular species, how are total mirror system connections allocated between nodes?	Repeated measures ANOVA with step-down T-tests (humans)	Ratio of mirror system streamlines that connect to SMG > ratio of mirror system streamlines that connect to STS	p=.014*	In humans, more mirror system streamlines are connected to SMG than STS or IT.
		Ratio of mirror system streamlines that connect to SMG > ratio of mirror system streamlines that connect to IT	p=.026*	
	Repeated measures ANOVA with step-down T-tests (chimps)	No comparisons with p<.05		In chimps, there is no significant difference in mirror system streamline distributed between nodes.
	Repeated measures ANOVA with step-down T-tests (macaques)	Ratio of mirror system streamlines that connect to STS > ratio of mirror system streamlines that connect to F5	p=.001	In macaques, more mirror system streamlines are devoted to STS than to F5 or IT.
		Ratio of mirror system streamlines that connect to STS > ratio of mirror system streamlines that connect to IT	p=.004	

Figure 2.1-3. Control tractography.



A. Geniculostriate pathway.

Probabilistic tractography between the optic chiasm and occipital white matter.

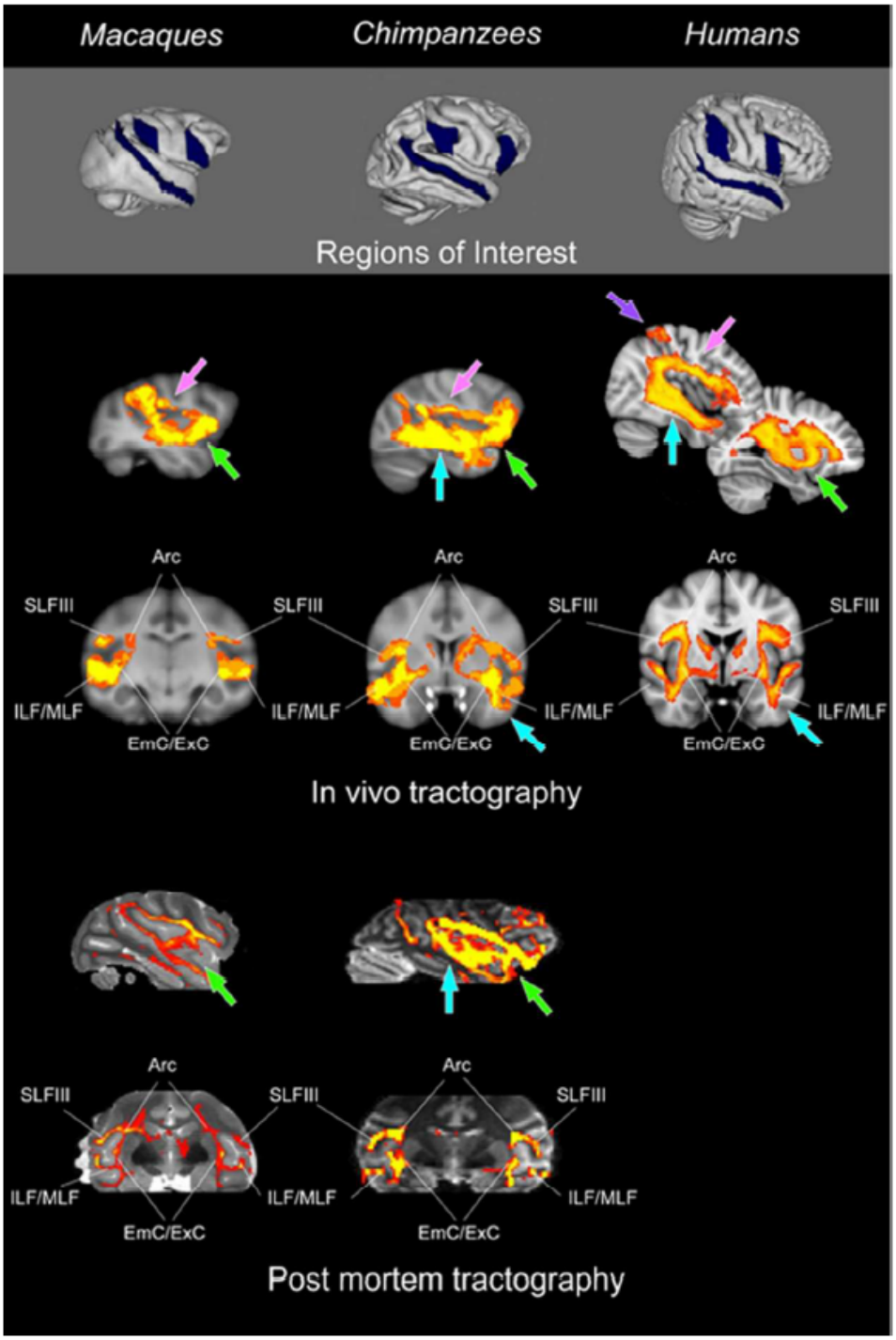
B. Corticospinal tract.

Probabilistic tractography between the internal capsule and the white matter beneath sensorimotor cortex.

Results are similar across species and between post mortem and in vivo subjects. Furthermore, the geniculostriate tract conforms to known species differences in the location of V1. Thus we can detect species differences in features known to vary across

species, but do not detect species differences in features known to be similar across species. This indicates that our analysis avoids both false positive and false negative results. Images are shown in radiological convention (right side of image corresponds to left side of brain).

Figure 2.1-4. Overview of mirror system tractography.



The mirror system as a whole: Connections between frontal mirror region, parietal

mirror region, and superior temporal sulcus. Probabilistic tractography between macaque F5, PF, and superior temporal sulcus; chimpanzee BA44, PF, and superior temporal sulcus; and human BA44, BA40, and superior temporal sulcus. Three major species differences are apparent. First, there is an increase from macaques to chimpanzees to humans in the ratio of dorsal versus ventral connections within the circuit (inferior/middle longitudinal fasciculi (ILF/MLF) and third branch of superior longitudinal fasciculus (SLFIII) versus extreme and external capsules (EmC/ExC); pink versus green arrows). Second, in humans and chimpanzees but not macaques, this circuit includes a robust connection to inferior and middle temporal areas associated with object and tool recognition (blue arrows). Third, in humans only, this circuit includes a connection to superior parietal cortex, a region associated with spatial attention and tool use (purple arrow). Images are shown in radiological convention (right side of image corresponds to left side of brain).

Figure 2.1-5. Additional views of connections between frontal mirror region, parietal mirror region, and superior temporal sulcus.

A. *In vivo* humans

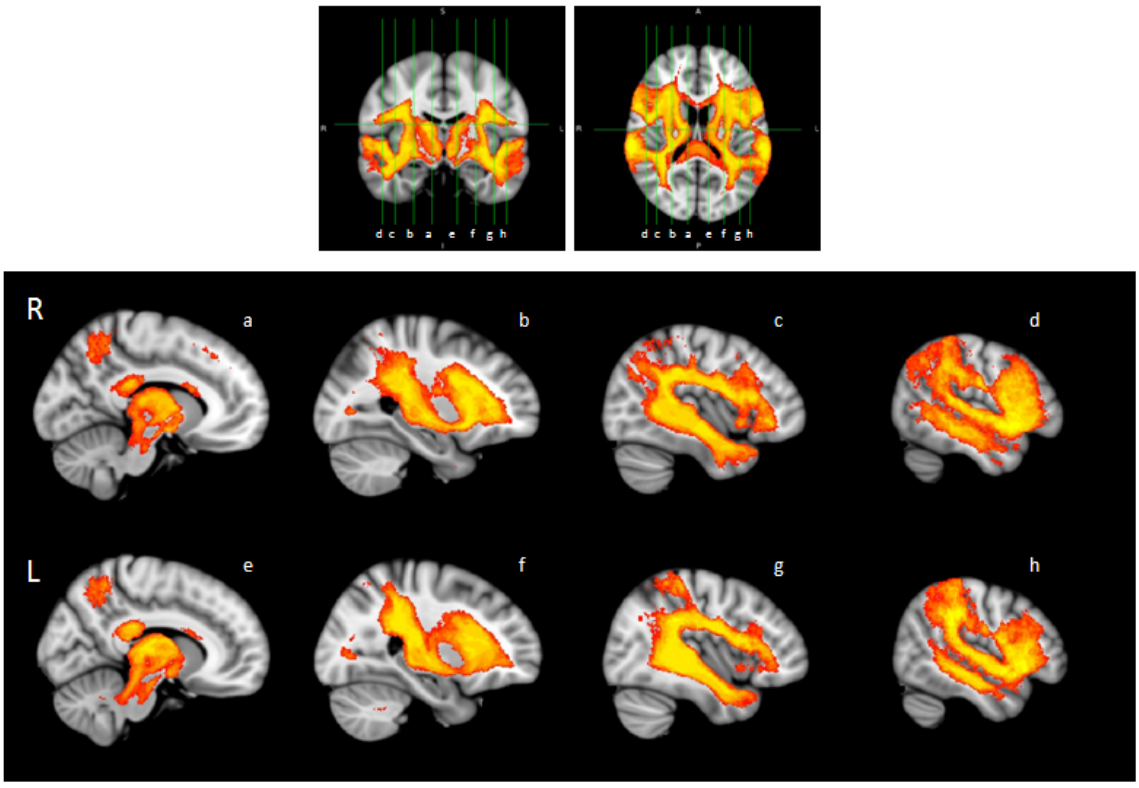


Figure 2.1-5 (continued). Additional views of connections between frontal mirror region, parietal mirror region, and superior temporal sulcus.

B. *In vivo* chimpanzees

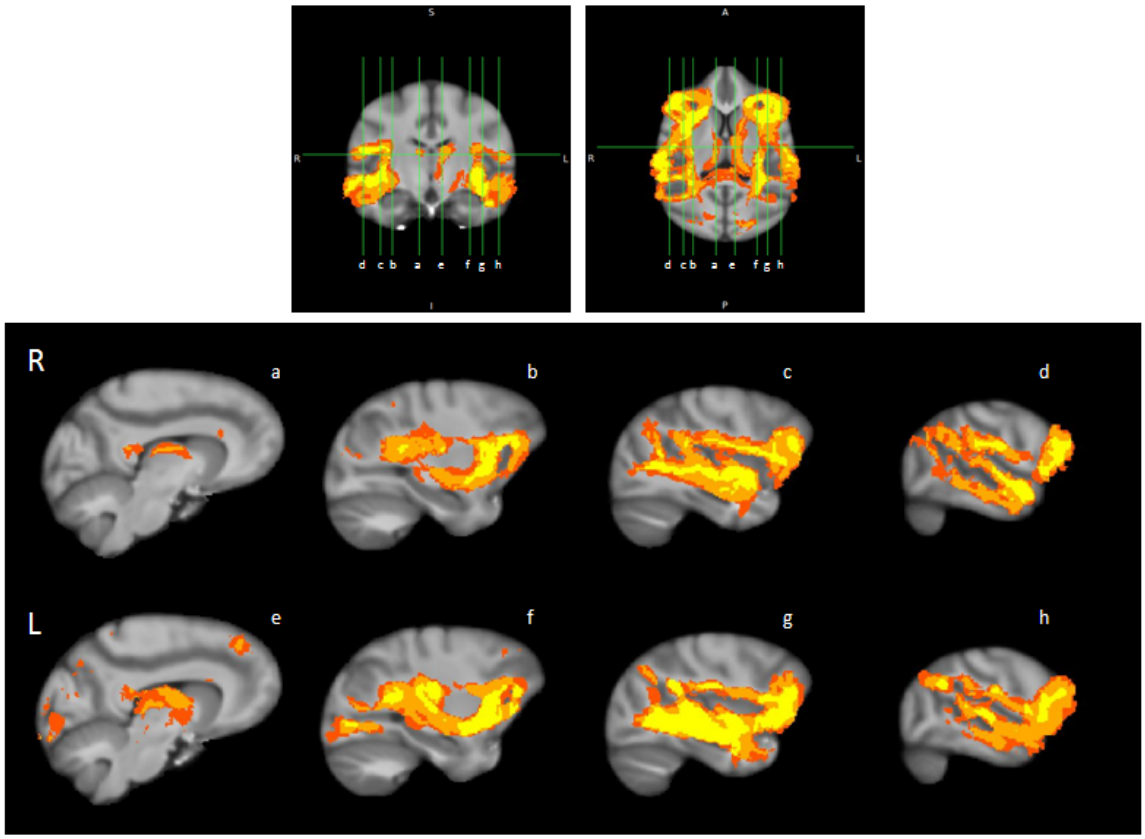


Figure 2.1-5 (continued). Additional views of connections between frontal mirror region, parietal mirror region, and superior temporal sulcus.

C. *In vivo* macaques

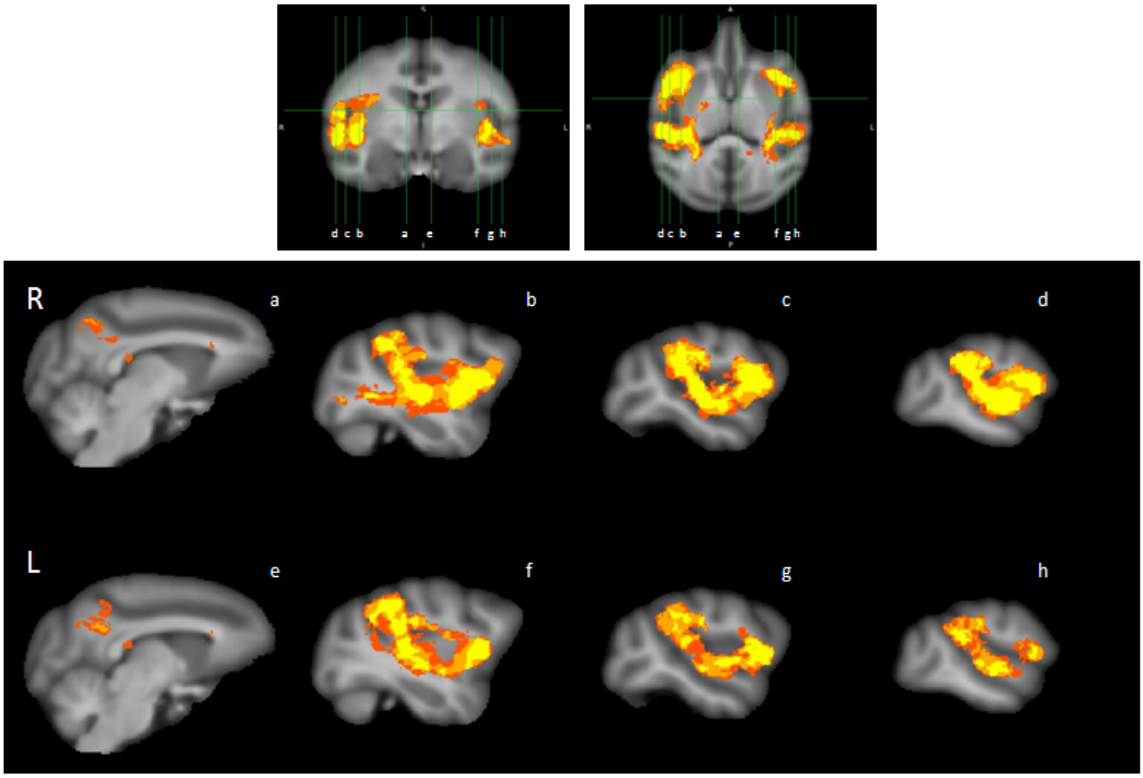
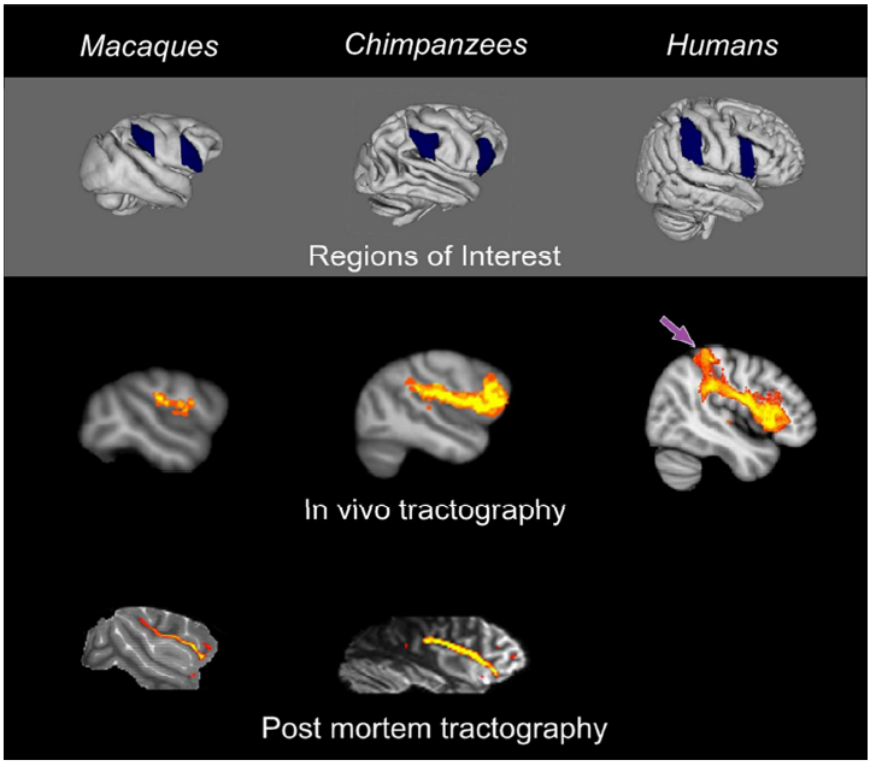


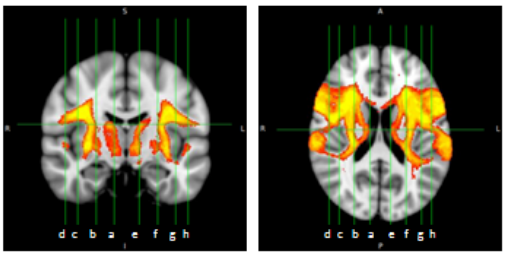
Figure 2.1-6. Overview of connections between frontal and parietal mirror regions.



Probabilistic tractography between macaque F5 and PF, chimpanzee BA44 and PF, and human BA44 and BA40. These connections follow the third branch of the superior longitudinal fasciculus in all three species. In humans, this tract appears more robust, and includes a connection with superior parietal cortex (purple arrow).

Figure 2.1-7. Additional views of connections between frontal and parietal mirror regions.

A. *In vivo* humans



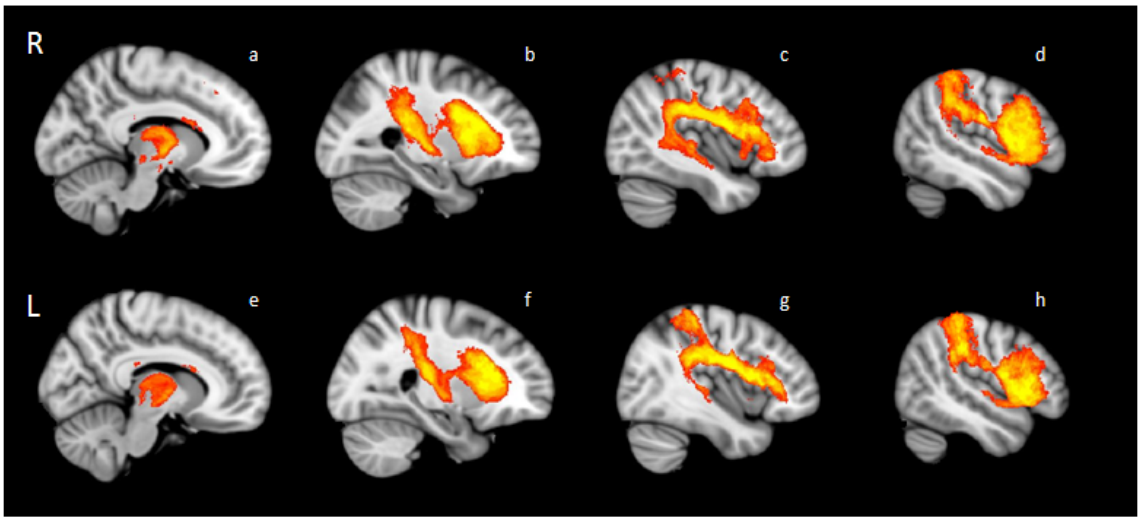


Figure 2.1-7 (continued). Additional views of connections between frontal and parietal mirror regions.

B. *In vivo* chimpanzees

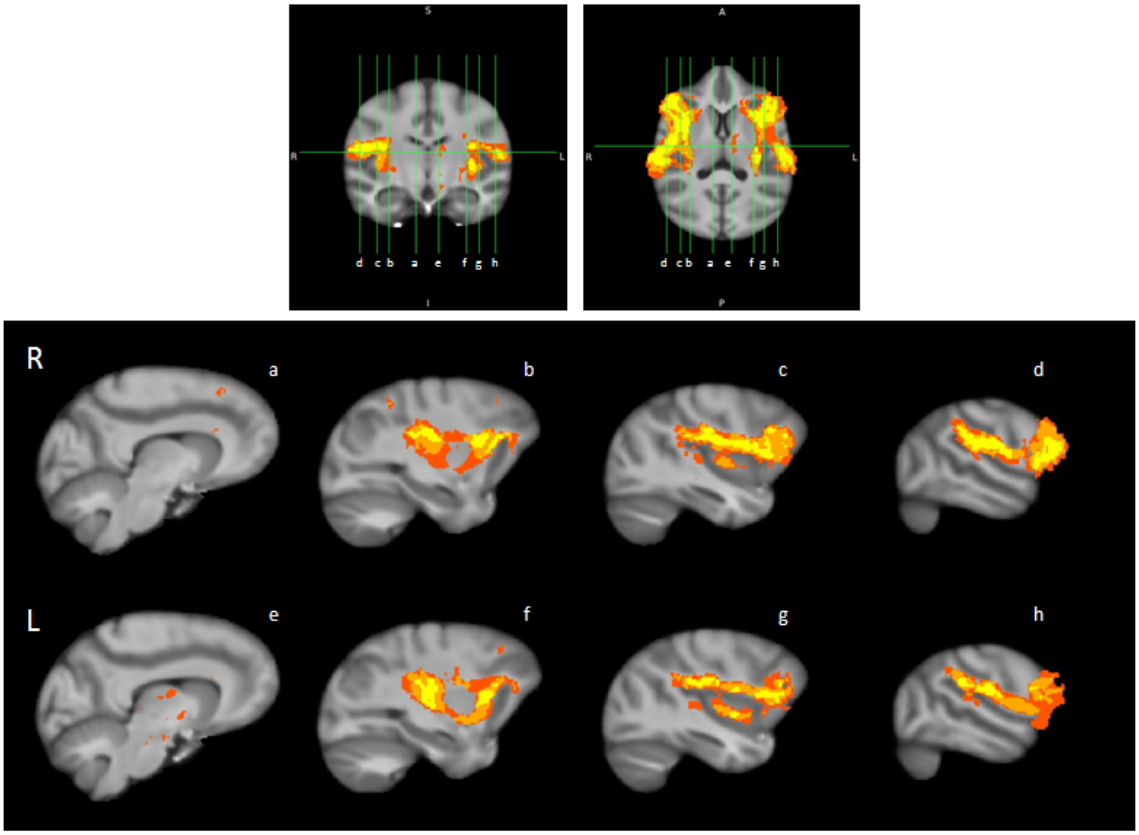


Figure 2.1-7 (continued). Additional views of connections between frontal and parietal mirror regions.

C. *In vivo* macaques

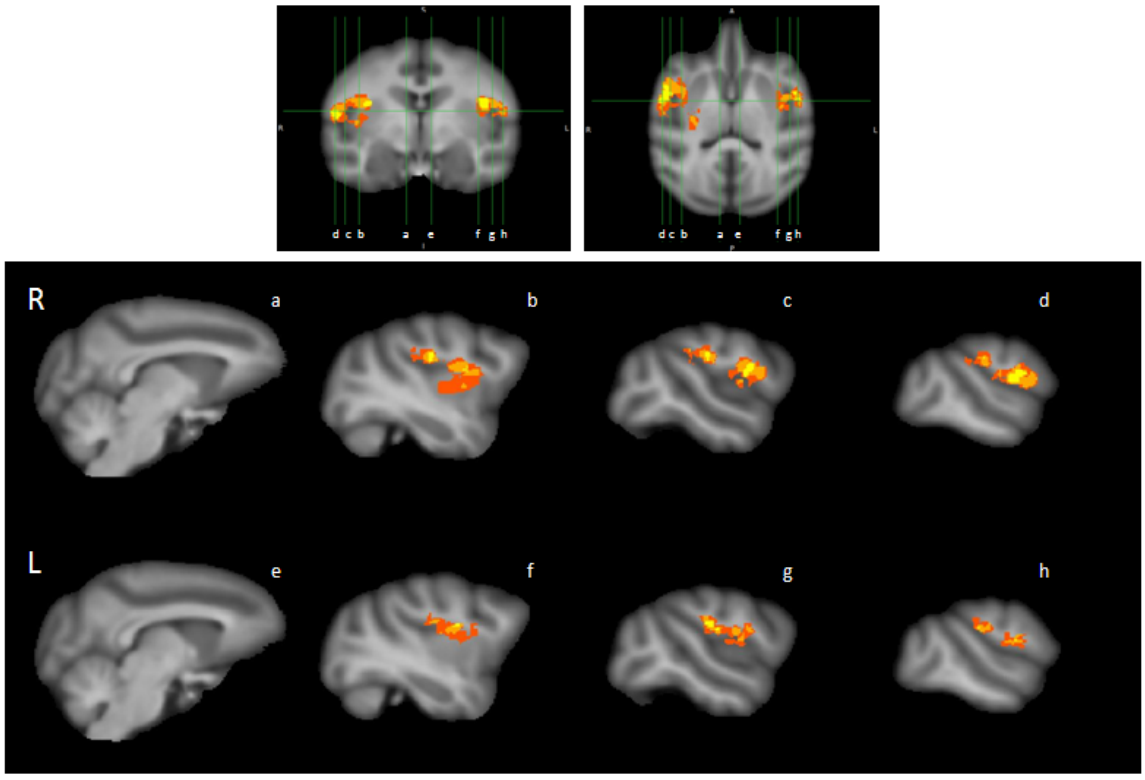
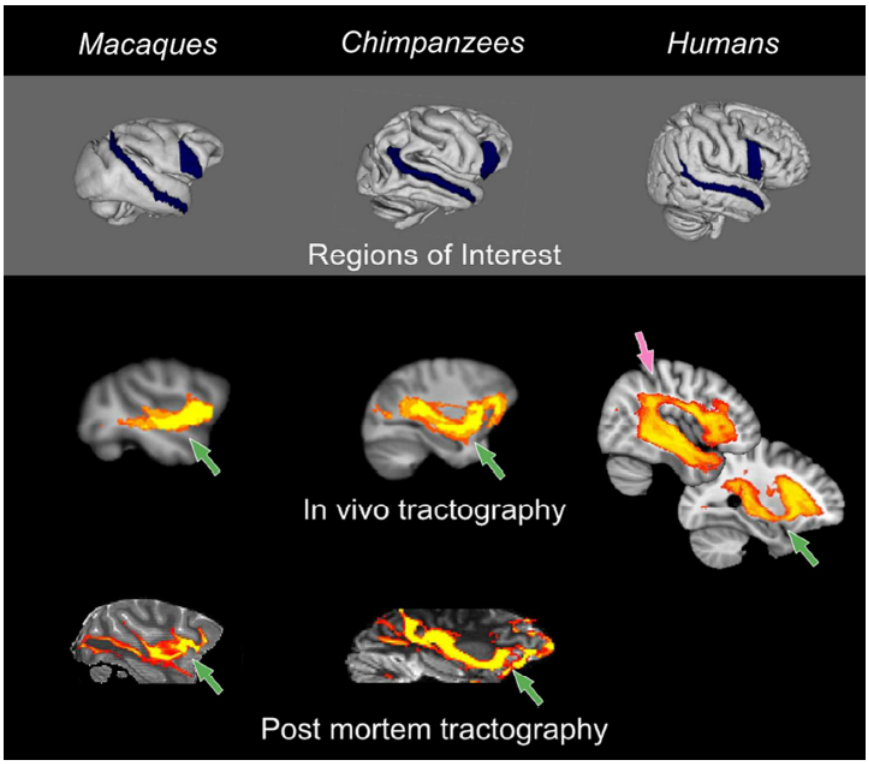


Figure 2.1-8. Overview of connections between superior temporal sulcus and frontal mirror region.



Probabilistic tractography between macaque F5 and superior temporal sulcus; chimpanzee BA44 and superior temporal sulcus; and human BA44 and superior temporal sulcus. In all 3 species, connections between these regions follow the extreme/external capsules and pass through more anterior regions of prefrontal cortex en route to the frontal mirror region (green arrows). In humans, a second, dorsal pathway is detected, which travels through the inferior/middle longitudinal fasciculi through inferior parietal cortex to the third branch of the superior longitudinal fasciculus (pink arrow). Connections through the arcuate fasciculus (not shown here) were also detected, but this tract travels deeper in the white matter beneath parietal cortex and does not reach parietal gray matter.

Figure 2.1-9. Additional views of connections between superior temporal sulcus and frontal mirror region.

A. *In vivo* humans

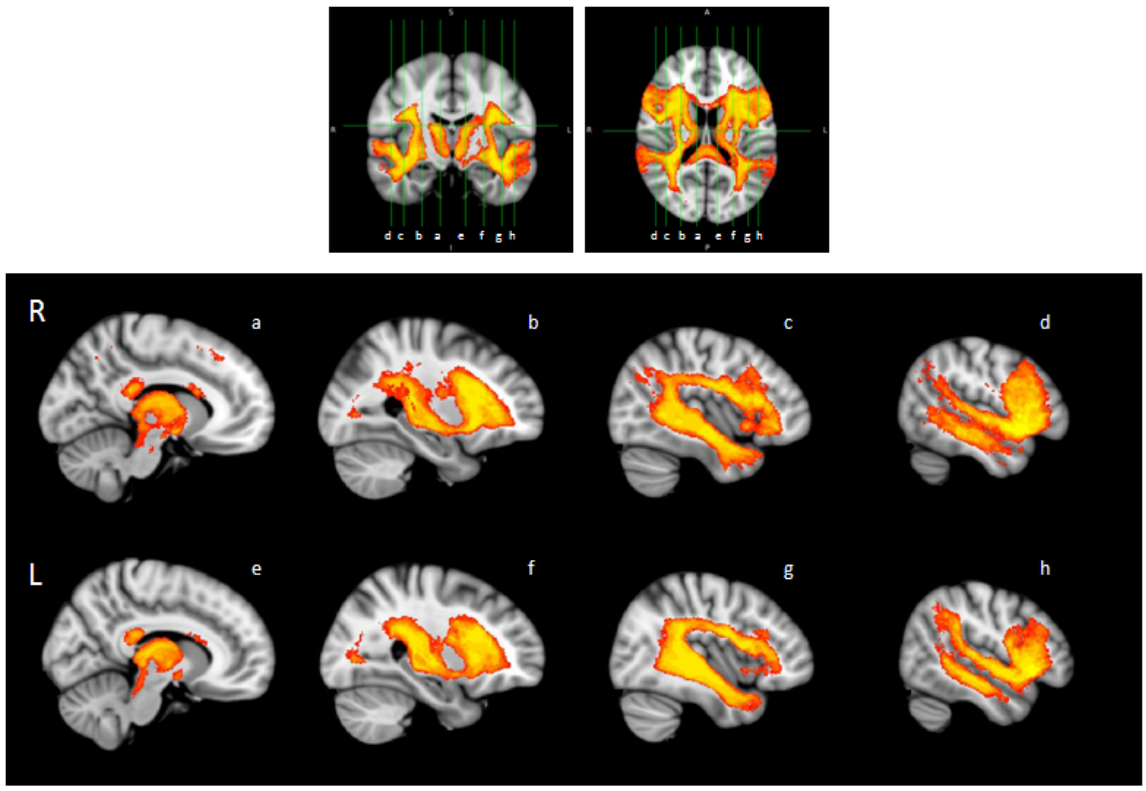


Figure 2.1-9 (continued). Additional views of connections between superior temporal sulcus and frontal mirror region.

B. *In vivo* chimpanzees

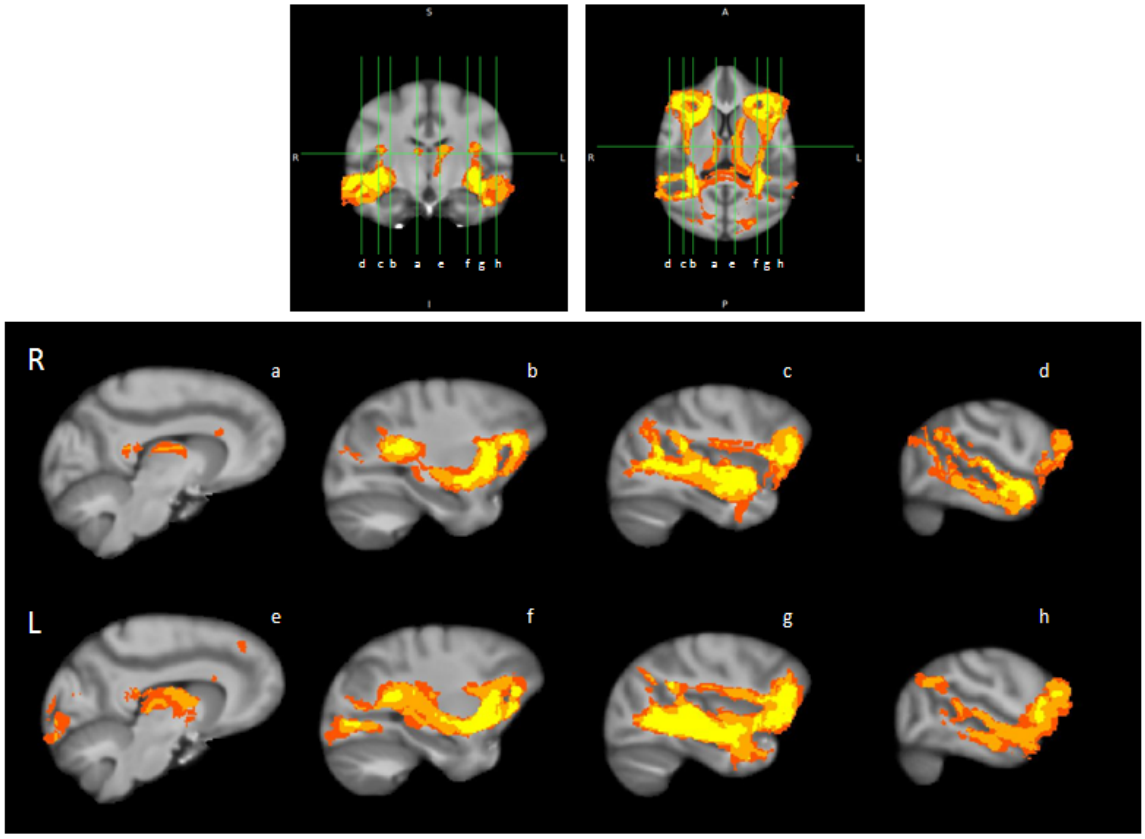


Figure 2.1-9 (continued). Additional views of connections between superior temporal sulcus and frontal mirror region.

C. *In vivo* macaques

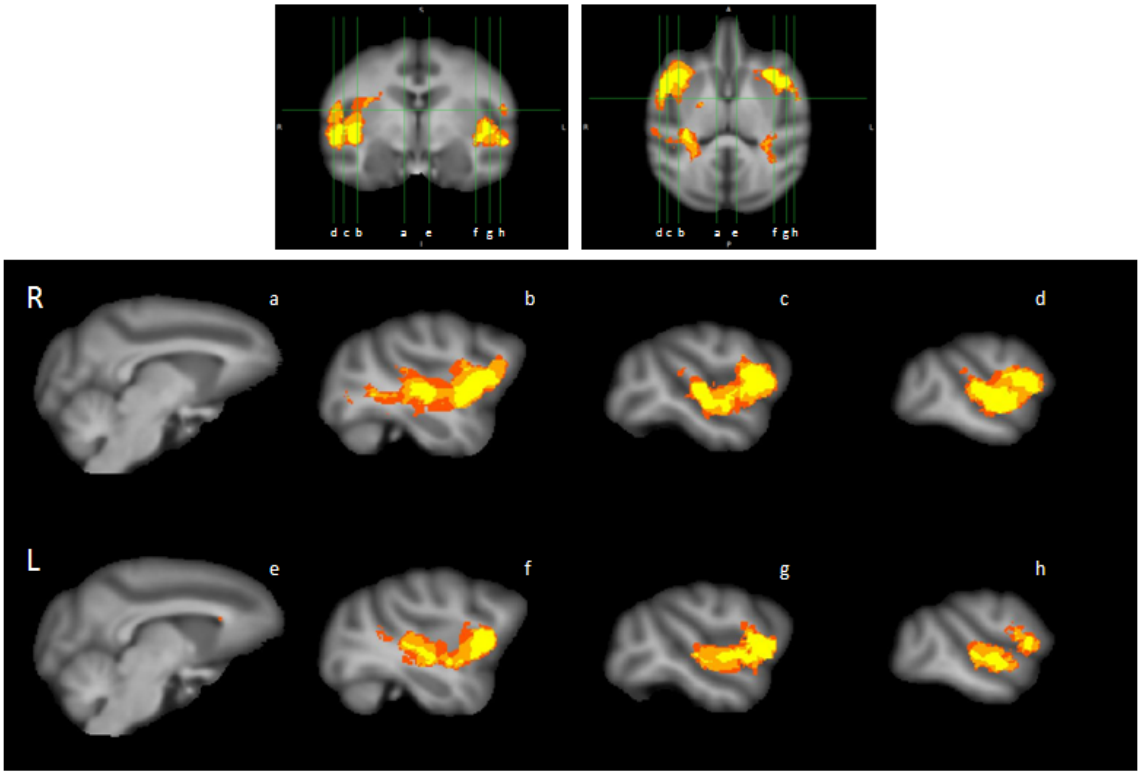
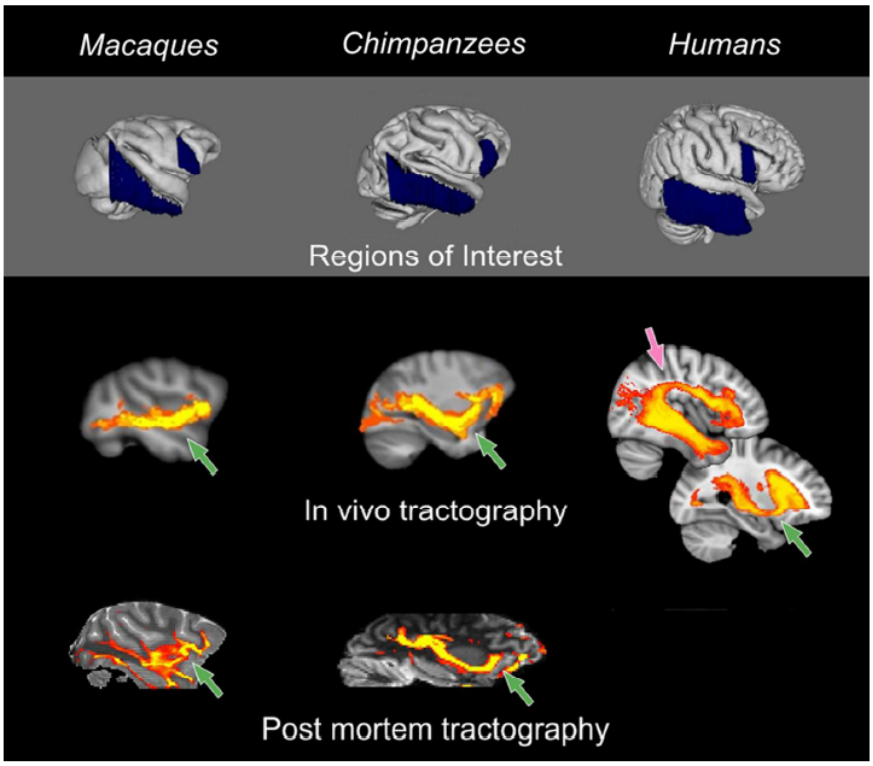


Figure 2.1-10. Overview of connections between inferior temporal cortex and frontal mirror region.



Probabilistic tractography between macaque F5 and inferior temporal cortex ROI (inferior temporal and fusiform gyri); chimpanzee BA44 and inferior temporal ROI (middle, inferior, and fusiform gyri); and human BA44 and inferior temporal ROI (middle, inferior, and fusiform gyri). In all three species, connections between these regions follow the extreme/external capsules and pass through more anterior regions of prefrontal cortex en route to the frontal mirror region (green arrows). In humans, a second, dorsal pathway is detected, which travels through the inferior/middle longitudinal fasciculi through inferior parietal cortex to the third branch of the superior longitudinal fasciculus (pink arrow). Connections through the arcuate fasciculus (not shown here) were also detected, but this tract travels beneath the white matter of parietal cortex and does not reach parietal gray matter.

Figure 2.1-11. Additional views of connections between inferior temporal cortex and frontal mirror region.

A. *In vivo* humans

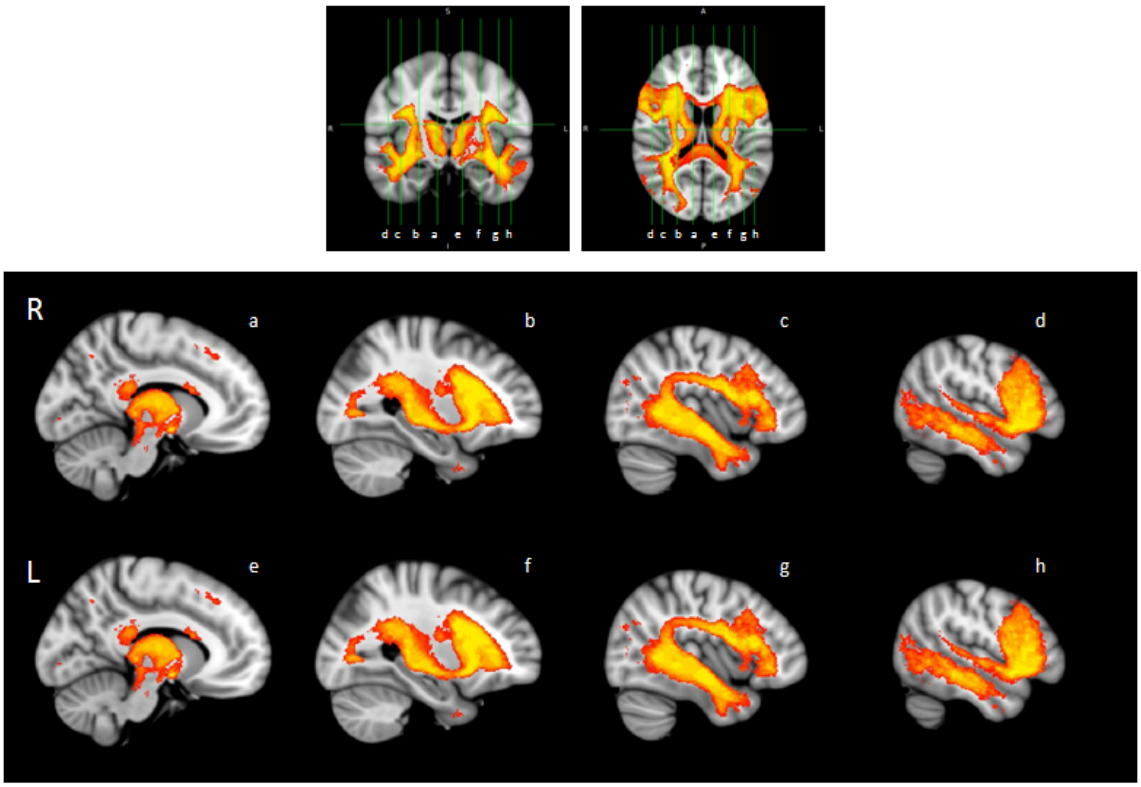


Figure 2.1-11 (continued). Additional views of connections between inferior temporal cortex and frontal mirror region.

B. *In vivo* chimpanzees

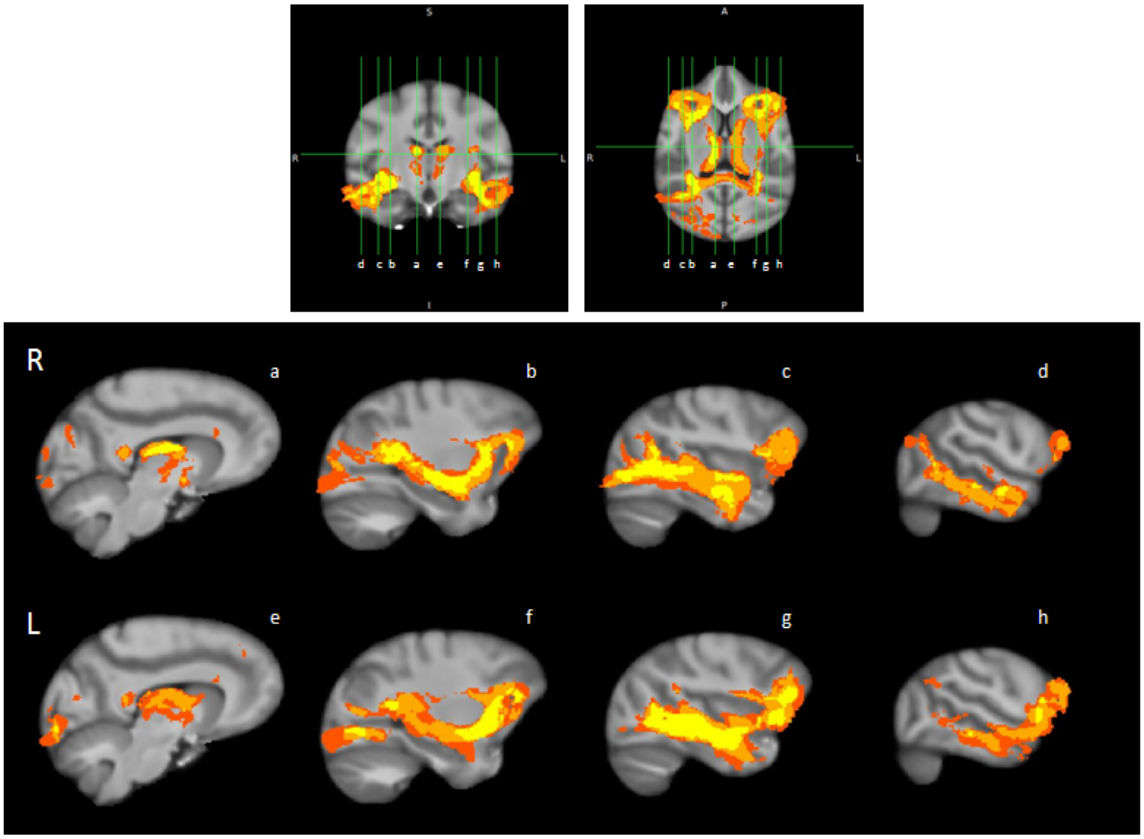


Figure 2.1-11 (continued). Additional views of connections between inferior temporal cortex and frontal mirror region.

C. *In vivo* macaques

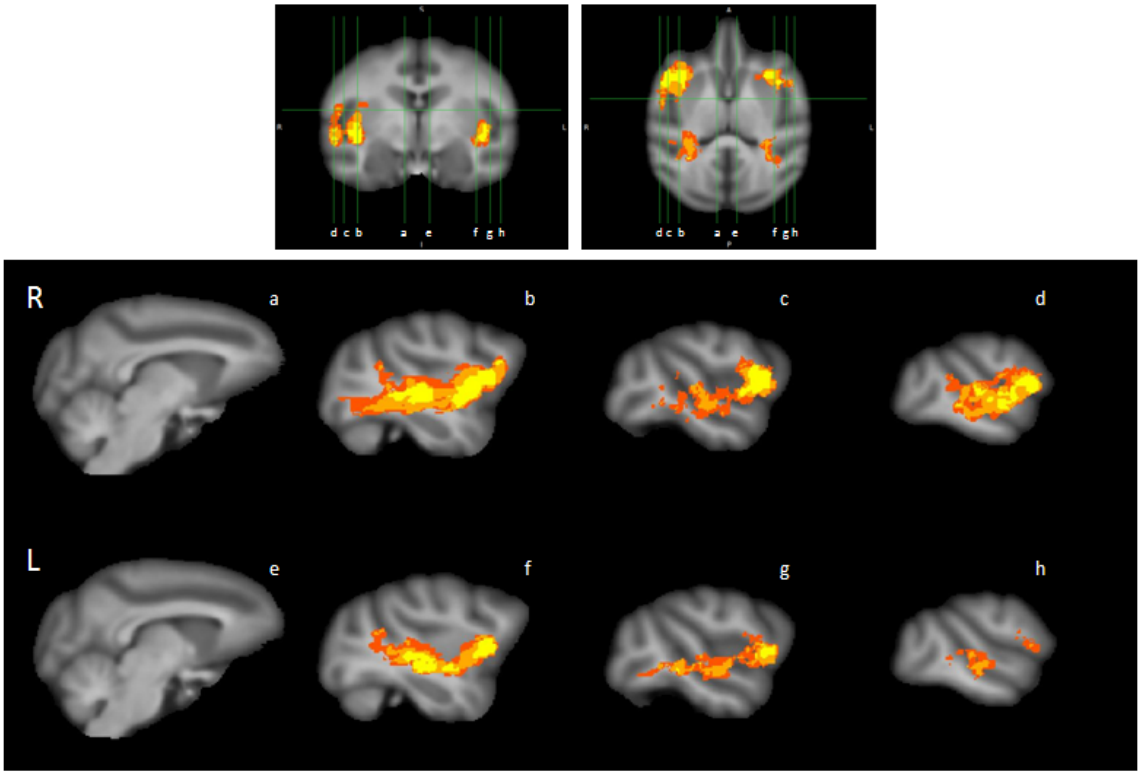
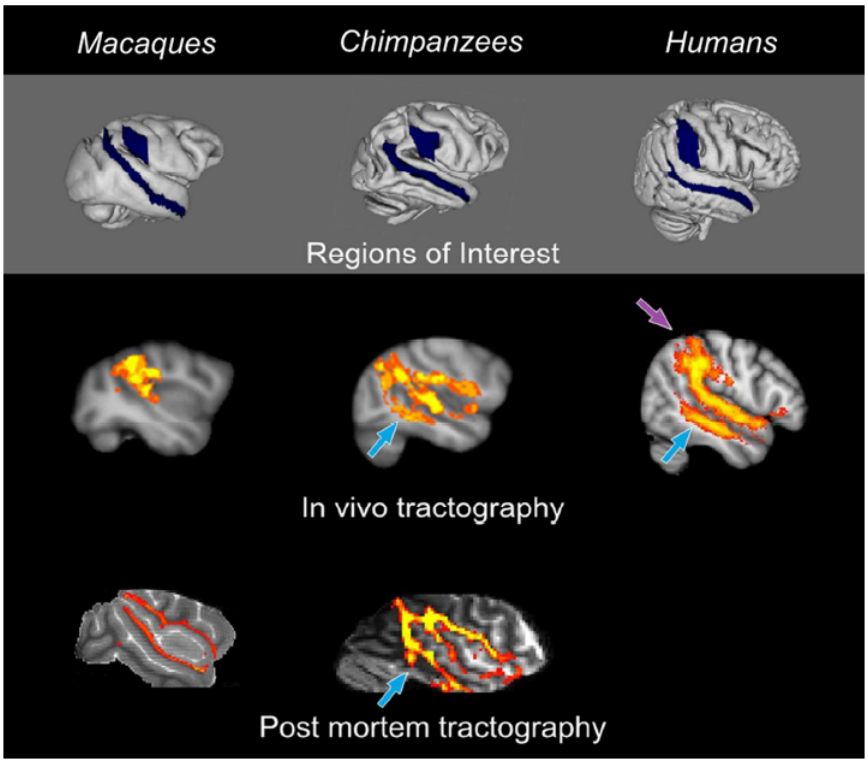


Figure 2.1-12. Overview of connections between superior temporal sulcus and parietal mirror region.



Probabilistic tractography between macaque PF and superior temporal sulcus; chimpanzee PF and superior temporal sulcus; and human BA40 and superior temporal sulcus. In all three species, these connections follow the middle longitudinal fasciculus, but these connections extend further in chimpanzees than macaques, and furthest in humans. Connections with inferior temporal cortex via the inferior/middle longitudinal fasciculi are also apparent in chimpanzees and humans, and are more robust in humans (blue arrows). These connections also included a projection to superior parietal cortex in humans (purple arrow).

Figure 2.1-13. Additional views of connections between superior temporal sulcus and parietal mirror region.

A. *In vivo* humans

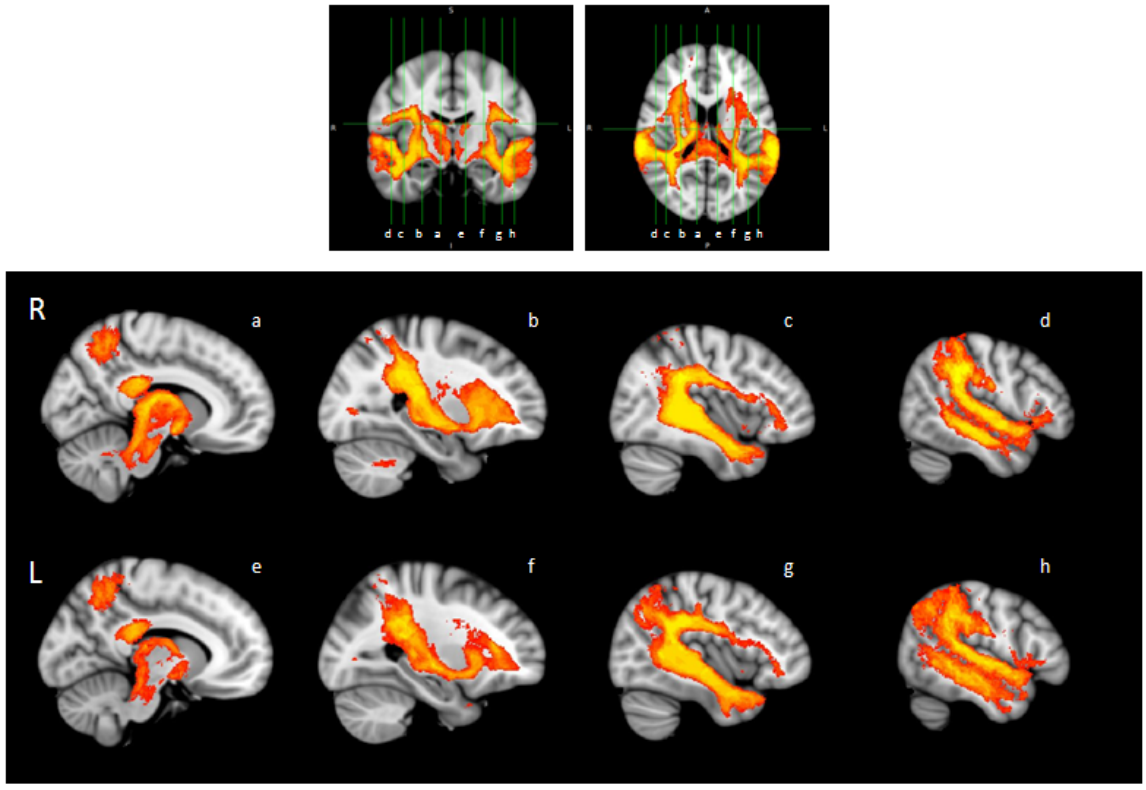


Figure 2.1-13 (continued). Additional views of connections between superior temporal sulcus and parietal mirror region.

B. *In vivo* chimpanzees

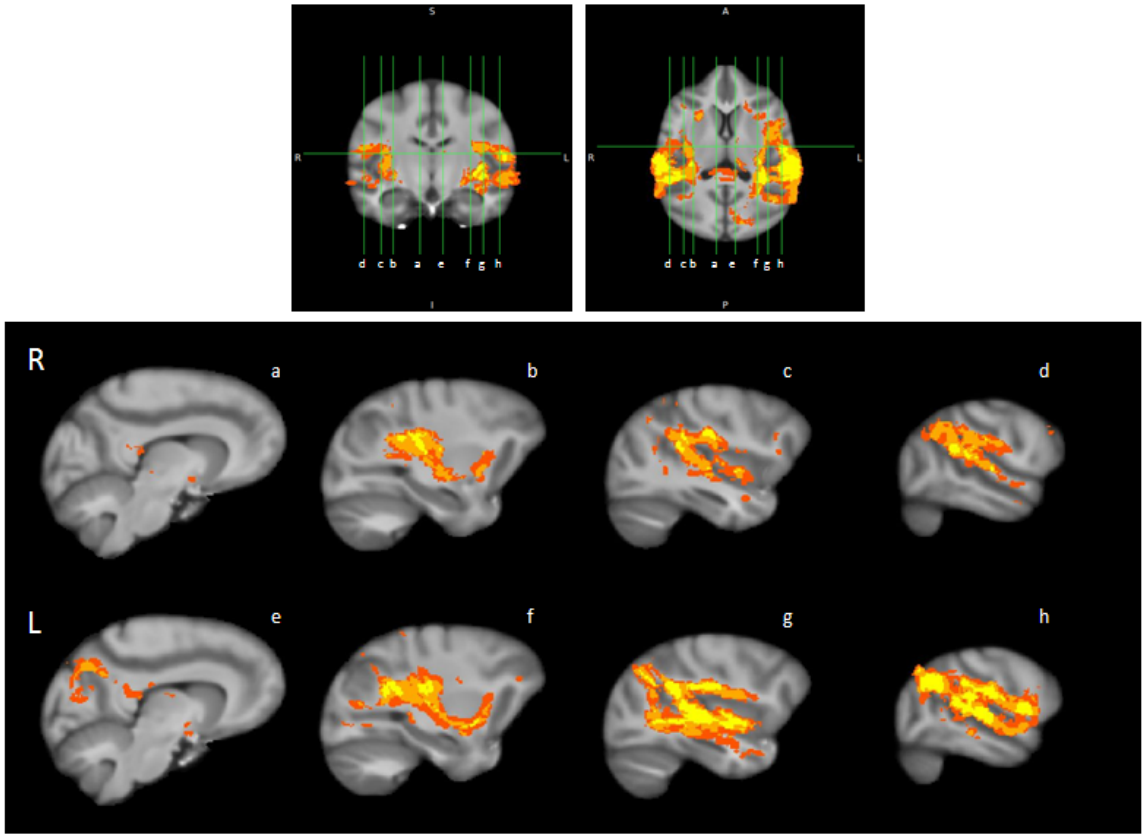


Figure 2.1-13 (continued). Additional views of connections between superior temporal sulcus and parietal mirror region.

C. *In vivo* macaques

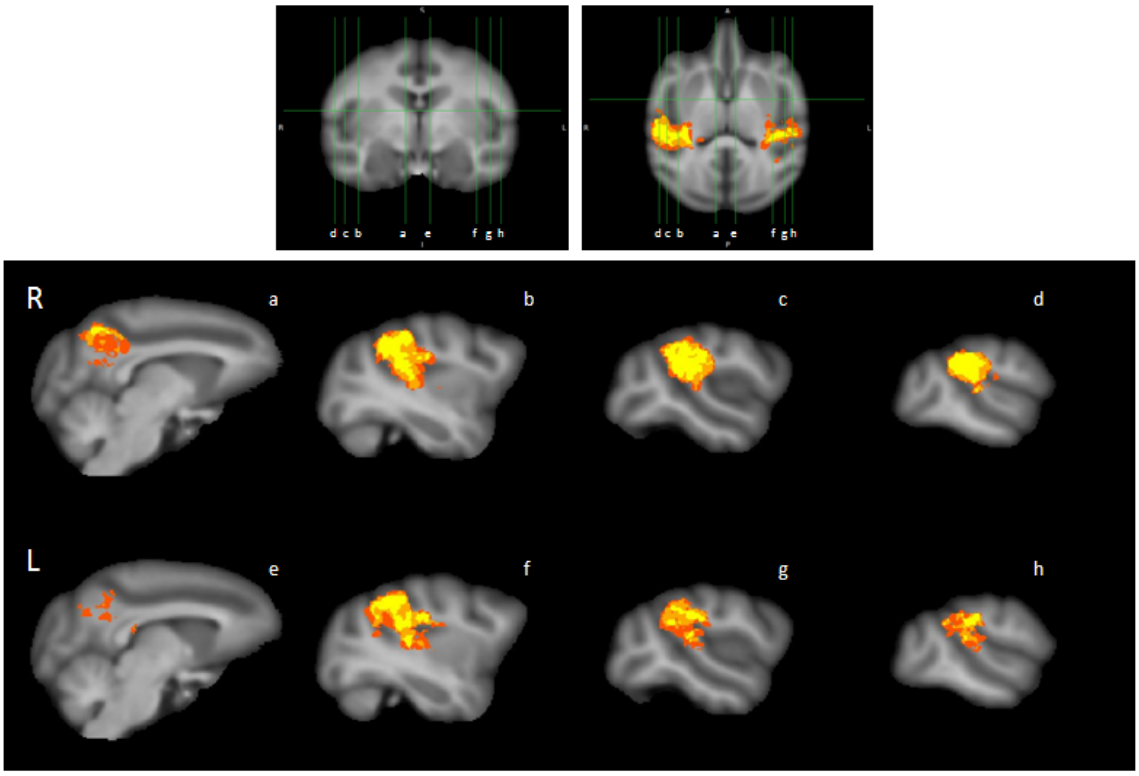
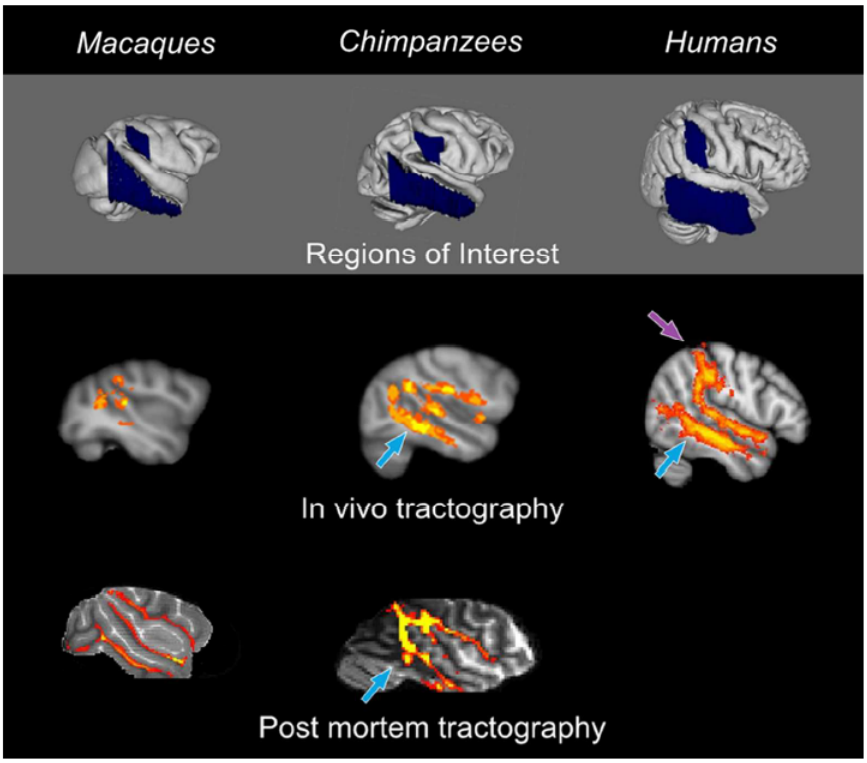


Figure 2.1-14. Overview of connections between inferior temporal cortex and parietal mirror region.



Probabilistic tractography between macaque PF and inferior temporal ROI (inferior and fusiform gyri); chimpanzee PF and inferior temporal ROI (middle, inferior, and fusiform gyri); and human BA40 and inferior temporal ROI (middle, inferior, and fusiform gyri). These connections travel through the inferior/middle longitudinal fasciculi in all three species. They are quite weak in macaques, robust in chimpanzees, and most robust in humans (blue arrows). In humans, a connection with superior parietal cortex is also apparent (purple arrow).

Figure 2.1-15. Additional views of connections between inferior temporal cortex and parietal mirror region.

A. *In vivo* humans

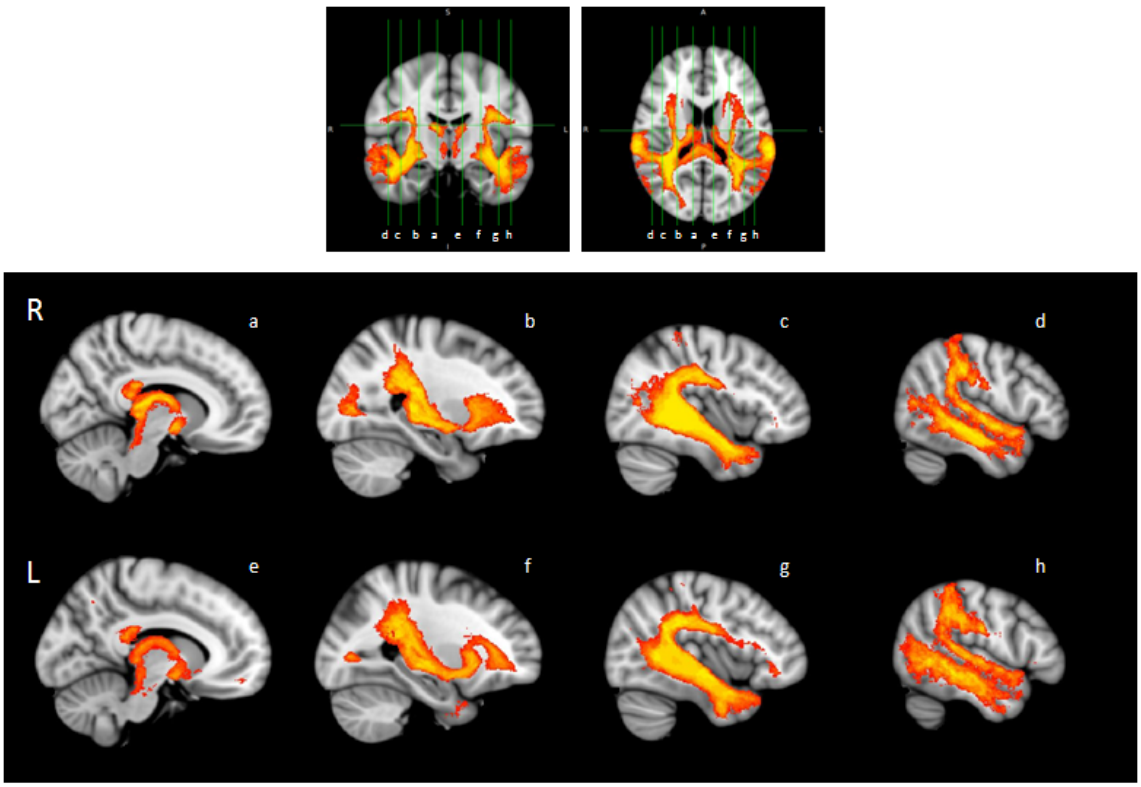


Figure 2.1-15 (continued). Additional views of connections between inferior temporal cortex and parietal mirror region.

B. *In vivo* chimpanzees

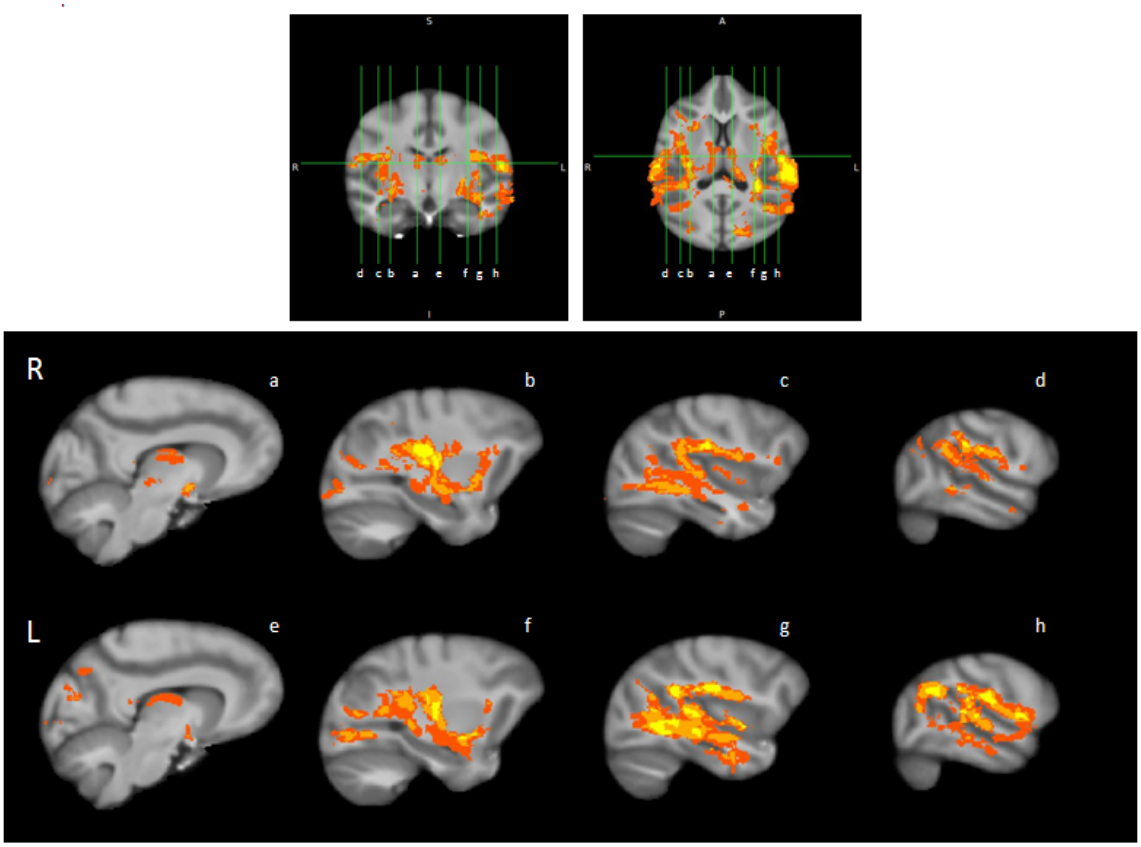


Figure 2.1-15 (continued). Additional views of connections between inferior temporal cortex and parietal mirror region.

C. *In vivo* macaques

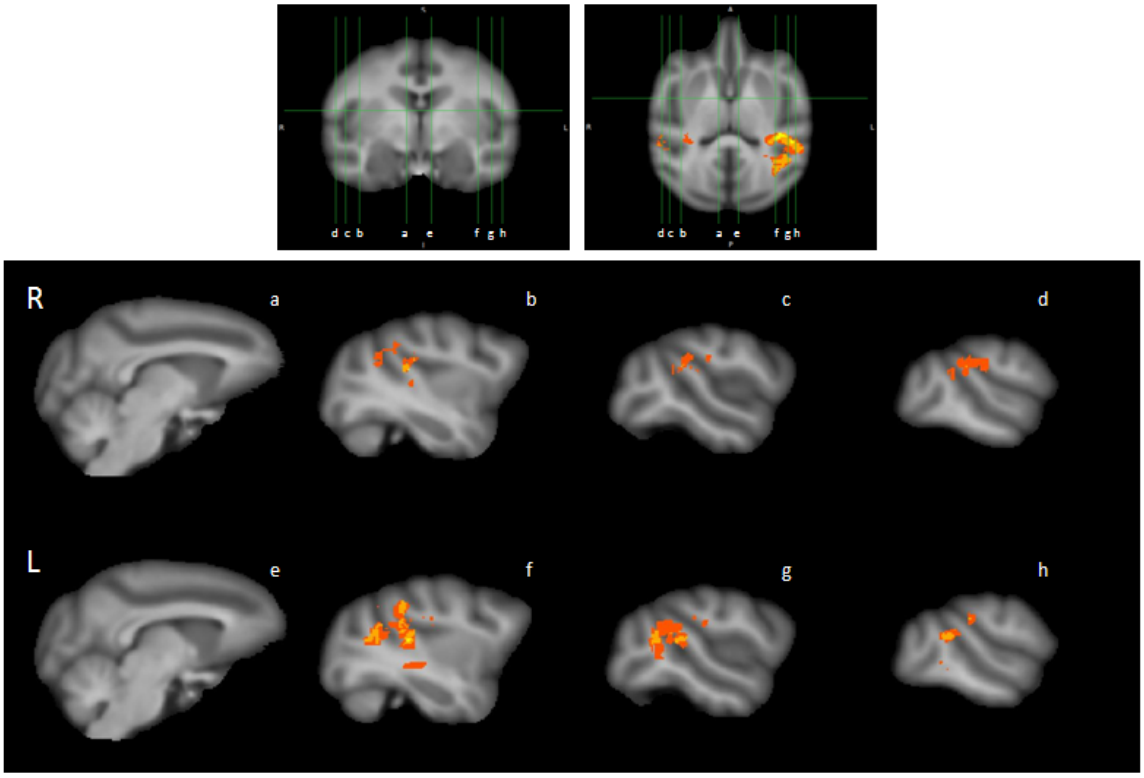
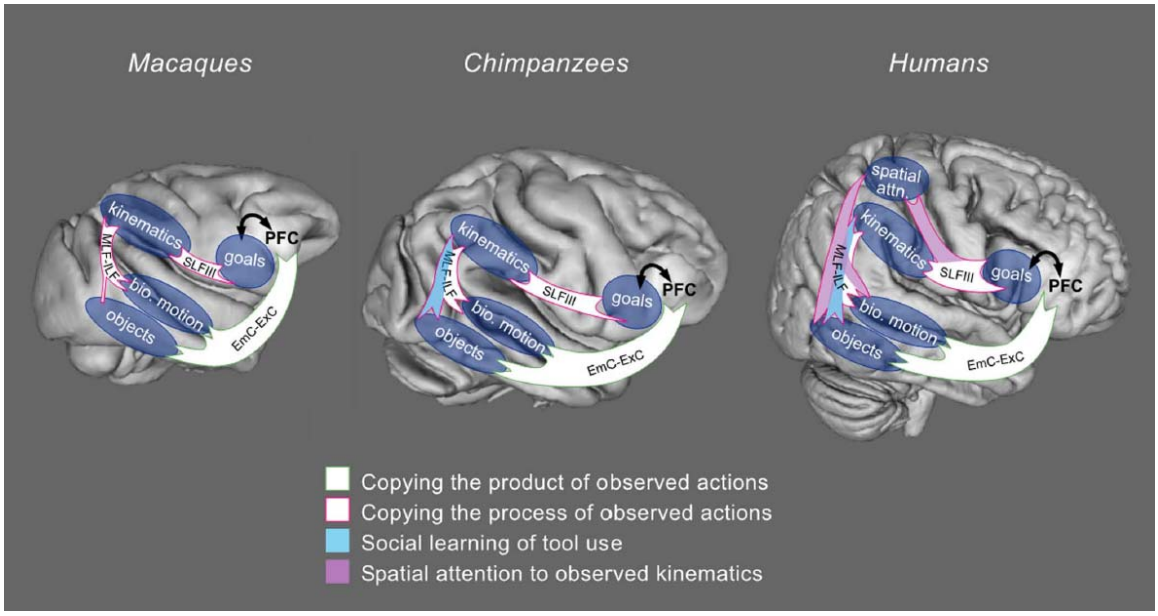


Figure 2.1-16. Product versus product in social learning: A model linking species differences in mirror system circuitry, mirror system functional responses, and social learning behavior.



In macaques and chimpanzees, temporal-frontal connections via the extreme/external capsules (green outlines) outweigh temporal-parietal and parietal-frontal connections via the inferior /middle longitudinal fasciculi and the third branch of the superior longitudinal fasciculus (pink outlines). This produces a circuit configured to mirror the product or goals of observed actions, rather than the process or kinematics. In humans, temporal-parietal and parietal-frontal connections (pink outlines) are more equally balanced with temporal-frontal connections (green outlines), producing a circuit that is better configured to mirror the process or kinematics of observed actions. Thus, the ratio of green-outlined to pink-outlined connections could support species' biases towards emulation versus imitation. Additionally, chimpanzees and humans but not macaques

have a substantial connection between the parietal mirror region and object- and tool recognition regions in middle and inferior temporal cortex; this adaptation may underlie the social learning of tool use. Finally, in humans alone, the mirror system includes a projection to superior parietal cortex, an adaptation that may support spatial attention to the kinematics of others' actions, particularly during tool use. MLF-ILF: Middle longitudinal fasciulus and inferior longitudinal fasciculus. EmC-ExC: Extreme capsule and external capsule. SLFIII: Third branch of the superior longitudinal fasciculus. PFC: Prefrontal regions anterior to the frontal mirror region, which are connected to temporal regions via EmC–ExC, and to the frontal region via cortical U-fibers (black arrows).

Chapter 3:

Activation

3.1. Characterization of chimpanzee regional cerebral glucose metabolism during the perception and execution of object-directed and non-object-directed grasping actions[9]

3.1.1. Summary

This chapter tests Hypothesis 2(a):

- ➔ Species differences in social learning are related to species differences in the neural response to observed action.
  - o Part A: The aspects of an observed action that are "mirrored" determine which aspects can be behaviorally copied. If this is true, whether or not a species is capable of copying action movements apart from results should align with whether or not its mirror system responds to actions which consist of movement without results.

This hypothesis was tested using FDG-PET, which is a functional neuroimaging method that measures regional cerebral glucose metabolism. This is the only functional neuroimaging method currently available to image the chimpanzee brain during awake behavior. We measured chimpanzee activations during action execution, transitive action observation, and intransitive action observation, and looked for overlaps between

[9] *Section 3.1 is reproduced with minor edits from Hecht, E. E., L. E. Murphy, D. A. Gutman, T. M. Preuss and L. A. Parr (Under revision). "Functional neuroimaging of the chimpanzee mirror system reveals human specializations for social learning." J Neurosci.*

execution and either observation condition. We compared this with published macaque and human findings. This yielded 3 main results:

1) Performance and observation of the same action activated a distributed fronto-parietal network similar to that reported in macaques and humans.

2) Like humans and unlike macaques, these regions were also activated by observing movements without results (intransitive actions).

3) However, unlike humans, parietal activation appeared to be relatively weak.

We discuss the potential relevance of these results for species differences in social learning.

3.1.2. Materials and methods

Subjects

Subjects were 4 chimpanzees housed at the Yerkes National Primate Research Center, 2 male and 2 female, ages 18-24. All had previous experience working on cognitive behavioral tasks.

Training for behavioral tasks

Subjects were trained on the behavioral tasks (**Figure 3-1**) using behavioral chaining. A subject was considered to be fully trained when he or she could perform the task for 30

minutes continuously, with less than 3 minutes of non-task-related behavior. Thus, by the time scans were acquired, subjects were very well practiced at the tasks. Both chimpanzee subjects and human demonstrators performed all actions with the right hand.

Behavioral uptake period for FDG-PET scanning

FDG-PET uses fluorodeoxyglucose, a glucose analog radiolabelled with ^{18}F. FDG is taken up by cells in the same manner as glucose but becomes temporarily trapped inside the cell; photons that result from decay are detected by the scanner, and metabolism then completes normally (Reivich, Kuhl et al. 1979). Subjects drank a 15 mCi dose of FDG mixed in sugar-free KoolAid™, then carried out the behavioral task for each condition, and then were anesthetized and scanned. Thus in scan images, brighter regions indicate areas of increased metabolism during the task. This method was developed at the Yerkes National Primate Research Center and is the only methodology available for functional neuroimaging in awake, behaving chimpanzees (e.g., (Rilling, Barks et al. 2007, Taglialatela, Russell et al. 2008, Parr, Hecht et al. 2009, Taglialatela, Russell et al. 2011)). FDG gray matter absorption rises slowly for about 10 minutes post-dosage and then rises sharply (Parr, Hecht et al. 2009). The behavioral training period described above revealed that it was difficult for our tasks to hold the chimpanzees' attention for sustained periods and we wanted to ensure maximally focused behavior during the period of greatest FDG uptake. Therefore, in the 10 minutes following dosage, subjects rested quietly in their cage. During this period, behavior was videotaped and monitored remotely via live feed to ensure that no actions took place that could confound image interpretation. Humans, other chimpanzees, and manipulatable objects were all removed from the subject's vicinity. Ten minutes post-dosage, the behavioral task

began.

Behavioral tasks are illustrated in **Figure 3-1**: performance of an object-directed reach-to-grasp motor task (action execution), observation of the experimenter performing this same task (transitive observation), and observation of the experimenter miming this task without grasping any object (intransitive observation condition). In the intransitive observation condition, a ball was moved into and out of the testing box along a string. The chimpanzee was unable to see the experimenter's hand moving the string, and no hand touched the ball within the chimpanzee's sight. This control was included in order to ensure that any differences in brain activation between the transitive and intransitive action observation conditions would not be due to the presence of a moving object in the transitive but not intransitive condition. All actions were carried out with the right hand. For the observation conditions, there was no "task" other than to sit quietly and pay attention to the experimenters. Scans of the same subjects resting quietly in their enclosures were also available and have been published previously; see Figure 2 in (Rilling, Barks et al. 2007). Subjects were offered small sips of sugar-free KoolAid™ when necessary to maintain motivation at the task. No subject received more than about 150 ml and the experimenter's hand motions when lifting the bottle were hidden.

Because each FDG-PET scan averages brain activity over the entire 45-minute uptake period, the homogeneity of the subject's behavior during that period is crucial for linking brain activation to the task. While the chimpanzees' behavior was unconstrained, we were able to ensure behavioral homogeneity across conditions by only scanning subjects when their behavior conformed to pre-defined criteria. If the total time of non-task-related hand or mouth activity exceeded predefined thresholds, the scan was cancelled and re-attempted at a later date. Between 1-5 scans were aborted for every one

successfully obtained. The thresholds for cancellation were: more than 3 minutes performing mouth movements or reaching/grasping actions with the hand or arm; more than 3 minutes in any other activity not involving the hands, arms, or mouth; more than 10 minutes being inactive but not engaged in the task. **Table 3-2** shows the amount and type of non-task-related activity for each subject in each condition; the average time was 2:32 (5.62% of total uptake time).

Image acquisition

45 minutes post-dosage, subjects were sedated with Telazol (4-5 mg/kg, i.m.) and anesthetized with propofol (10 mg/kg/hr). They were then transported to the Wesley Woods Imaging Center at Emory University, where they were scanned in a Siemens high resolution research tomograph using previously described procedures (Rilling, Barks et al. 2007, Parr, Hecht et al. 2009). PET image resolution was 1.22 mm isotropic. Prior to the current FDG-PET study, subjects had also undergone structural T1-weighted MRI scans in a 3T Siemens Trio scanner as described previously (Rilling, Barks et al. 2007, Parr, Hecht et al. 2009). MRI resolution was 0.63 x 0.63 x 0.60 mm.

Image analysis

PET images were coregistered to and masked with skull-stripped MRI images, so that only voxels relating to the brain would be analyzed. Each image was normalized by dividing it by its own mean voxel value, so that images could be compared across subjects and conditions. Each image was smoothed using a 4-mm kernel. In the group statistical analyses, scans were analyzed using a full factorial model in SPM5 with one factor (condition) with 4 levels (execution, transitive observation, intransitive

observation, rest). We used a statistical threshold of $p < .05$. No voxels survived the analysis when correcting for multiple comparisons (using SPM5's algorithm for family-wise error), so results are reported without correction for multiple comparisons. In the within-subjects analyses, each image was thresholded to include only the top 1% of the robust mean of the histogram of voxel values in that condition. This threshold was chosen in the interest of providing a relatively conservative map of the wider distributed network involved in the tasks (e.g., (Rilling, Barks et al. 2007) used 5%). As with any neuroimaging study, the lack of "activated" voxels in a particular region in our results does not necessarily mean a region was not involved in the task, just that it was not involved in the task to a degree that surpassed this threshold. We calculated the number of activated voxels in each ROI, in each condition, in each subject. 3D images of brain activations were created using MRIcron with an 8mm search depth. PET activations were overlaid on our nonlinearly-averaged, 36-subject chimpanzee brain template (Li, Preuss et al. 2010) for the group analyses, and on each subject's own T1 MRI scan for the within-subjects analyses.

ROI definition

Regions of interest were drawn by hand in each subject's T1 MRI image (**Figure 3-3**). Macaque F5 and human Brodman area 44 are homologous to chimpanzee FCBm, which occupies the pars opercularis of the inferior frontal gyrus (Bailey, Bonin et al. 1950). Macaque areas PF/PFG and human Brodman area 40 are homologous to chimpanzee areas PFD/PF, which occupy the anterior part of the supramarginal gyrus in inferior parietal cortex (Bailey, Bonin et al. 1950).

3.1.3. Results

Group-level analyses

Initial whole-brain group-level comparisons between the experimental conditions and rest revealed that the major difference between these conditions occurred in cerebellum and brainstem (**Figure 3.1-4**). Therefore, for further group-level statistical analyses, we masked the cerebellum and brainstem in order to more directly investigate activation differences in the cerebrum.

Results obtained using this approach to compare the experimental conditions against rest are rendered on the 3D chimpanzee template brain in **Figure 3.1-5**; coronal slices are shown in **Figure 3.1-6**. The contrast between action observation and rest revealed left-lateralized clusters of activation in primary motor cortex (in the vicinity of the hand and arm representations), ventral premotor cortex, inferior frontal gyrus, inferior parietal cortex, and lateral temporal cortex. Similar regions were significantly more active in the transitive observation > rest contrast, although primary motor and inferior parietal activation appears to be less extensive.

The cerebrum-only contrasts for transitive observation > execution and intransitive observation > execution produced clusters in lateral temporal cortex, especially on the right side (3D renderings, **Figure 3.1-7**; coronal slices, **Figure 3.1-8**). This contrast also produced clusters in anterior inferior frontal gyrus, probably area FCBm (homologous to BA 44), as well as scattered small clusters in dorsal premotor and dorsolateral prefrontal cortex, probably including the frontal eye fields (area FDΓ).

The cerebrum-only contrasts for execution > transitive observation and execution > intransitive observation produced clusters in inferior parietal cortex (3D renderings,

Figure 3.1-9; coronal slices, **Figure 3.1-10**. Small clusters also occurred around the border of the precentral gyrus (area FBA, homologous to BA 6) and pars opercularis of the inferior frontal gyrus (area FCBm, homologous to BA 44).

The cerebrum-only contrast for transitive observation > intransitive observation produced clusters at the border between the left precentral and inferior frontal gyri, left inferior parietal cortex, left dorsal premotor cortex, right dorsal premotor or primary motor cortex, right orbitofrontal cortex, and bilateral lateral temporal cortex (3D renderings, **Figure 3.1-11**; coronal slices, **Figure 3.1-12**). The opposite contrast, intransitive observation > transitive observation, produced small clusters at the border of the left precentral and inferior frontal gyri (located more ventrally than the transitive > intransitive cluster), left anterior superior temporal sulcus and middle temporal gyrus, and right inferior parietal cortex.

Individual subject-level analyses

Figure 3.1-13 shows the top 1% of activity in each subject's scan in each condition. All action conditions activated similar fronto-parietal regions, including central sulcus, pre- and post-central gyri, dorsal and ventral premotor cortex, ventrolateral prefrontal cortex, dorsolateral prefrontal cortex (probably including the frontal eye fields), and inferior and superior parietal cortex. Individual subjects' activations are overlaid in a group composite map (3D renderings, **Figure 3.1-14**; coronal slices, **Figure 3.1-15**), which shows the number of subjects with above-threshold activation at a given voxel in each condition. Notably, the transitive and intransitive observation conditions activated visibly similar regions, both at the individual subjects level and at the group level (**Figures 3.1-13 – 3.1-15**).

In order to identify brain regions that mapped observed actions onto the same substrates used to perform them, we performed a conjunction analysis, selecting voxels that were active in *both* the execution and transitive or intransitive observation conditions. **Figure 3.1-16** shows these overlaps in individual subjects; **Figure 3.1-17** shows 3D renderings of a group composite map; **Figure 3.1-18** shows coronal slices of this group composite map. Regions of overlap between execution and transitive action observation included central sulcus, pre- and post-central gyri, dorsal and ventral premotor cortex, ventrolateral prefrontal cortex, dorsolateral prefrontal cortex, and inferior and superior parietal cortex. Regions of overlap between execution and intransitive action observation are visibly very similar, both at the individual subjects level and at the group level (**Figures 3.1-16 – 3.1-18**).

Finally, we compared the ratio of the frontal and parietal ROI's volumes that contained above-threshold activation (**Figure 3.1-19**). Activity in both the frontal and parietal regions of interest was significantly greater in each of the experimental conditions than in the rest condition (**Figure 3.1-19A**). Again, activity in the ROIs was not significantly different between the transitive and intransitive observation conjunction analyses (**Figure 3.1-19B**).

3.1.4. Discussion

This research identified fronto-parietal chimpanzee brain regions that are activated while producing grasping actions, observing grasping actions, and observing hand movements which do not involve objects. Group-level statistical comparisons between each of these conditions and rest highlighted small, focused clusters (**Figures 3.1-5-3.1-12**); conservatively thresholded scans in individual subjects revealed a distributed

network (**Figures 3.1-13-18**). Chimpanzee regions that are more activated by observing than producing grasping actions include portions of superior temporal sulcus, inferotemporal cortex, occipitotemporal cortex, and inferior frontal gyrus (**Figure 3.1-7 – 3.1-8**); regions that are more activated by producing than observing grasping include portions of inferior parietal cortex including anterior intraparietal sulcus and probably the chimpanzee homologue of area AIP, somatosensory cortex, and premotor cortex (**Figures 3.1-9 – 3.1-10**) as well as cerebellum (**Figure 3.1-4**).

As with any neuroimaging study, the lack of "activated" voxels in a particular region in our results does not necessarily mean a region was not involved in the task, just that it was not involved in the task to a degree that surpassed this threshold. Importantly, primary visual cortex activations are not to be expected in the observation > execution or observation > rest contrasts, because subjects were able to freely view their surroundings in all conditions, including the rest condition (they were simply unable to observe any grasping movements, their own or others', in the execution condition).

All actions were carried out with the right hand (most chimpanzees are right-handed (Hopkins, Taglialatela et al. 2010)). This would be expected to cause greater left hemisphere activations during the execution condition. The effect of handedness on action observation is unclear. Some human studies have suggested that the human action observation network is left-lateralized (Hamzei, Rijntjes et al. 2003, Fecteau, Lassonde et al. 2005), while others suggest that it is bilateral (Cochin, Barthelemy et al. 1999, Aziz-Zadeh, Koski et al. 2006). Future chimpanzee studies with larger sample sizes could investigate whether chimpanzee action observation activations are lateralized – a particularly interesting topic given that the mirror system has been postulated to be a precursor to language systems (Rizzolatti and Arbib 1998, Arbib, Billard et al. 2000, Arbib 2005, Arbib, Liebal et al. 2008).

The findings of this study highlight two points which may be relevant to the evolution of action understanding, social learning, and culture. First, in chimpanzees, brain activations for observing transitive actions are very similar to activations for observing intransitive actions, both at the group level (**Figures 3.1-5 – 3.1-6**) and at the individual subjects level (**Figures 3.1-13 – 3.1-15**). There are a few small, constrained portions of chimpanzee fronto-parietal cortex that are activated more by transitive than intransitive observation (**Figures 3.1-11 – 3.1-12**), but the regions of overlap between execution and transitive observation are nearly identical to the regions of overlap between execution and intransitive observation (**Figure 3.1-16 – 3.1-18**). Furthermore, in regions of interest homologous to macaque regions which contain mirror neurons, there is no significant difference in activation for transitive and intransitive observation or in the overlap between execution and transitive or intransitive observation (**Figure 3.1-19**). This suggests that when a chimpanzee observes another individual performing hand movements, these are mapped onto almost the same brain regions that the chimp would use to produce those movements himself – regardless of whether the movements lead to a physical result. This is similar to humans, who also map observed intransitive actions onto one's own motor system with somatotopic specificity (Buccino, Binkofski et al. 2001, Binkofski and Buccino 2006, Filimon, Nelson et al. 2007, Lui, Buccino et al. 2008). It is in notable contrast to macaques, whose mirror neurons do not respond to intransitive actions (Rizzolatti, Fadiga et al. 1996). Macaque mirror neurons only respond to movements in the context of a goal, even if the goal is only implied (Umilta, Kohler et al. 2001). Importantly, though, neuroimaging data on whole-brain responses during transitive and intransitive action observation are needed for a full understanding of how macaque action perception differs from chimpanzees and humans.

Lyons et al. (Lyons, Santos et al. 2006) propose that the macaque brain performs "intentional compression," boiling observed actions down to their environmental results. Our results suggest that the chimpanzee brain does not "compress" observed actions in this way. Chimpanzees map not only the results but also the movements of observed actions to the same brain regions that produce those actions. We propose that this is a correlate of, and a prerequisite to, the ability to copy specific movements. In other words, in order for an individual to copy the specific movements of an action, their brain must be capable of mapping not only the action's results but also its movements onto the same neural circuitry used to produce them. Thus, perhaps macaques emulate results but do not imitate movements because their brains "mirror" interactions between hands and objects, but not manual movements apart from objects. Perhaps chimpanzees are capable of some limited imitation of movements because their brains, like ours, *do* "mirror" movements. This hypothesis could be investigated in other species found to copy not only the results but also the specific movements of observed actions.

This research also highlights a second point that may be relevant to the evolution of social learning. This is a potential difference in chimpanzee and human neural responses to observed action. Chimpanzees had significantly more activity in the frontal ROI than the parietal ROI, both in the individual conditions and in the conjunction analyses (**Figure 3.1-19**). In contrast, human metanalyses of action observation and imitation report more balanced fronto-parietal activations (Molenberghs, Cunnington et al. 2009, Caspers, Zilles et al. 2010, Molenberghs, Cunnington et al. 2012). Notably, these human neuroimaging studies have used fMRI or $H_2{}^{15}O$ PET. In order to verify that humans have significantly more inferior parietal activation than chimpanzees for observed action, similar methodologies are necessary in both species to enable a direct

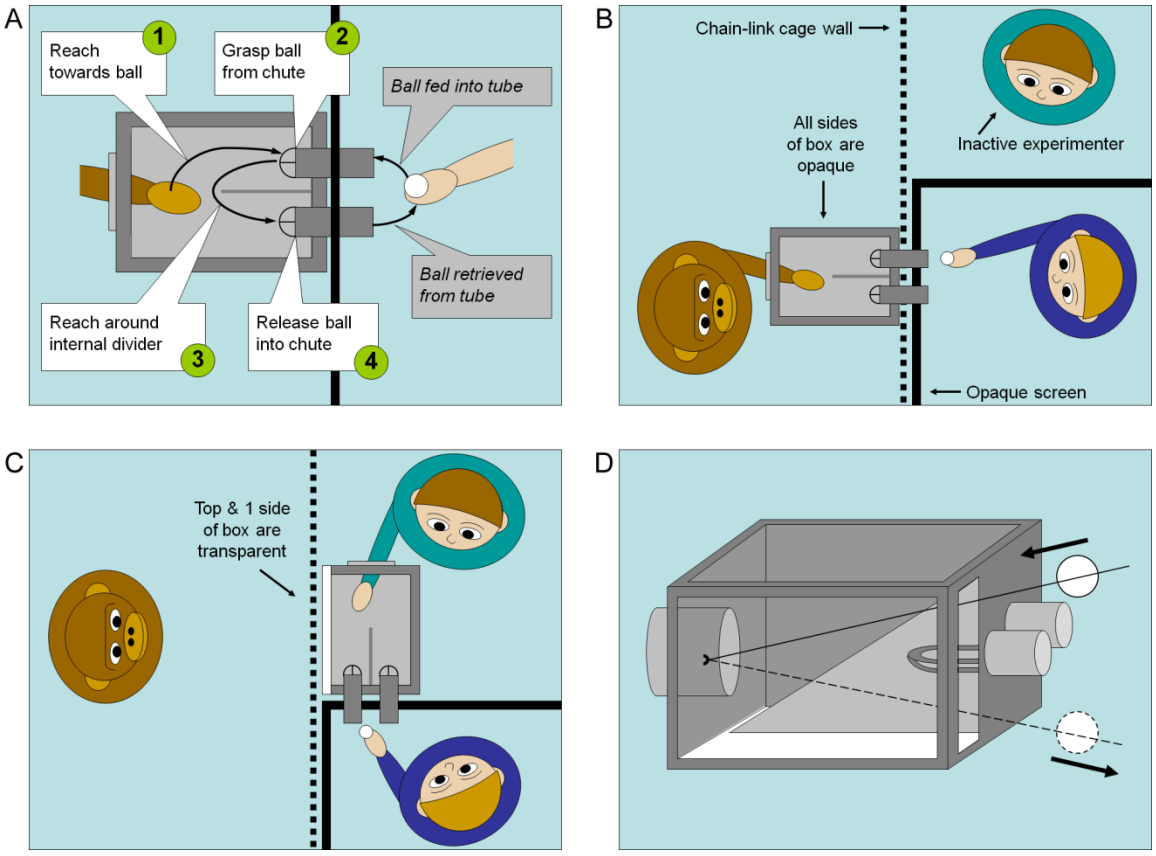
quantitative comparison (see Chapter 3.2). In macaques, transitive action observation has been investigated using 2-deoxyglucose, another method of measuring regional cerebral glucose metabolism during a task. Observing grasping action caused signal increases between 7-19% in macaque F5, and 2-11% in macaque PF/PFG (Raos, Evangeliou et al. 2004, Raos, Evangeliou et al. 2007), which is similar to the pattern we see in chimpanzee inferior frontal and inferior parietal cortex.

The finding that chimpanzee inferior frontal cortex is more responsive to observed action than inferior parietal cortex correlates well with our recent comparison of white matter connectivity in these brain regions (Hecht, Gutman et al. 2012) (Chapter 2). We found greater connectivity in the frontal component of this network in chimps, and in the parietal component in humans. It seems likely that the difference in anatomical structure underlies the difference in functional activation.

We propose the hypothesis that the balance between frontal and parietal components of this network, both in terms of connectivity and activation, is related to the balance between copying results (emulation) and copying movements (imitation). Both chimpanzees and humans are capable of both emulation and imitation, but chimpanzees have a strong bias towards emulation, and humans have a strong bias towards imitation. In macaques, the inferior frontal mirror region (F5) is thought to contain a "vocabulary of motor acts," coding actions on a schematic, conceptual level (Rizzolatti, Camarda et al. 1988, Bonini, Rozzi et al. 2010), while the inferior parietal mirror region (PF/PFG) is thought to incorporate somatotopic, visual, and motor information about action into the body schema in order to spatially and temporally organize the constituent movements of an action (Rozzi, Ferrari et al. 2008, Bonini, Rozzi et al. 2010). Assuming that the chimpanzee and human homologues serve similar purposes, chimps' greater activation

in inferior frontal cortex may reflect greater processing of actions' results or goals; humans' more balanced inferior frontal and inferior parietal activations may reflect relatively more processing of movements or methods. This might explain why although both chimpanzees and humans are capable of imitation, only humans have a proclivity for it that is great enough to lead to cumulative culture.

Figure 3.1-1. Behavioral tasks for functional neuroimaging.



A. Reach-to-grasp action used in tasks. The ball is fed into a downward-slanting chute. The chimpanzee reaches toward and grasps the ball, navigates around the internal divider, and places the ball into another chute, where it rolls back to the experimenter.

B. Action execution condition. The chimpanzee performed the reach-to-grasp action while an experimenter passed the ball through the chutes. This experimenter was hidden behind an opaque screen, but a second, inactive experimenter was visible. This controlled for the presence of a visible human in the observation condition and also allowed the chimpanzee's behavior to be monitored. All sides of the box were opaque, so the chimpanzee could not see his own hand movements.

C. Transitive and intransitive observation conditions. The top and 1 side of the box were replaced with clear Plexiglas. The experimenter performing the actions was visible, but

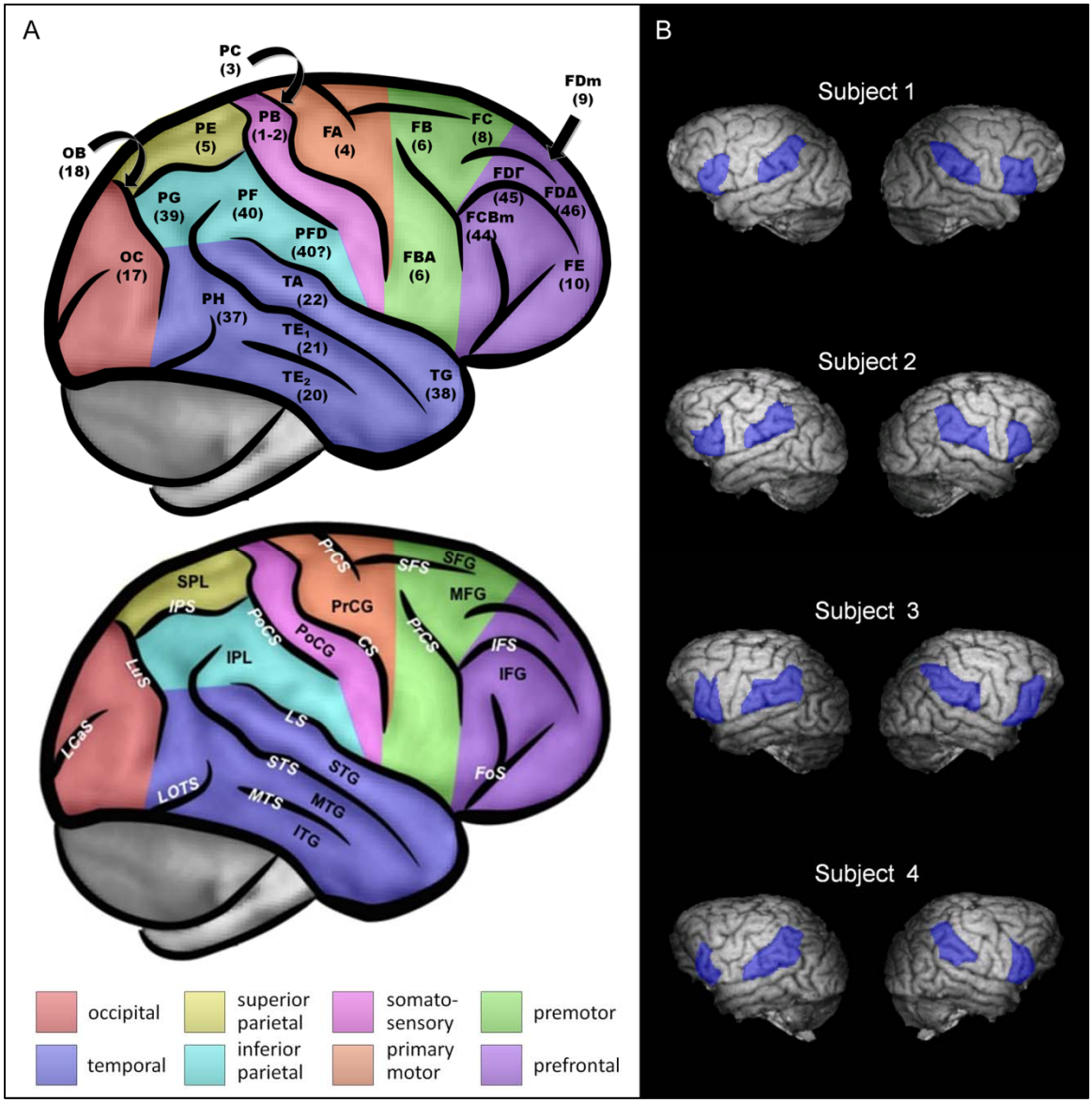
the second experimenter was hidden. In the transitive observation condition, the experimenter performed the actions as in (A). In the intransitive observation condition, the experimenter mimed these same actions without touching any object.

D. Control for the perception of object movement in the intransitive observation condition. The ball was slid in and out of the box along a transparent thread, interspersed with the experimenter's mimed grasping actions. The chimpanzee was unable to see the experimenter's hand moving the thread.

Table 3.1-2. Chimpanzee behavior during FDG uptake periods prior to scans.

Condition	Subject	Time spent in non-task-related activity	Description of non-task-related activity
Action execution	Scott (S1)	3:08	Chew on ball, scratch/groom self, return ball through cage mesh, raspberry, aggression display
	Katrina (S2)	1:59	Chew on ball, bite fingernails, scratch/groom self
	Patrick (S3)	1:20	Swing, climb, move barrel, manipulate cage lock
	Faye (S4)	5:00	Food beg, spit water at experimenters
Transitive observation	Scott (S1)	1:00	Groom self
	Katrina (S2)	2:15	Swing, climb, manipulate own feet, bite fingernails, food beg, aggression display, throw feces at experimenters, scratch/groom self, pat own head, manipulate cage locks
	Patrick (S3)	1:18	Scratch/groom self, aggression display
	Faye (S4)	1:36	Suck thumb, poke finger through cage mesh, scratch/groom self
Intransitive observation	Scott (S1)	3:55	Scratch/groom self, spit water at experimenters
	Katrina (S2)	3:34	Pick up hairs from floor, bite/lick cage mesh, scratch/groom self, climb
	Patrick (S3)	0:37	Climb
	Faye (S4)	4:42	Spit water at experimenters, scratch/groom self, manipulate own feet, gurgle juice, food beg

Figure 3.1-3. Chimpanzee cortical anatomy and regions of interest.



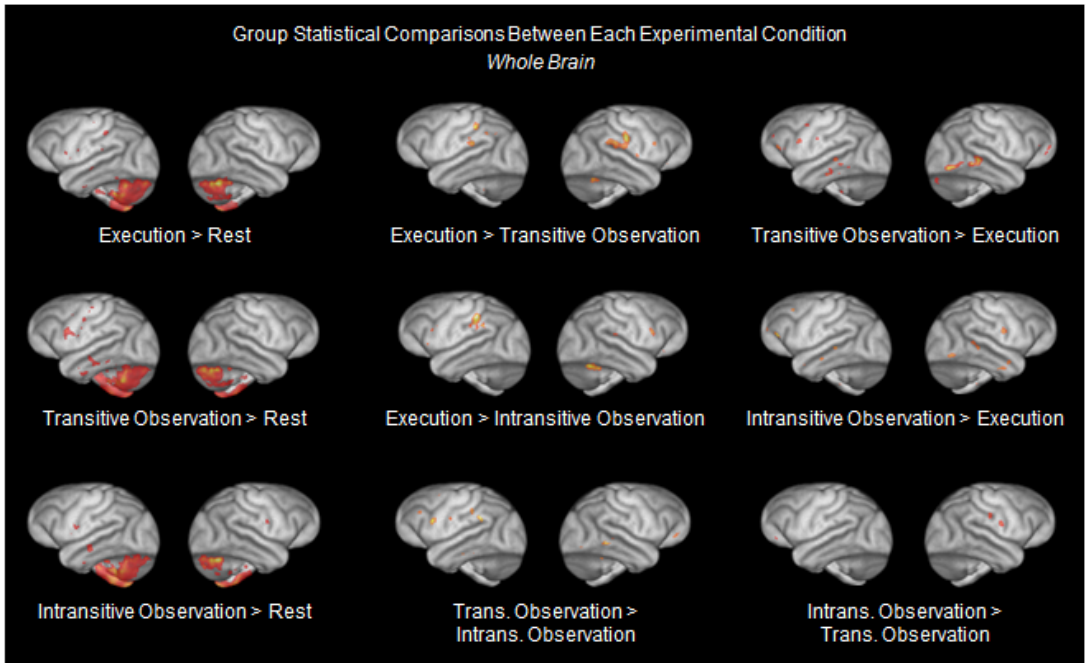
Left hemispheres on left.

A. Chimpanzee cortical anatomy. The location of regions of interest with respect to the surface morphology of cerebral cortex (above) and architectonic areas (below) in chimpanzees. The nomenclature for sulci and gyri is based on Bailey et al. (Bailey, Bonin et al. 1950), although our abbreviations follow more modern conventions. Cortical areas are denoted according to the system of Bailey et al. (Bailey, Bonin et al. 1950) and Bailey (Bailey 1948), based on Economo's system in humans (Economo and Parker 1929). For

most areas, there is a fairly straightforward correspondence between the Bailey et al. areas and their counterparts in Brodmann's human map (Brodmann 1909) (see, e.g., (Bonin 1948), and we have added Brodmann numbers in parentheses below the Bailey et al. symbols. Areas thought to be homologous to Brodmann's areas 44 and 45 of humans, occupy the posterior inferior frontal gyrus and adjacent part of the inferior frontal sulcus in chimpanzees, as discussed by Schenker et al. (Schenker, Hopkins et al. 2010). Abbreviations for gyri and sulci: CS - central sulcus; FOS - fronto-orbital sulcus; IFG - inferior frontal gyrus; IFS - inferior frontal sulcus; IPL - inferior parietal lobule; IPS - intraparietal sulcus; LCaS - lateral calcarine sulcus; LOTS - lateral occipitotemporal sulcus; LS - lateral sulcus; LuS - lunate sulcus; MFG - middle frontal gyrus; MTG - middle temporal gyrus; MTS - middle temporal sulcus; PoCG - postcentral gyrus; PoCS - postcentral sulcus; PrCG - precentral gyrus; PrCS - precentral sulcus; SFG - superior frontal gyrus; SFS - superior frontal sulcus; SPL - superior parietal lobule.

B. Regions of interest drawn in individual subjects' MRI scans in homologues to macaque regions that contain mirror neurons (FCBm and PF/PFD).

Figure 3.1-4. Group statistical comparisons between experimental conditions and rest before masking cerebellum and brainstem.



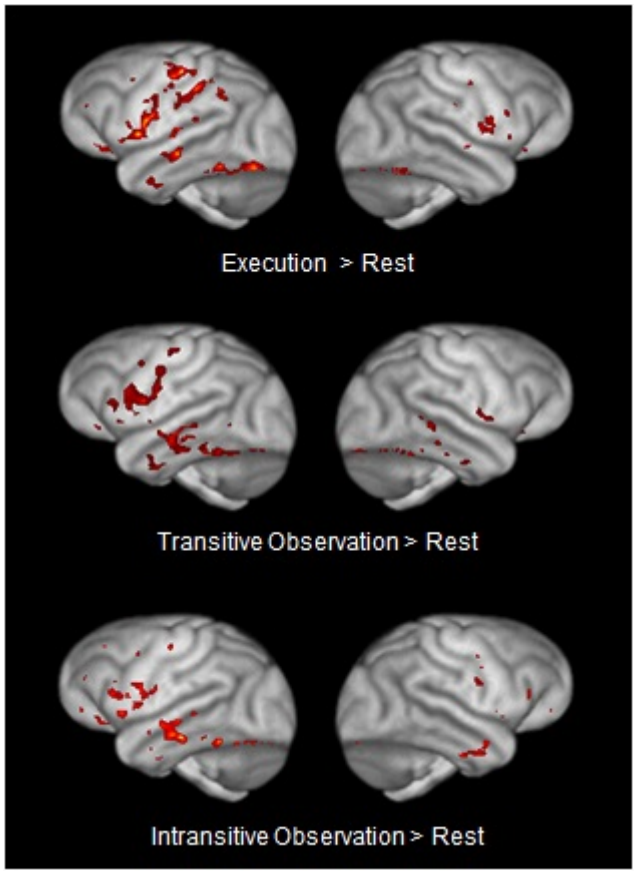
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Comparisons between the experimental conditions and rest: Significant activations for each contrast included broad regions of cerebellum and brainstem as well as small, focused clusters in the left ventral premotor and primary motor cortex in the vicinity of the hand representation, and in left superior temporal sulcus and inferotemporal cortex. Additionally, the execution > rest contrast produced clusters in the left inferior parietal lobule and adjacent somatosensory cortex. The intransitive observation > rest contrast produced a cluster inside the right central sulcus.

Comparisons between each experimental condition: Both the execution > transitive observation and execution > intransitive observation contrasts produced significant clusters in the left anterior inferior parietal lobule and adjacent left somatosensory cortex, right cerebellum, and right ventral premotor cortex. Both the transitive observation > execution and intransitive observation > execution contrasts produced

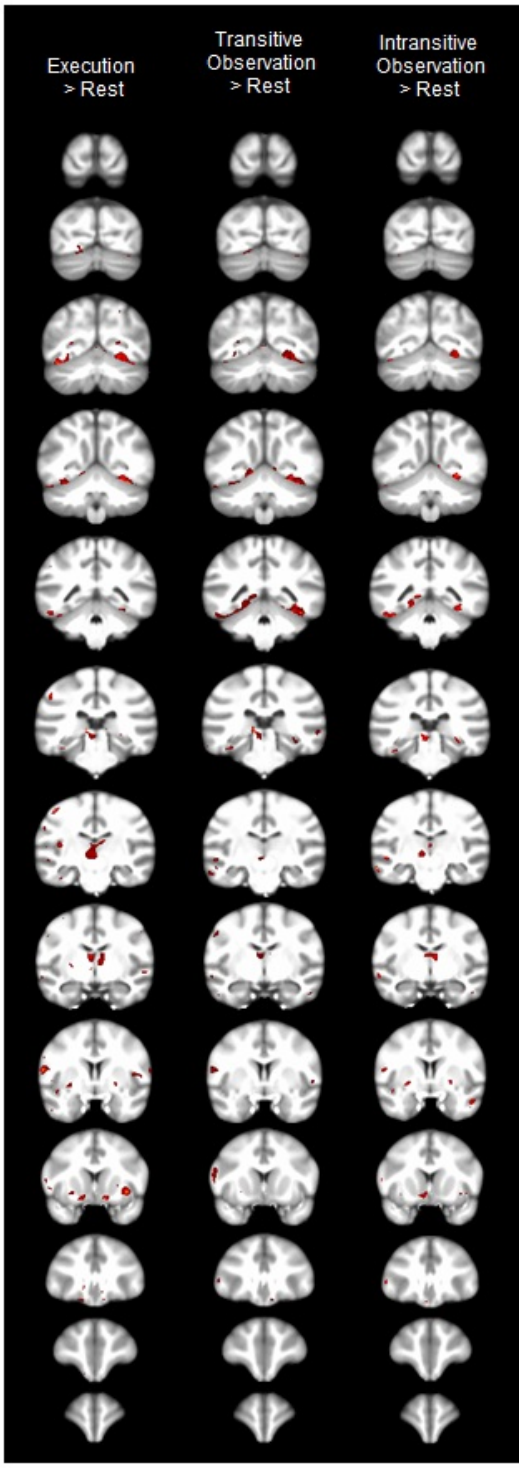
significant clusters of activation in bilateral superior temporal sulcus and inferotemporal cortex, as well as right occipitotemporal cortex and left inferior frontal gyrus. Additionally, the transitive observation > execution contrast produced clusters in left premotor cortex, left somatosensory cortex, right frontal pole, and bilateral cerebellum, and the intransitive observation > execution contrast produced a cluster inside the right central sulcus. The transitive > intransitive observation contrast produced small clusters in left inferior frontal gyrus, left ventral premotor cortex, left somatosensory cortex, left inferior parietal cortex, and right superior temporal sulcus, and right inferotemporal cortex. The intransitive > transitive observation contrast produced clusters in right central sulcus and postcentral sulcus cortex.

Figure 3.1-5. 3D surface renderings of group statistical comparisons between experimental conditions and rest.



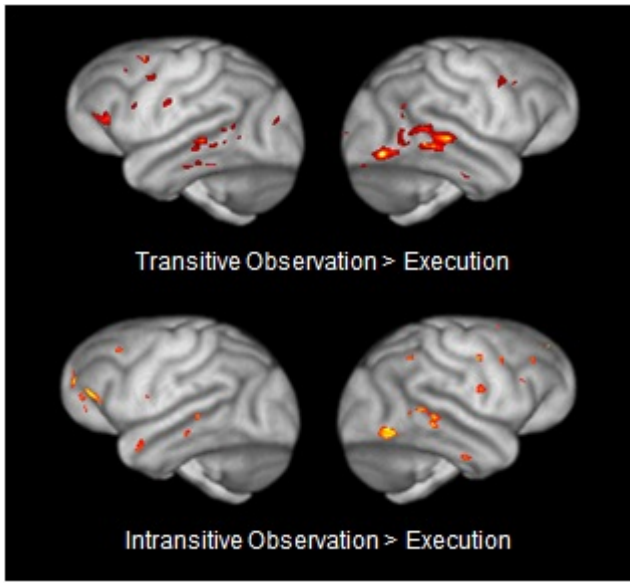
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Figure 3.1-6. Coronal slices of group statistical comparisons between experimental conditions and rest.



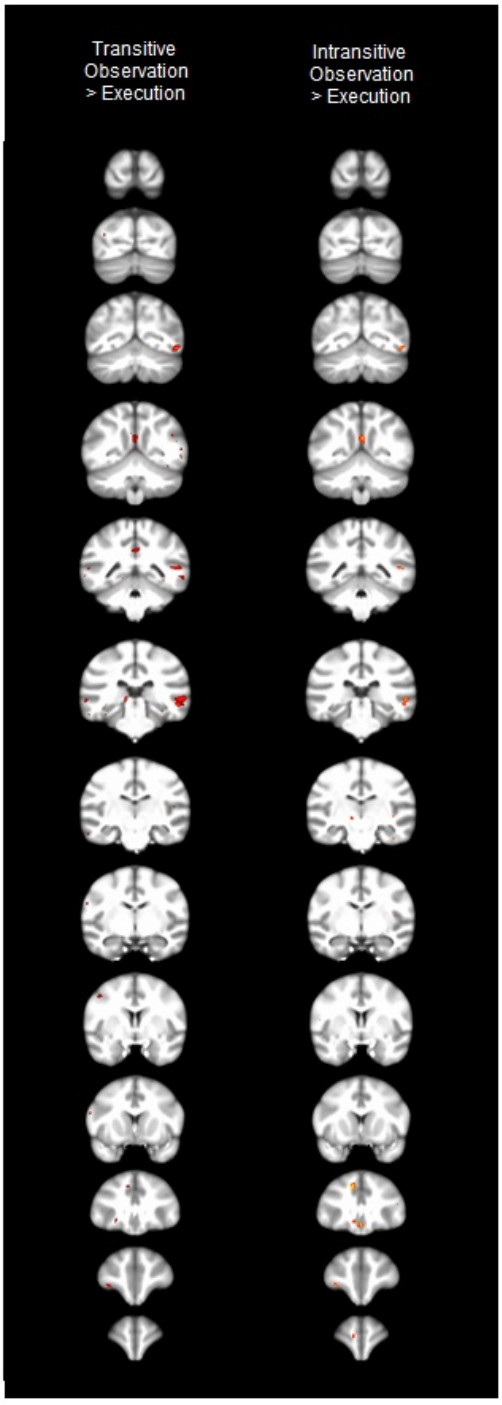
Left hemispheres on left. Top 1% of activated voxels in each condition in each subject.

Figure 3.1-7. 3D surface renderings of group statistical comparisons for observation > execution.



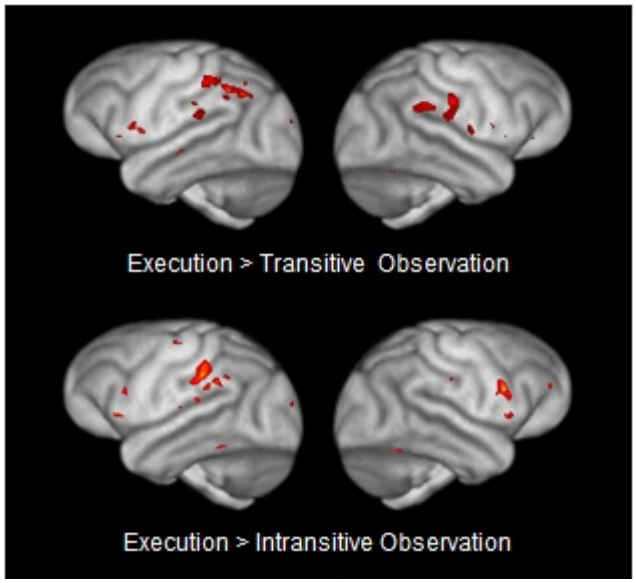
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Figure 3.1-8. Coronal slices of group statistical comparisons for observation > execution.



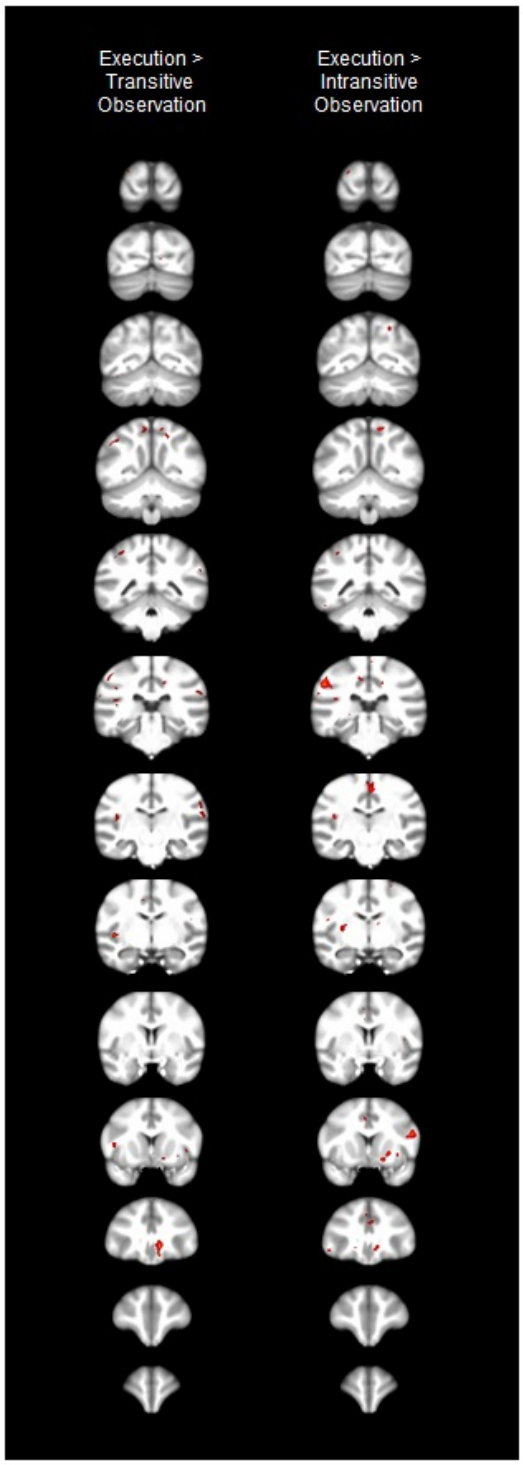
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Figure 3.1-9. 3D surface renderings of group statistical comparisons for execution > observation.



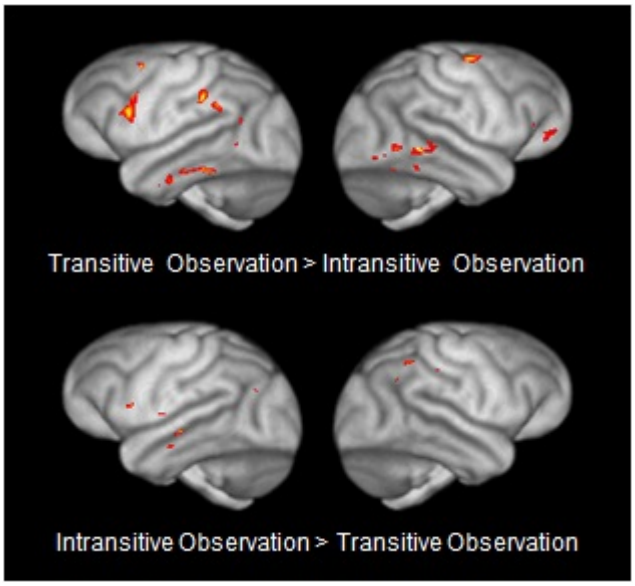
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Figure 3.1-10. Coronal slices of group statistical comparisons for execution > observation.



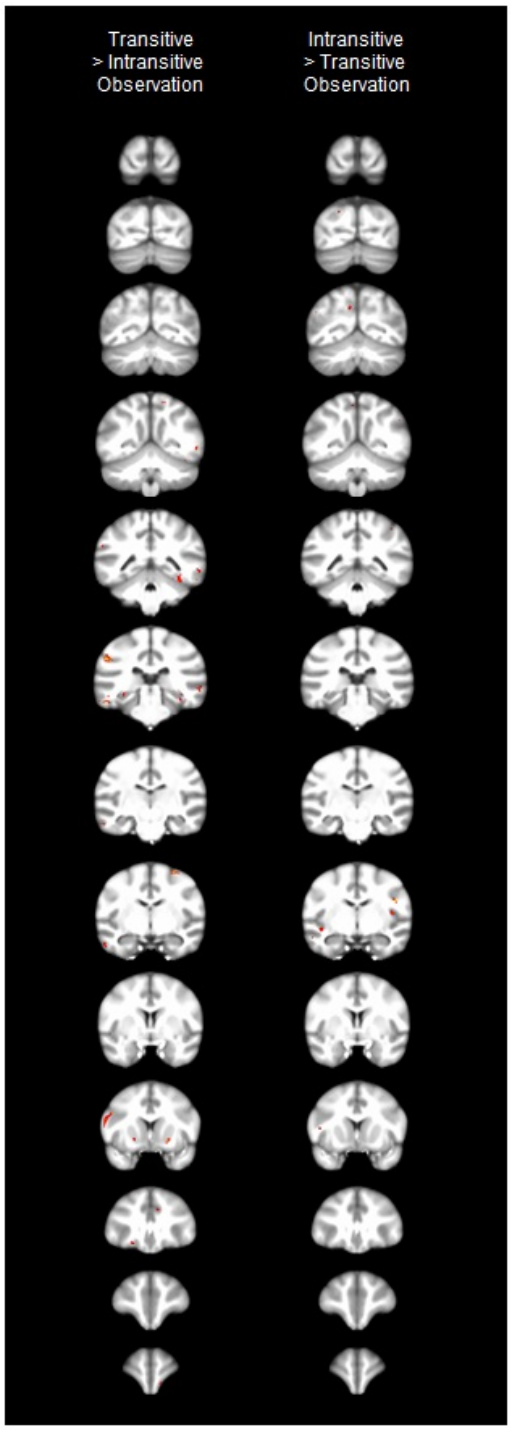
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Figure 3.1-11. 3D surface renderings of group statistical comparisons between transitive and intransitive observation.



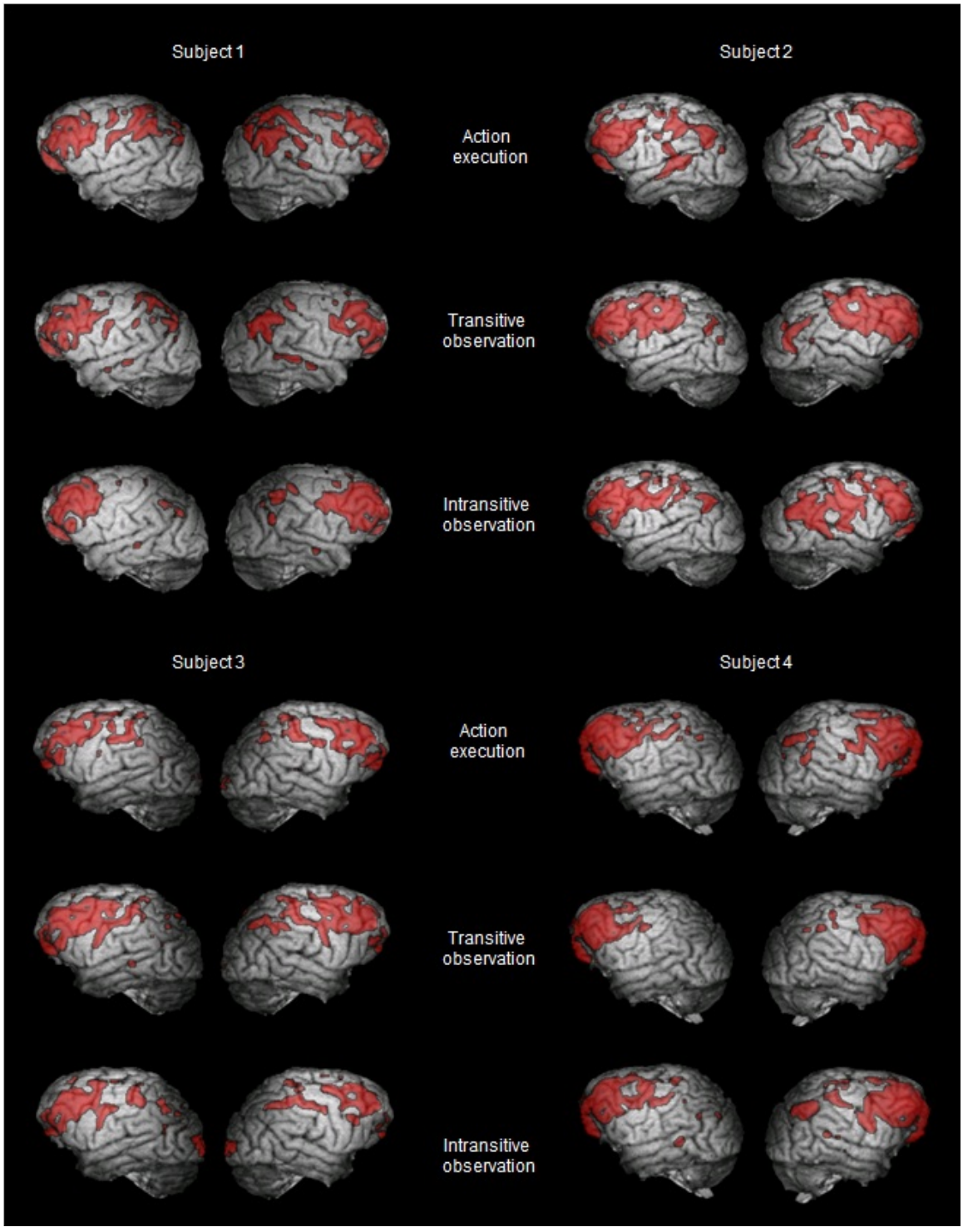
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Figure 3.1-12. Coronal slices of group statistical comparisons between transitive and intransitive observation.



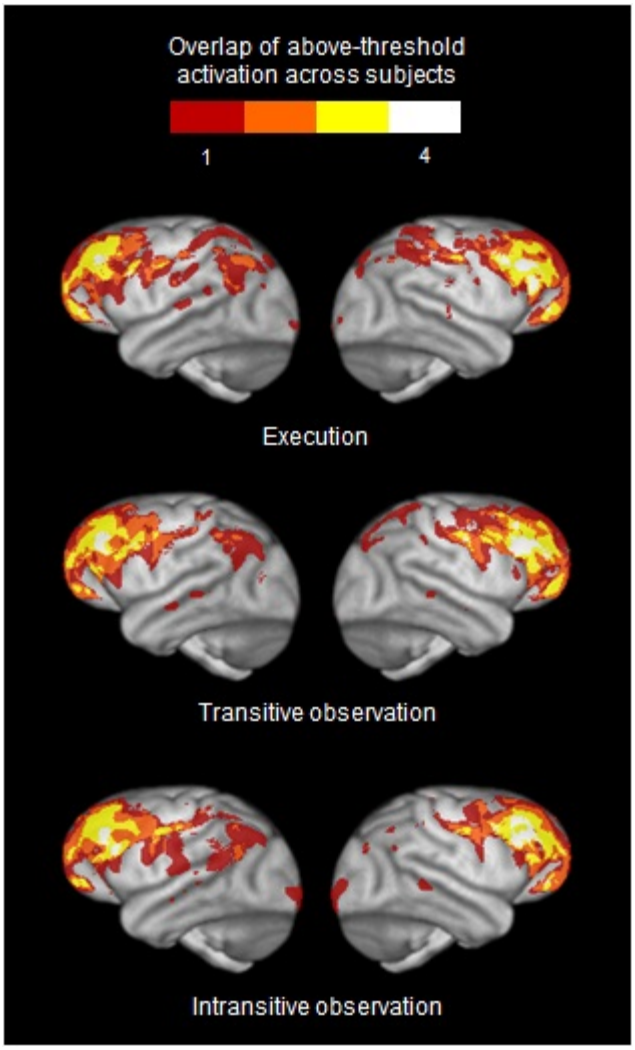
Left hemispheres on left. SPM5 analysis thresholded at $p < .05$.

Figure 3.1-13. Top 1% of activity in chimpanzee brains during each individual scan.



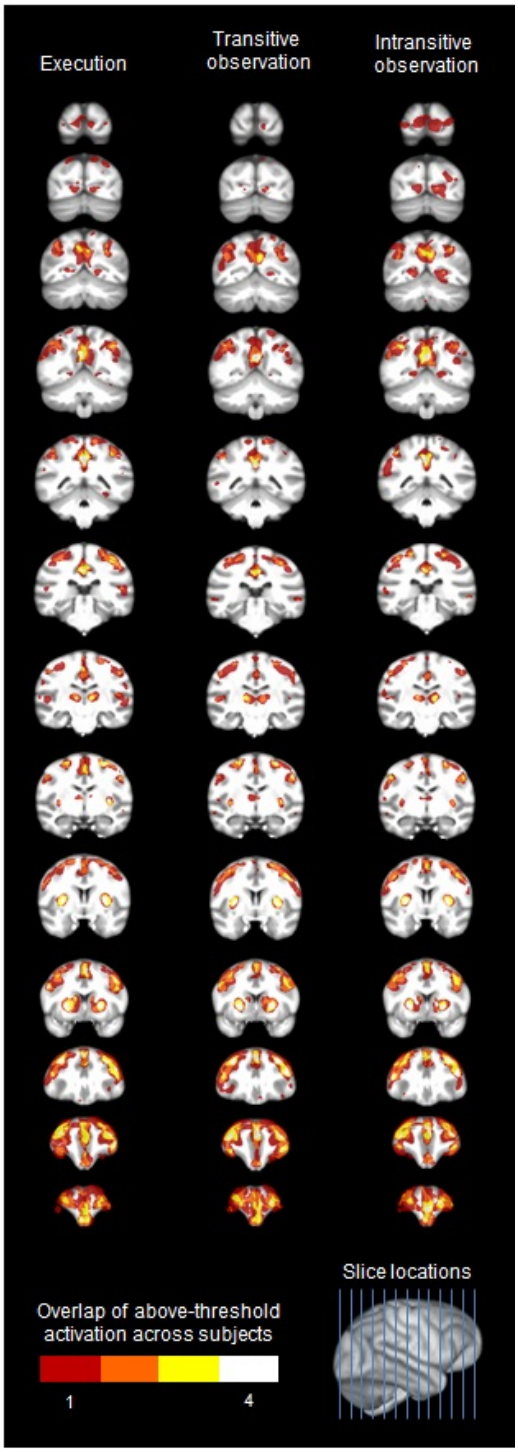
Left hemispheres on left. Top 1% of activated voxels in each condition in each subject.

Figure 3.1-14. 3D surface renderings of composite group map of top 1% of activity in chimpanzee brains during each individual scan.



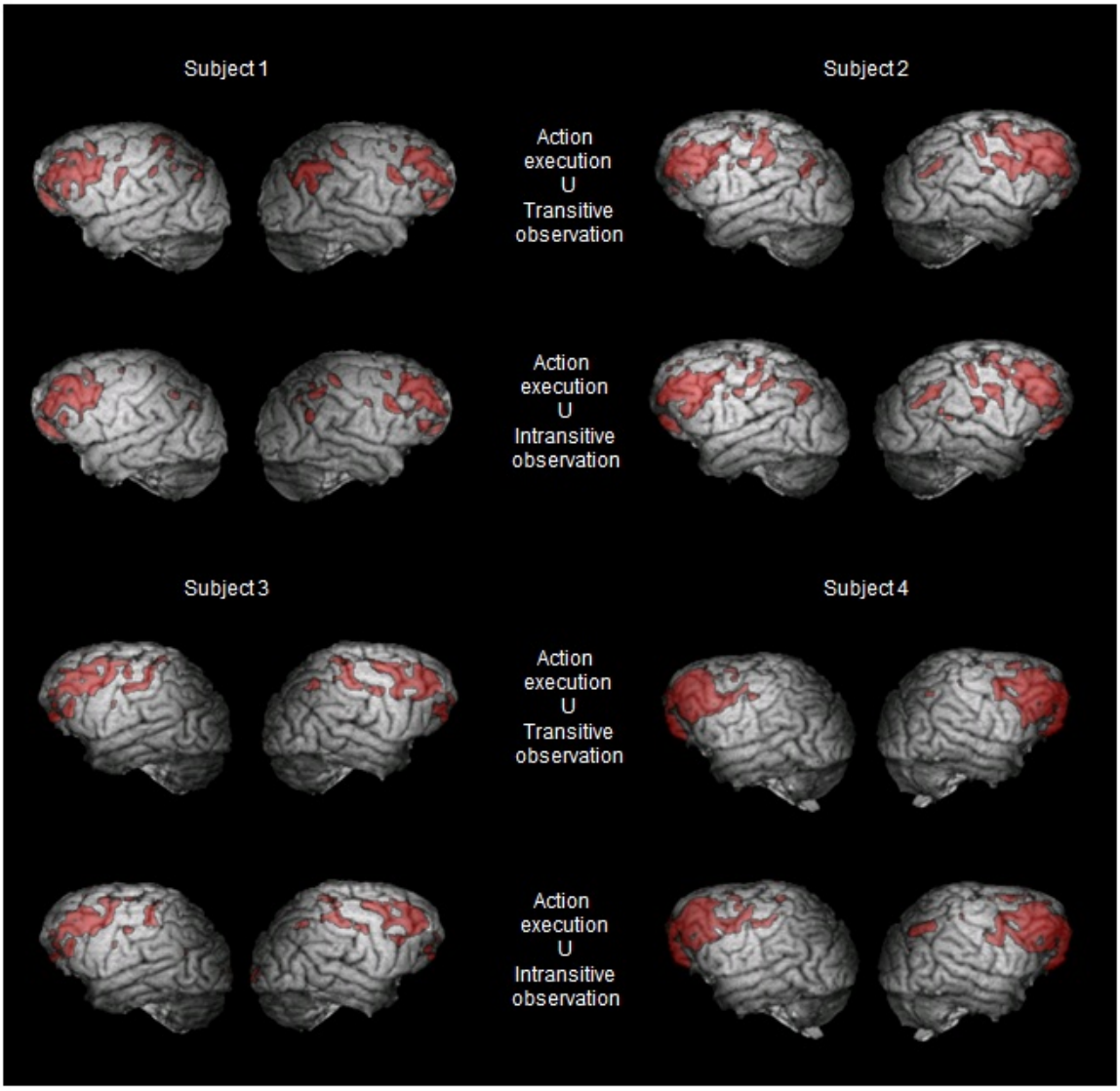
Left hemispheres on left. Individual, thresholded scans from each condition were binarized and summed, so that color corresponds to the number of subjects with above-threshold activation at that voxel.

Figure 3.1-15. Coronal slices of composite group map of top 1% of activity in chimpanzee brains during each individual scan.



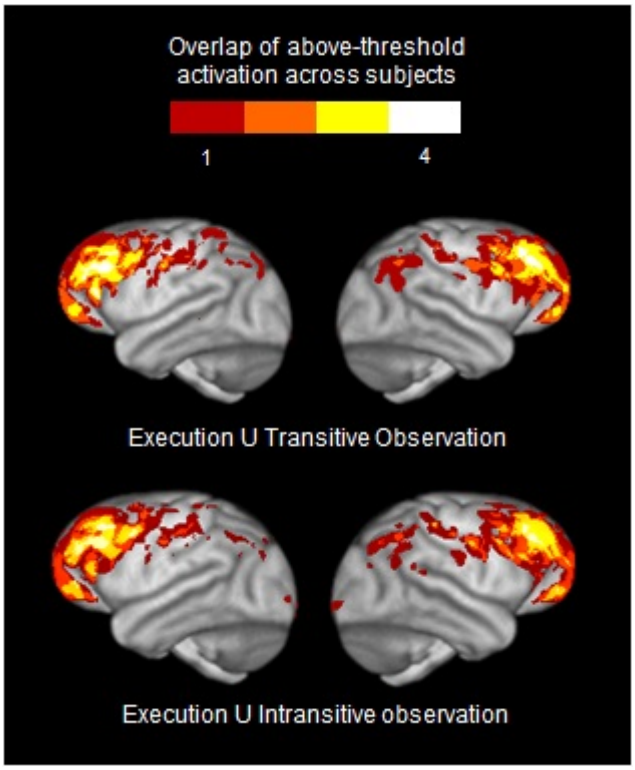
Left hemispheres on left. Individual, thresholded scans from each condition were binarized and summed, so that color corresponds to the number of subjects with above-threshold activation at that voxel.

Figure 3.1-16. Overlapping activity in individual subjects between action execution and both transitive and intransitive action observation.



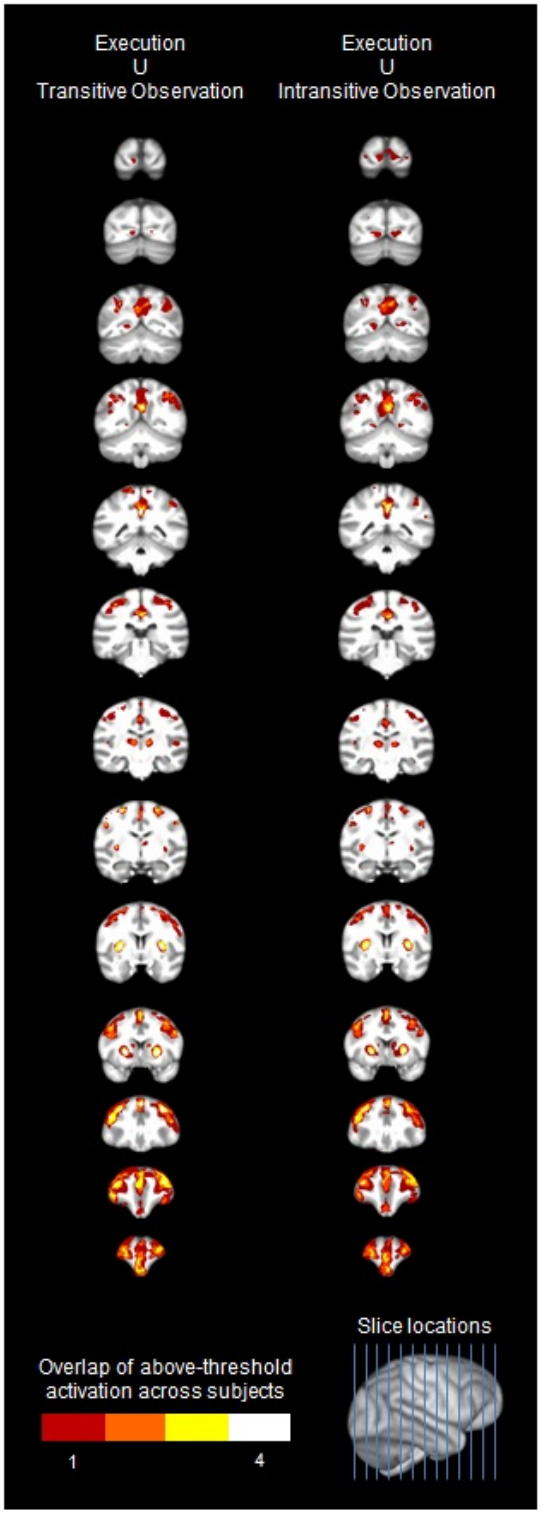
Left hemispheres on left. Voxels that were in the top 1% of activated voxels in both the execution and transitive observation conditions, and in both the execution and intransitive observation conditions, in each subject.

Figure 3.1-17. 3D surface rendering of composite group maps of overlapping activity for action execution and transitive and intransitive action observation.



Left hemispheres on left. Thresholded overlap images from each subject were binarized and summed, so that color corresponds to the number of subjects with above-threshold overlapping execution/observation activation at that voxel.

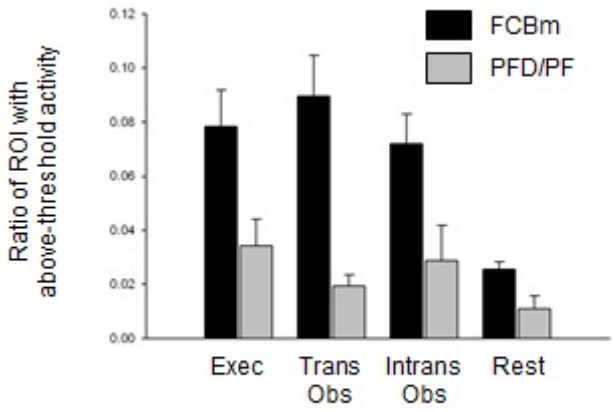
Figure 3.1-18. Coronal slices of composite group maps of overlapping activity for action execution and transitive and intransitive action observation.



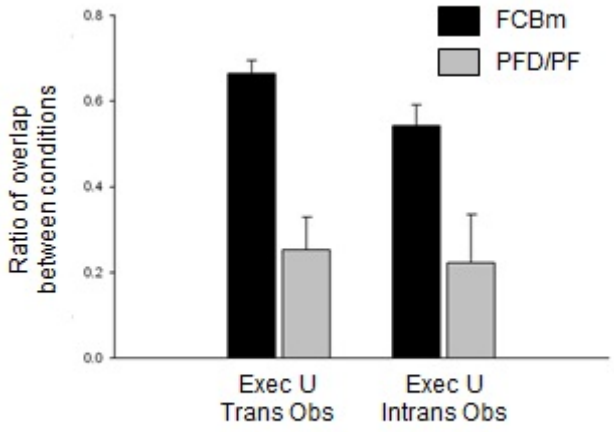
Left hemispheres on left. Thresholded overlap images from each subject were binarized and summed, so that color corresponds to the number of subjects with above-threshold overlapping execution/observation activation at that voxel.

Figure 3.1-19. Quantification of activity in individual conditions.

A



B



(A) ROI activation in individual conditions. Percent of ROIs active in each condition, averaged across subjects. An initial repeated measures ANOVA showed no effect of hemisphere, so data were averaged bilaterally for each ROI. Activation was greater in execution, transitive observation, and intransitive observation relative to rest, as measured with a repeated measures ANOVA (main effect of task condition, $F(3) = 14.185$, $p < 0.001$; individual comparisons, $p = 0.004$, 0.007, and 0.026, respectively).

Additionally, the FCBm was more active than PFD/PF (main effect of region, $F(1) = 17.386$, $p = 0.014$).

(B) ROI activation in conjunction analyses. Percent of voxels in top 1% of execution condition which were also in top 1% of transitive observation or intransitive observation conditions in FCMb and PF, averaged across subjects. A repeated measures ANOVA revealed no effect of condition, but a main effect of region ($F(1) = 16.076$, $p = .028$); the frontal ROI was more active than the parietal ROI.

3.2. Comparison between chimpanzee and human regional cerebral glucose metabolism during the perception of object-directed grasping[10]

3.2.1. Summary

This experiment tests Hypothesis 2, Part B:

- ➔ Hypothesis 2: Species differences in social learning are related to species differences in the neural response to observed action.
    - o Part B: Behavioral differences in social learning are the result of underlying neural differences in the component processes involved in action observation. If this is true, the distributed pattern of activation during action observation should differ between species.

This was tested by comparing human FDG-PET scans during transitive action observation to the chimpanzee transitive observation scans in Chapter 3.1. These human scans were acquired as pilot data for another study and the comparison was opportunistic rather than pre-planned, so stimuli and methods were not identical. However, we took several measures to control for these differences. We then compared the amount of activation in homologous regions of human and chimpanzee frontal, parietal, and temporal cortex. This yielded 2 main results:

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[10] *Section 3.2 is reproduced with minor edits from Hecht, E. E., L. E. Murphy, D. A. Gutman, D. M. Schuster, J. R. Votaw, T. M. Preuss, L. A. Parr and G. A. Orban (In preparation). "Differences in regional cerebral glucose metabolism during action perception in humans and chimpanzees."*

1) Most of the chimpanzee activation was concentrated in frontal cortex, with relatively little parietal or occipitotemporal activation. In contrast, human activation was more evenly distributed between frontal, parietal, and occipitotemporal cortex.

2) Some brain regions had activation differences between humans and chimpanzees. In humans, a greater proportion of above-threshold activation fell into inferior parietal cortex, inferotemporal cortex, and ventral premotor cortex. In chimpanzees, a greater proportion of above-threshold activation fell into ventrolateral prefrontal cortex.

We discuss the potential relevance of these results to species differences in social learning.

3.2.2. Materials and methods

Subjects

Subjects were 6 humans, 3 male and 3 female, all neurologically normal and right-handed, plus the same chimpanzee subjects described in Chapter 3.1.2 (we re-analyzed these existing scans in comparison with the new human data).

Stimuli

Human subjects viewed videos of a hand grasping an object (sample screenshot shown in **Figure 3.2-1**). Grip type varied (whole-hand or precision), as did object type (a small

ball, block, or stone). Each clip was 2 seconds long. Clips were arranged in pseudo-random order with no repeats. Chimpanzee stimuli are described in Chapter 3.1.2 and are depicted in **Figure 3.1-1**.

Uptake period for FDG-PET scanning

Subjects sat in a chair in a small room near the PET scanner during the FDG uptake period. They received an intravenous injection of 10 mCi of FDG simultaneous with the onset of the video. The videos were presented on a laptop which the experimenter positioned on a stand over the subject's lap. Subjects were instructed to sit still, watch the video, and avoid using their hands. The experimenters dimmed the lights, left the subject alone in the room, and closed the door. A video camera recorded subject behavior during the uptake period. These videos were later scored in the same manner as the chimpanzee videos by the same researcher (Lauren Murphy). Human behavior during FDG uptake is shown in **Table 3.2-2**, alongside chimpanzee behavior in the comparable transitive action observation condition. After 45 minutes, the subject was escorted to the PET scanner for image acquisition.

Image acquisition

Human subjects were scanned in the same Siemens high resolution research tomograph as was used to collect the chimpanzee scans in Chapter 3.1. Subjects also underwent structural T1-weighted MRI scans.

Image analysis

Human PET images were pre-processed in exactly the same way as the chimpanzee PET images (described in Chapter 3.1.2). MRI images were aligned to template space (using the MNI152 nonlinear 1mm template); PET images were aligned to MRI images and masked to remove non-brain voxels; PET images were normalized to their own mean whole-brain value so that intensities could be compared both across subjects within a species, and across species; and finally, PET images were smoothed using a 4-mm kernel. Both human and chimpanzee PET images were thresholded to show the top 1% of the robust range of the histogram of voxel values. To produce composite group images, these thresholded images were binarized and summed so that each voxel's intensity corresponded to the number of subjects with above-threshold activation at that location (e.g., an intensity of 3 denotes that 3 subjects had above-threshold activity in that voxel).

ROI definition

Regions of interest were drawn using published chimpanzee and human atlases and cytoarchitectonic reports (Brodmann 1909, Economo and Parker 1929, Bailey 1948, Bonin 1948, Bailey, Bonin et al. 1950, Schenker, Hopkins et al. 2010). Regions of interest are depicted in **Figure 3.2-3** and their anatomical definitions in each species are listed in **Table 3.2-4**.

3.2.3. Results

Upon examination of the individual subjects' scans (**Figure 3.2-5**), it is grossly evident that chimpanzee activation is focused mainly in frontal and prefrontal cortex, with a lesser amount of activation in parietal and occipitotemporal cortex. In contrast, human

activation is more evenly distributed between frontal, parietal, and occipitotemporal cortex. When each species' individual thresholded scans were binarized and summed into a composite group image (**Figure 3.2-6**), this difference became even more evident. Examination of group-averaged, unthresholded scans (**Figure 3.2-7**) reveals that chimpanzees do have regions of activation in parietal and occipitotemporal cortex, especially in the right hemisphere, but that this is overshadowed by frontal activation so that the parietal and occipitotemporal activation does not surpass threshold.

In order to quantitatively assess these qualitative differences, we drew regions of interest (ROIs) in a set of frontal, parietal, and temporal regions in chimpanzees and humans (depicted in **Figure 3.2-3**; anatomically defined in **Table 3.2-4**). We measured the activity in each ROI as a percentage of total above-threshold activity in the scan (number of above-threshold voxels in ROI divided by total above-threshold voxels in the brain). This controls for differences in the amount of above-threshold activation that may have been caused by differences in live vs. video stimulus presentation.

When ROIs were ranked according to mean activation in each species, the order of ranks showed a non-significant correlation of .309 ($p = .186$, Kendall's tau test), indicating that the order of ROIs from most to least activated is not significantly correlated between species. Broca's area was significantly more active in chimpanzees, while ventral premotor cortex, inferior parietal lobule, and inferotemporal cortex were significantly more active in humans (**Figure 3.2-8**). ($p=.033$, $p=.036$, $p<.001$, and $p<.001$, respectively; independent measures t-tests).

3.2.4. Discussion

Our results indicate a broad species difference in the relative allocation of metabolic resources for neural processing of observed action. In chimpanzees, there is a prefrontal bias for this processing, especially in ventrolateral prefrontal cortex. In humans, there is a relatively more robust response in parietal and occipitotemporal cortex, especially ventral premotor cortex, inferior parietal lobule, and inferotemporal cortex.

It is important to note that our scans represent the entire mosaic of neural processes involved in grasping perception, many of which probably subserve related, component functions like the control of eye movements, biological motion perception, etc. Additional research is needed to pinpoint potential underlying differences in these underlying component processes. Although chimpanzee and human stimuli were not identical, our various normalization steps controlled for potential global differences in glucose metabolism, and previous research suggests that local differences in the amount of activation of different brain regions would have been opposite to what we observed (**Table 3.2-9**).

Our findings are consistent with previously published studies in macaques and humans. Meta-analyses of human fMRI studies on grasping observation depict a roughly even balance between frontal and parietal activation (Caspers, Zilles et al. 2010, Molenberghs, Cunnington et al. 2012). Studies in macaque monkeys have reported greater frontal activations that may be comparable to these chimpanzee results: in an fMRI study, macaques have more prefrontal activation than humans when viewing objects (Denys, Vanduffel et al. 2004), and in a set of 2-deoxyglucose studies, object-directed grasp perception caused more activation in ventral premotor than inferior parietal cortex (Raos, Evangeliou et al. 2004, Raos, Evangeliou et al. 2007). Given that these macaque findings are similar to our chimpanzee findings, a prefrontal bias may represent the

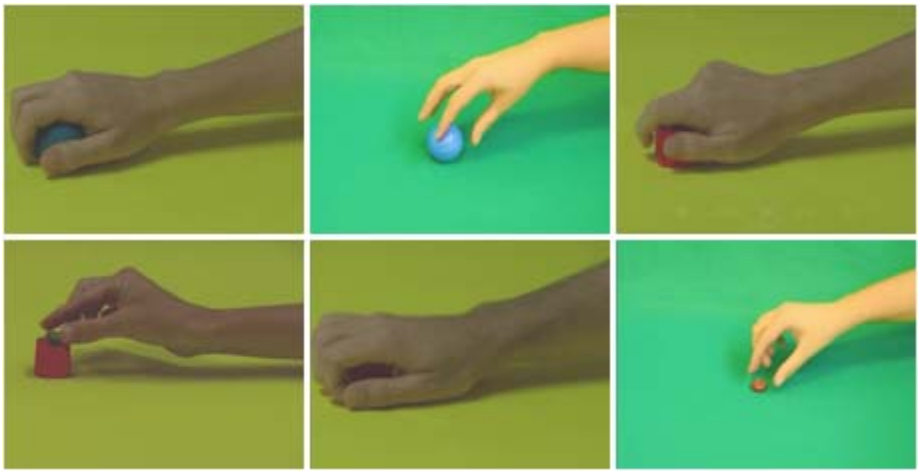
primitive condition which existed before the macaque/chimpanzee divergence. Humans' shift toward parietal and occipitotemporal processing may represent a relatively recent adaptation that occurred after the chimpanzee/human divergence.

These PET results are also consistent with our recent comparison of white matter connectivity in macaques, chimpanzees and humans, in which humans had increased connectivity with inferior parietal and inferotemporal nodes of the network (Hecht, Gutman et al. 2012) (Chapter 2). These differences in connectivity may underlie the differences in activation.

What might be the functional relevance of these results? Action understanding relies on multiple levels of information processing in a tightly integrated network including inferotemporal cortex, superior temporal sulcus, inferior parietal lobule, dorsal and ventral premotor cortex, and ventrolateral prefrontal cortex. While the precise functional contributions of each region across species remain to be resolved, there is substantial evidence that ventrolateral prefrontal cortex, compared to ventral premotor cortex or postcentral regions, supports more abstract action representations such as context, outcomes, or intentions (Nelissen, Luppino et al. 2005, Hamilton and Grafton 2008, Bonini, Rozzi et al. 2010) and/or top-down cognitive control processes such as rule-based action selection, information retrieval and hierarchical control (Petrides 2005, Koechlin and Jubault 2006, Badre and D'Esposito 2009). Conversely, occipitotemporal and parietal regions have been associated with more specific representations like kinematics or proximate goals (Bonini, Rozzi et al. 2010), and/or bottom-up perceptual-motor processes like recognition, categorization, and sequencing (Jubault, Ody et al. 2007, Jastorff, Begliomini et al. 2010). The observed prefrontal bias in chimpanzee brain response during transitive action observation thus suggests greater

functional investment in high-level representations and top-down control processes, whereas humans' increased parietal and occipitotemporal activation suggests a relatively greater reliance on specific representations and bottom-up perceptual recognition. This functional difference parallels behavioral evidence of a chimpanzee preference for copying action outcomes (results or ends), and a human propensity for copying action details (means or movements) (Whiten, McGuigan et al. 2009). Humans' focus on these details has been identified as a key component for cumulative culture (Dean, Kendal et al. 2012), so these results may be relevant to its evolution.

Figure 3.2-1. Visual stimuli for human functional neuroimaging.



Humans subjects viewed a montage of video clips of a hand grasping an object; these images represent screenshots from the video clips.

Figure 3.2-2. Human behavior during FDG uptake periods prior to scans, with comparison chimpanzee behavior.

Subject	Total time spent in non-task-related activity	Description of non-task-related activity
Human 1	0:48	Manipulate wristwatch, scratch face, yawn, adjust shirt
Human 2	*No video due to error*	
Human 3	04:46	Head nod, fall asleep
Human 4	04:29	Yawn, manipulate blanket
Human 5	01:38	Rearrange blanket, yawn
Human 6	00:00	Yawn, stretch, scratch face
Chimpanzee 1	1:00	Groom self
Chimpanzee 2	2:15	Swing, climb, manipulate own feet, bite fingernails, food beg, aggression display, throw feces at experimenters, scratch/groom self, pat own head, manipulate cage locks
Chimpanzee 3	1:18	Scratch/groom self, aggression display
Chimpanzee 4	1:36	Suck thumb, poke finger through cage mesh, scratch/groom self

Figure 3.2-3. Regions of interest.

Regions of interest in dorsolateral prefrontal cortex (DLPFC), Broca's area (Broca), dorsal premotor cortex (PMd), ventral premotor cortex (PMv), primary motor cortex (M1), primary and secondary somatosensory cortex (S1-S2), inferior parietal lobule (IPL), lateral occipital cortex (LOC), inferotemporal cortex (IT), and superior temporal sulcus (STS). Homologies were identified using chimpanzee and human cortical maps (Brodmann 1909, Economo and Parker 1929, Bailey 1948, Bonin 1948, Bailey, Bonin et al. 1950, Schenker, Hopkins et al. 2010).

Table 3.2-4. Anatomical definitions of regions of interest.

Region of interest	Chimpanzees		Humans	
	Anatomical description	**Cyto-architectonic region(s)**	**Anatomical description**	**Cyto-architectonic region(s)**
Lateral occipital cortex	Its anterior border is a line drawn straight up from the occipital notch, following the inferior extension of the STS. Its posterior border includes both the banks and the fundus of the lunate sulcus. It includes both banks of the medial parieto-occipital fissure.	OA (BA 19)	Same, except its posterior border is a curved line placed half way to the pole.	BA 19
Infero-temporal cortex	Lateral temporal cortex inferior to the superior central sulcus, extending ventrally to the border with the hippocampal formation. Its anterior border is the temporal pole, and its posterior border is an imaginary vertical line drawn up from the occipital notch.	TE1 (BA21), TE2 (BA 20), PH (BA 37)	Same.	BA 21, BA 20, BA 37
Superior temporal sulcus	Includes both banks and fundus. Its posterior border is the imaginary extension of the inferior terminus of the STS, parallel to but anterior to the lunate sulcus.		Same, except its posterior termination is vertical line from occipital notch.	
Inferior parietal cortex	Its anterior border is the posterior bank of post-central sulcus. Its posterior border is a vertical line drawn up from the termination of the inferior sulcus that extends off the posterior end of the STS.	PFD, PF (BA 40/7b), PG (BA 39/7a)	Its anterior border is the fundus of the post-central sulcus. Its posterior border is vertical line drawn up from the occipital notch.	BA 40, BA 39
Superior parietal cortex	Its anterior border is the posterior bank of post-central sulcus. Its posterior border is a vertical line drawn up from the termination of the inferior sulcus that extends off the posterior end of the STS.	Pem (BA 5), PEp (BA 5)	Its anterior border is the fundus of the post-central sulcus. Its posterior border is a vertical line drawn up from the occipital notch.	BA 5, BA 7
Primary and secondary somato-sensory cortex	Its anterior border is the fundus of the central sulcus. Its posterior border is the fundus of postcentral sulcus.	PC (BA 3), PB (BA 1, BA 2)	Same.	BA 3, BA 1, BA 2

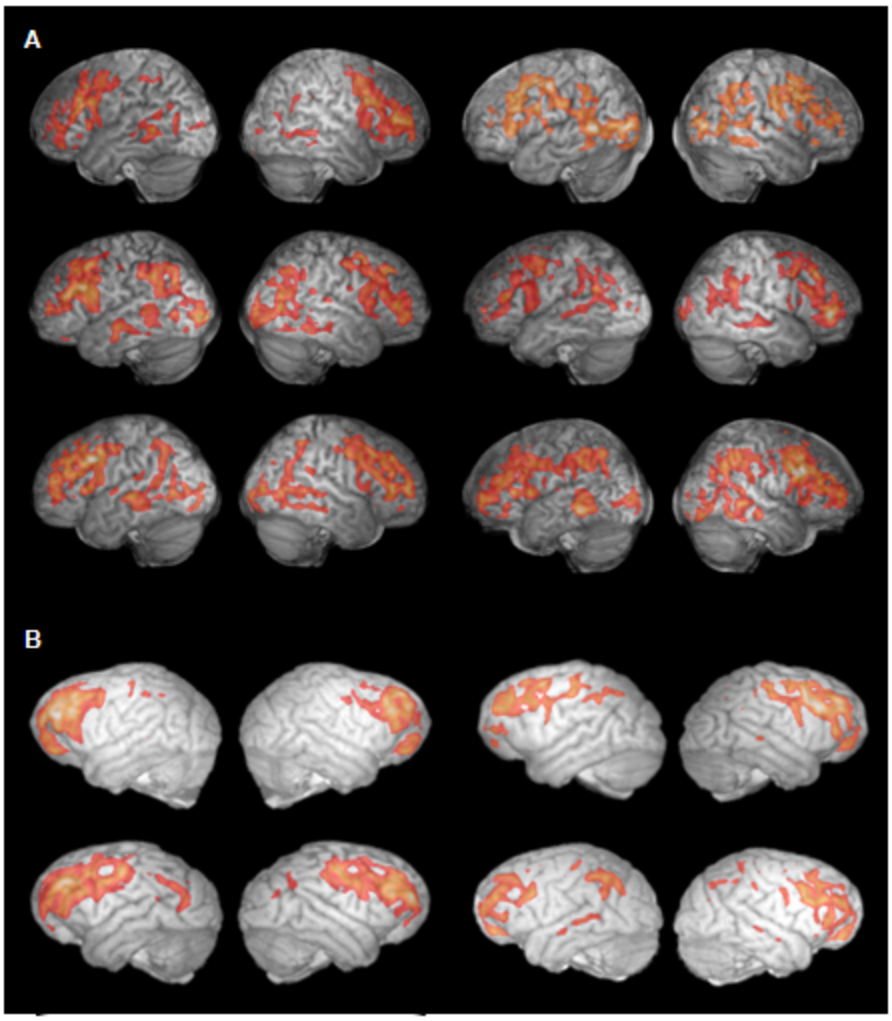
Table 3.2-4 (continued). Anatomical definitions of regions of interest.

Region of interest	Chimpanzees		Humans	
	Anatomical description	**Cyto-architectonic region(s)**	**Anatomical description**	**Anatomical description**
Primary motor cortex	Its posterior border is the fundus of the central sulcus. Its anterior border is an imaginary line drawn straight up from the intersection of the inferior frontal sulcus and the central sulcus. At its inferior aspect, the ROI exists entirely inside the central sulcus. At its superior aspect, the ROI extends past the dorsal precentral sulcus.	FA (BA 4)	Its posterior border is the fundus of the central sulcus. Its anterior border is a vertical line from the lateral sulcus to the superior tip of superior pre-central sulcus.	BA 4
Dorsal premotor cortex	At its dorsal aspect, it extends anteriorly to an imaginary line drawn from the tip of the inferior pre-central sulcus at a 90 degree angle with the lateral sulcus. The inferior part of the ROI is bordered anteriorly at the inferior frontal sulcus, curving down and back to meet the PMv ROI. The border between PMd and PMv is an imaginary line drawn parallel to the lateral sulcus at the dorsal tip of the fronto-occipital sulcus so that the superior borders of PMv and Broca's area are continuous.	FB (BA 6), FC (BA 8)	Its posterior border is a vertical line from the lateral sulcus to the superior tip of the superior pre-central sulcus. Its anterior border is a 45 degree line from the antero-superior edge of the PMv ROI. The border between PMd and PMv is the gyrus that splits the superior and inferior precentral sulci.	BA 6, BA 8
Ventral premotor cortex	Bordered posteriorly by the M1/S1 ROI, superiorly as described above, and anteriorly by the inferior precentral sulcus.	FBA (BA 6)	Its anterior border is the inferior precentral sulcus. Its posterior border is a vertical line from the lateral sulcus to the superior tip of superior pre-central sulcus (M1). Its superior border is the gyrus that splits the inferior and superior pre-central gyri.	BA 6
Dorso-lateral prefrontal cortex	Bordered dorsally by the interhemispheric fissure, posteriorly by the PMd ROI, inferiorly by the Broca's area ROI, and anteriorly by an imaginary line which is an extension of the orbital sulcus drawn past the tip of the middle frontal sulcus.	FDm (BA 9), Fddelta (BA 46)	Its inferior border is the inferior frontal sulcus. Its anterior border is a 45 degree line drawn from tip of anterior horizontal ramus (the sulcus that borders the anterior edge of Broca's area).	BA 9, BA 46

Table 3.2-4 (continued). Anatomical definitions of regions of interest.

Region of interest	Chimpanzees		Humans	
	Anatomical description	**Cyto-architectonic region(s)**	**Anatomical description**	**Anatomical description**
Ventro-lateral prefrontal cortex	Includes the pars opercularis and pars triangularis of the inferior frontal gyrus. Bordered posteriorly by the inferior precentral sulcus, anteriorly by the small sulcus that extends anteriorly from the fronto-orbital sulcus, and superiorly by the inferior frontal sulcus.	FCBm (BA 44), FDp (BA 45)	Same.	BA 44, BA 45

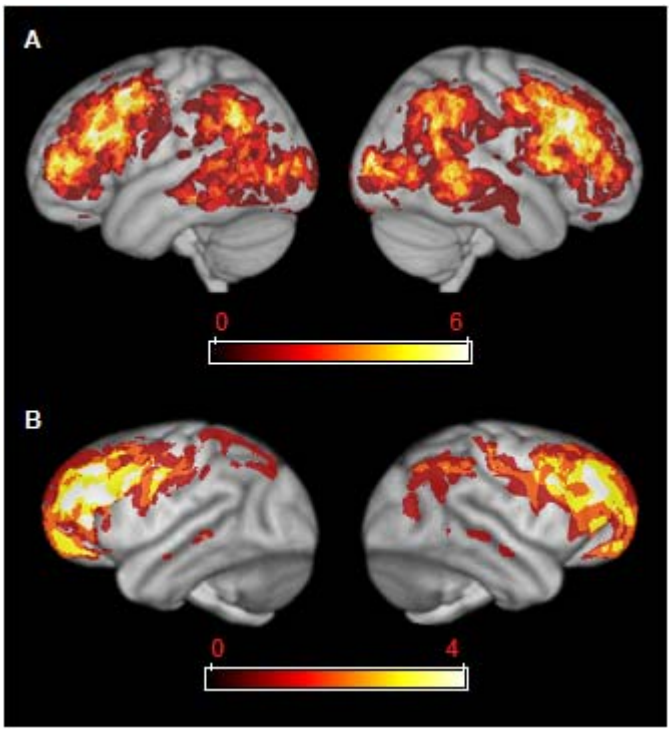
Figure 3.2-5. Individual scans.



A. Humans. Human subjects show broad activation over frontal, parietal, and temporal cortex.

B. Chimpanzees. Chimpanzee subjects show more concentrated activation in frontal cortex. All images were normalized to their own mean intensity value and thresholded to show the top 1% of the robust mean of voxel values. Activations are rendered on each subject's own T1-weighted MRI scan.

Figure 3.2-6. Composite group analysis of thresholded images.

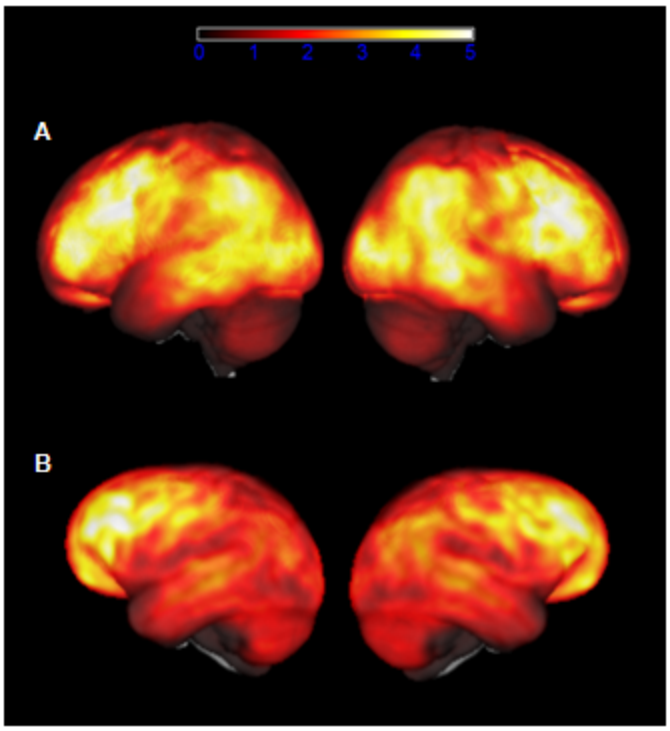


A. Humans.

B. Chimpanzees.

Individual thresholded scans were binarized and summed so that intensity corresponds to number of subjects with overlapping above-threshold activation at a particular location, as indicated by the color bars.

Figure 3.2-7. Composite group analysis of unthresholded images.

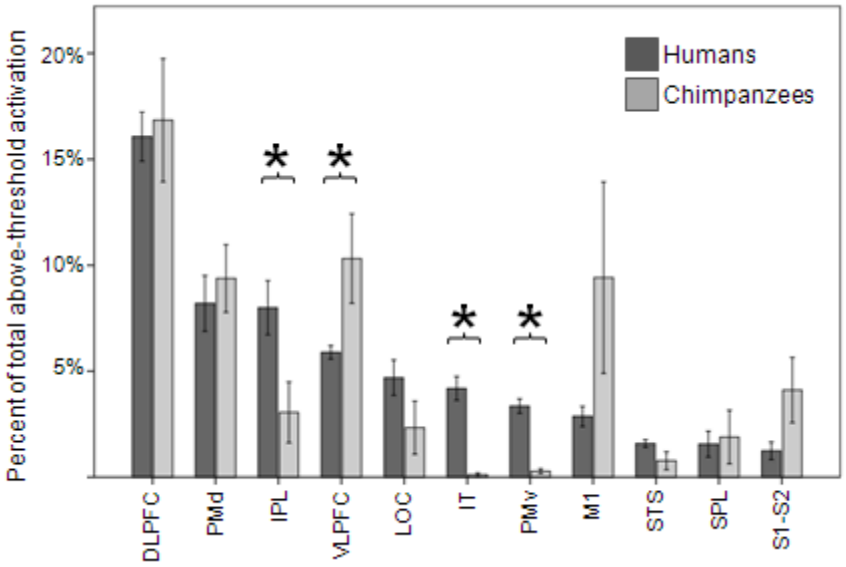


A. Humans.

B. Chimpanzees.

Individual thresholded scans were averaged without thresholding so that intensity corresponds to average activation at a particular location, as indicated by the color bar.

Figure 3.2-8. Quantification of above-threshold activation in humans and comparison to chimpanzees



Percent of total above-threshold activation that fell into each region of interest. Inferior parietal lobule, inferotemporal cortex, and ventral premotor cortex accounted for a significantly greater proportion of overall activation in humans than in chimpanzees ($p=.036$, $p<.001$, and $p<.001$, respectively; independent measures t-tests). Broca's area accounted for a significantly greater proportion of overall activation in chimpanzees than in humans ($p=.033$, independent measures t-test). Each region was compared to only one other region (i.e., human region compared to its chimpanzee homolog), so we did not correct for multiple comparisons.

Table 3.2-9. Methodological differences between chimpanzees and humans

Methodological difference	Possible effect	Discussion
Chimpanzees viewed live demonstrations; humans viewed videos	Might cause less mirror system activation in humans (since videos are less effective at activating the mirror system in macaques)	Actually observed greater activation in PMv and IPL in humans
Chimpanzee stimuli were 3D; human stimuli were 2D	Might cause greater PMv activation in chimpanzees (since stereopsis increases PMv activation in humans)	Actually observed greater PMv activation in humans
Human stimulus showed a more constrained field of view on the action	Might cause more limited frontal activations in humans (since viewing a grasping hand opposed to a whole actor activates fewer regions of monkey ventral premotor and ventral prefrontal cortex)	Actually observed widespread frontal activation in both chimpanzees and humans
Reaching may have been a more prominent characteristic of the chimpanzee stimulus	Might cause greater PMd activation in humans, since observed reaching activates PMd in humans	Actually observed no difference in PMd activation between humans and chimpanzees
Humans received IV doses of FDG; chimpanzees received oral doses	Might cause absolute level of signal to differ between species; human brain might be "hotter" overall	Both species' scans were normalized by their own mean intensity so that the average intensity of every image is equal to 1, putting intensity values on the same relative scale. Also, ROI activation was measured as a percent of total activation above a relative threshold, controlling for differences in absolute amount of activation
One species may have been more interested in or attentive to the stimulus	Might cause absolute level of signal to differ between species	Same as above
There may be quantitative differences in brain metabolism between species	Might cause the range of values to be larger in one species, so that even after normalization one species might have "hotter hots" and "colder colds"	Both species' scans were thresholded using the robust range (middle 96%) of the histogram of voxel values, so that the post-threshold images are minimally affected by outlier voxels and more accurately reflect the bulk of voxel values
Chimpanzee non-task-related behaviors were more locomotive than human non-task related behaviors (they moved around more)	Might cause greater activation in M1 and S1-S2 in chimpanzees	This difference was observed, although it was not significant. Chimpanzees 2 & 3 had the most M1 activation, and also had the most locomotive non-task-related behavior (see **Table 3.2-2**)

Chapter 4:

Behavior

4.1. Correlations between behavior and brain activation in chimpanzees

4.1.1. Summary

This experiment tests Hypothesis 3:

➔ Hypothesis 3: Differences in activation patterns in the action observation network will correlate with differences in social learning behavior.

This was tested by looking for correlations between individual variation in copying behavior and brain activation during action observation. The same chimpanzees who participated in the PET studies were presented with a variety of familiar and unfamiliar objects and were allowed to interact with them freely. A human experimenter then demonstrated a specific use of each object without giving the chimpanzee any specific instruction or reward for copying. Voluntary, spontaneous behavior after the demonstration was scored for the frequency of copying the means (methods) of the demonstrated action, the frequency of copying the ends (results) of the demonstrated action, and the frequency of successful tool use. We then investigated whether measurements in these behavioral categories correlated with measurements in PET activation during the transitive and/or intransitive action observation conditions. This yielded 3 main results:

1) In line with previously published research, chimpanzees were better at copying the ends than the means of demonstrated actions.

2) Chimpanzees who participated in a 1995 imitation-training study were better at copying means and successfully using tools in familiar actions. These chimpanzees also had more activation in ventral premotor cortex and lateral occipital cortex while observing object-directed grasping actions.

3) In the transitive action observation PET scans, activation in ventral premotor cortex was correlated with chimpanzees' ability to use tools in ways that they frequently saw demonstrated by human experimenters in daily life, but had rarely or never attempted themselves (such as using a key to open a lock). Activation in lateral occipital cortex was correlated with the ability to copy the means of familiar and unfamiliar actions and the ends of unfamiliar actions. In the intransitive action observation PET scans, activation in somatosensory cortex was negatively correlated with the ability to copy the means of unfamiliar actions.

4.1.2. Materials and methods

Subjects

Subjects were the same as those used in Chapter 3: 4 chimpanzees housed at the Yerkes National Primate Research Center, 2 male and 2 female, ages 18-24. All had previous experience working on cognitive behavioral tasks. One male and 1 female , Scott and Katrina, had been previously trained to imitate non-object-oriented actions ("do as I do") in a 1995 study (Custance, Whiten et al. 1995). The other male and female, Patrick and Faye, received no such training.

Behavioral task

The behavioral task was based on two previous chimpanzee studies which successfully measured chimpanzees' tendencies to copy the means versus the ends of observed actions (Tomasello, Savage-Rumbaugh et al. 1993, Bjorklund, Yunger et al. 2002). The objects and demonstrated actions are listed in **Table 4.1.1**. Unfamiliar actions, as far as we could determine, had never been observed or carried out by the chimps before – for example, opening a carabineer or blowing on a pinwheel. Familiar actions were frequently demonstrated by human experimenters in the chimps' daily environment, but the chimpanzees were rarely or never able to attempt these actions themselves – for example, putting on a glove or using a key to open a lock.

For each object, the chimpanzee was allowed 5 minutes of free play with the object. This was termed the "baseline" trial and allowed the chimpanzee's spontaneous interactions with the object to be recorded. After 5 minutes, the chimpanzee was called to the cage front where the experimenter and videographer were sitting. The experimenter demonstrated the action once and then waited for 30 seconds, during which time the chimpanzee could interact with the object. This was termed a "demonstration trial." Demonstration trials were repeated until the chimpanzee's behavior did not change for 3 consecutive demonstrations. The experimenter did not instruct the chimpanzee in any way. Chimpanzees received occasional sips of sugar-free KoolAid to maintain their involvement in the interaction, regardless of whether they copied the demonstration. All behavior was recorded on video.

Data analysis

Chimpanzees received points for copying the means (movements/methods) of demonstrated actions, copying the ends (results), or successfully using tools. The component means and ends used to score each video are listed in **Table 4.1.1**. One point was given for successful means or ends copying or for successful tool use. One-half point was given for unsuccessful, incomplete, or approximated means or ends copying or tool use. Subjects did not receive points for copying unfamiliar actions if they spontaneously produced the action during the baseline trial. Subjects did receive points if a familiar action was produced in the baseline trial (since the action had effectively been previously demonstrated in the subject's normal daily life). The tool use scale was not intended to measure social learning, but simply to measure proficiency at using tools, so points were given for successful tool use even if this occurred prior to the experimenter's demonstration or in a manner that was not congruent with the demonstration. Each subject received a score for Copying Means, Copying Ends, and Tool Use.

Unfortunately, a video camera was dropped and some videos were lost. If a baseline and/or demonstration trial video was missing, that action was not scored for that chimp. Actions were not reattempted since multiple exposures to the actions/objects might influence results. In order to control for different numbers of actions/objects in different subjects, each score was divided by the total number of points possible for that category.

4.1.3. Results

Analysis of behavior

Behavior scores are shown in **Figure 4.1-3**. These scores were inputted in a repeated measures ANOVA with factors of familiarity (2 levels: familiar or unfamiliar) and scale (3 levels: Copy Means, Copy Ends, and Tool Use), and a between-subjects measure of training (participation in the 1995 study). This revealed a significant main effect of scale ($F=30.497$, $df=2$, $p=.004$). Follow-up paired t-tests showed that regardless of participation in the 1995 study and regardless of the familiarity of the demonstrated action, chimpanzees received higher scores on the Copy Ends scale than the Copy Means scale ($t=7.344$, $df=3$, $p=.005$), and higher scores on the Tool Use scale than either the Copy Ends or Copy Means scale ($t=4.238$, $df=3$, $p=.024$ and $t=6.128$, $df=3$, $p=.009$, respectively).

The repeated measures ANOVA also revealed a significant interaction between familiarity and scale ($F=7.248$, $df=2$, $p=.047$). Follow-up paired t-tests showed that this interaction effect was attributable to the fact that, regardless of participation in the 1995 imitation-training study, chimps had significantly greater Tool Use than Copying Means scores for unfamiliar actions ($t=3.85$, $df=3$, $p=.031$). There was no significant difference between Copying Means scores for familiar vs. unfamiliar actions, Copying Ends scores for familiar vs. for novel actions, or Tool Use scores for familiar vs. for novel actions (respectively, $t=1.796$, $df=3$, $p=.170$; $t=.943$, $df=3$; $p=.415$; $t=-.711$, $df=3$, $p=.528$).

The repeated measures ANOVA also revealed a significant interaction between familiarity, scale, and training ($F = 10.364$, $df = 2$, $p = .026$). An independent samples t-test showed that subjects who received “do as I do” training as part of the 1995 study received higher Copying Means and Tool Use scores for familiar actions ($t=4.841$, $df=2$, $p=0.40$ and $t=4.333$, $df=2$, $p=.049$, respectively).

Training X activation effects

Because chimpanzees who participated in the 1995 imitation-training study were significantly better at some behavioral measures (copying means and tool use for familiar actions), membership in that study was used as a grouping variable in an independent measures t-test on ROI activation values in the transitive and intransitive action observation PET scans. Chimpanzees who participated in the 1995 imitation-training study had significantly more activation in the PMv ROI during transitive action observation (t=4.710, p=.042, **Figure 4.1-4**). Imitation-trained chimpanzees also showed a trend toward more activation in the LOC ROI during transitive action observation, although this did not reach significance (t=3.262, p=.083).

Correlations between behavior and PET scan activation

Scores on each scale were inputted to a bivariate correlation analysis with the number of above-threshold voxels in each ROI shown in the previous section, **Figure 3.2-5**. The threshold was the top 1% of the robust mean of the histogram of voxel values, as described in Sections 3.1 and 3.2. A one-tailed significance threshold of $p<.05$ was used since the *a priori* hypothesis was that increased copying behavior would correlate with increased activation in regions of the social learning network during action observation.

Correlations between activation and behavior or training are shown in **Figure 4.1-5**. In the transitive action observation PET scans, the number of activated voxels in the PMv ROI was correlated with Tool Use scores for familiar actions (r=.919, p=.030). Activation in the LOC ROI was correlated with Copying Means scores for unfamiliar (r=.900, p=.050) and familiar actions (r=.926, p=.037) and with Copying Ends scores for unfamiliar actions (r=.985, p=.007). In the intransitive action observation PET

scans, the number of activated voxels in the S1-S2 ROI was negatively correlated with Copying Means scores for unfamiliar actions (r=-.919, p=.040).

4.1.4. Discussion

We found that chimpanzees are better at copying the results than the methods of observed actions, which is congruent with a long body of past research (reviewed in (Whiten, McGuigan et al. 2009)).

Subjects who participated in the 1995 study received training to copy non-object-directed limb movements. Over a decade later, these subjects still had measurable behavioral differences from subjects who did not receive this training. These behavioral differences may actually be a result of this training, but we cannot discount the possibility that these chimpanzees were simply chosen for the "do as I do" study because they were naturally better imitators. Regardless of the reason, these chimpanzees were significantly better at copying the means (specific component movements) of familiar actions. They were also better at using tools in ways which were frequently demonstrated by human experimenters in their daily lives but which had rarely or never been carried out by the chimps themselves, like using keys to open locks. While viewing transitive grasping actions, these imitation-trained chimpanzees had more activation in ventral premotor cortex and perhaps lateral occipital cortex. This suggests that greater activation in PMv and perhaps LOC while observing others' actions may be a determinant of the ability to later copy those actions. This possibility is supported by previous research on the roles of PMv and LOC in action observation.

Ventral premotor cortex in macaques is thought to contain a "vocabulary of motor acts" (Rizzolatti, Camarda et al. 1988). Macaque PMv contains mirror neurons which respond

to both performed and observed object-directed grasping actions similar to those in this chimpanzee study (Rizzolatti, Fadiga et al. 1996). Performed and observed object-directed actions also active human ventral premotor cortex (Caspers, Zilles et al. 2010, Molenberghs, Cunnington et al. 2012), and disruption of human ventral premotor cortex via transcranial magnetic stimulation impairs perception and discrimination of biological motion (Candidi, Urgesi et al. 2008, van Kemenade, Muggleton et al. 2012). Human imitation involves ventral premotor cortex and the adjacent section of the inferior frontal gyrus (Buccino, Vogt et al. 2004, Iacoboni 2005, Rumiati, Weiss et al. 2005, Molenberghs, Cunnington et al. 2009). These findings suggest that the imitation-trained chimps' greater PMv activation may be related to their greater ability to copy demonstrated actions. Future great ape or human studies could address whether an individual's ability to copy observed actions is related to the amount of PMv activation during action observation or to neuroanatomical measurements in PMv.

Lateral occipital cortex is part of the ventral visual stream (the "what" pathway) involved in object recognition (Goodale and Milner 1992, Grill-Spector, Kourtzi et al. 2001). It is activated during not only visual but also haptic object discrimination, and is hypothesized to contain modality-independent representations of geometric shape (Lacey, Tal et al. 2009, Lacey and Sathian 2011). Patterns of responses in LOC to hands and tools are very similar (Bracci, Cavina-Pratesi et al. 2012). This region is also implicated in tool use. Successful tool use is thought to rely on the integration of semantic knowledge about object and tool identities, functions, and uses (stored in LOC) with information from the dorsal visual stream (the "how" pathway) (Frey 2007, Valyear and Culham 2010). LOC is activated during the observation of tool-grasping actions (Valyear and Culham 2010). In addition, activation in LOC shows practice effects as human subjects learn to make stone tools of the earliest kind found in the archaeological

record (Oldowan tools) (Stout and Chaminade 2007), suggesting that the kind of processing that this region performs was important in the evolution of human tool use. These findings suggest that greater LOC activation might confer more successful tool use. However, in the present study, LOC activation was greater, but not significantly greater, in imitation-trained vs. untrained chimpanzees. Perhaps a study with a larger subject size would be able to determine whether greater LOC activation may be related to a greater ability to copy tool-use actions. Future great ape or human studies could address whether an individual's ability to copy tool use actions is related to the amount of LOC activation during tool use observation or to neuroanatomical measurements in LOC.

Interestingly, despite the seemingly straightforward mapping between PMv activation and imitation and LOC activation and tool use, PMv activation was correlated with tool use and LOC activation was correlated with copying ends and means of demonstrated actions. In fact, these correlations are also consistent with other published results. LOC shows sensitivity to action goals (Vingerhoets, Honore et al. 2010), and a posterior portion of lateral occipitotemporal cortex "mirrors" observed action in the sense that it is activated by both seeing and doing similar actions (Caspers, Zilles et al. 2010, Molenberghs, Cunnington et al. 2012), functions which are typically more associated with PMv. In the Oldowan tool-making study, PMv also showed practice effects, suggesting that this region was also important in the evolution of human tool use (Stout and Chaminade 2007). This suggests that the nature of action representation in the brain cannot be boiled down to a simple "region X does function Y" schematic. Imitation and tool use, along with other complex cognitive abilities like gesture and language, rely on overlapping brain networks and are hypothesized to have co-evolved

(Arbib 2005, Frey 2008, Iriki and Taoka 2012). More research is needed in order to fully understand the localized vs. distributed nature of these functions.

It is notable that many of our observed effects hold only for familiar and not unfamiliar demonstrated actions. The experiments on which this one was based (Tomasello, Savage-Rumbaugh et al. 1993, Bjorklund, Yunger et al. 2002), as well as most other chimpanzee social learning experiments, have used actions which were novel to the subjects. However, it may be difficult for chimpanzees to socially learn a completely unfamiliar action after only a few demonstrations, especially when the novel action is embedded in a contrived experimental context rather than a naturalistic goal-directed behavior. This experiment demonstrates that a viable alternative approach is to measure whether chimps spontaneously "pick up" actions that they frequently see demonstrated by their human caretakers. This approach is limited because the demonstration actions need to be frequently enacted by caretakers but infrequently or never available for the chimps themselves to carry out – and the number of such actions is small. However, it has the benefit of being more "ecologically relevant," and may capture a fuller range of chimpanzees' social learning abilities.

It should be pointed out that this behavioral study involved only a few chimpanzees and a relatively small number of demonstrated actions. Other similar studies have typically used a larger number of subjects and actions, and caution should be taken in interpreting such a small dataset. However, this study does replicate those earlier findings, and it adds a novel piece of information which is the correlation between copying and tool use behavior and brain activation in PMv and LOC. These behavior/activation correlations are in line with previous research in humans and macaques, suggesting that the results

of this small study might be used as a foundation for future, more in-depth investigations.

Table 4.1-1. Objects and actions for test of means/ends copying

Object and demonstrated action			Definition of ends	Definition of means
NOVEL ACTIONS *(no points for means/ends if target action occurs in baseline)*	**Tool use**	TONGS AND GRAPE Grasp tongs with hand; use tongs to pick up grape and bring it to self	Tongs moving grape; chimps get grape	Use hands not feet to manipulate; use tongs to pinch not nudge grape; chimp gets grape via tongs not another method
		PASTA SPOON AND GRAPE Turn spoon upside down to use it as a rake; extend spoon toward grape and capture it; pull back toward self to retrieve grape	Grape moves toward cage mesh; chimp gets grape	Grasp spoon with hand not foot; flip spoon so that the bowl is pointing downwards; capture grape under spoon
		POKER STICK AND BANANA Grasp flat end of poker stick; use pointy end to spear banana; retrieve stick with banana on end	Banana proximity decreases; get banana	Use hands not feet to manipulate; use pointy end not flat end to touch banana; get banana by spearing not nudging or other method
		BACK SCRATCHER BRUSH Grasp brush by handle; reach over shoulder; scratch back repetitively	Brush directed toward body; bristles in contact with body; body is scratched (by any object)	Grasp brush by handle not head; use hand not foot to manipulate; reach over shoulder not around ribcage
	Non-tool use	PIPE RATTLE Remove cap from pipe; pour balls into pipe from cup; put cap back on pipe; shake to produce noise	Cap is off of pipe; banana balls are out of cup; banana balls are inside pipe; cap is back on pipe; noise is produced	Use hands not feet to manipulate; grasp cap with one hand and pipe with the other; pour balls directly from cup to pipe; shake pipe
		PINWHEEL Take a deep breath; orient face toward pinwheel; pucker lips; blow on pinwheel	Pinwheel spins	Take a breath; orient face toward pinwheel; pucker lips; blow
		CARABINEER ATTACHED TO CHAIN Grasp carabineer in hand; use other hand to depress lever; unhook from chain; release lever	Carabineer is "open;" carabineer separated from mesh/chain	Use hand not foot to grasp; use fingers not toes to depress lever

Table 4.1-1 (continued). Objects and actions for test of means/ends copying

		Object and demonstrated action	Definition of ends	Definition of means
FAMILIAR ACTIONS *(Points for target action in baseline)*	**Tool use**	LOCK AND KEY Hold key and lock, one in each hand; insert key into lock and turn; open lock; remove key from lock	Key inside lock; lock is opened; key removed from lock	Use one hand to grasp key and other to grasp lock; turn key inside lock; use hand not foot to open lock; turn key the other way
		CRAYON AND CARDBOARD Pick up crayon and cardboard with hands; orient pointed end of crayon toward cardboard; draw a circle	Markings on cardboard; markings are circular	Use hands not feet to grasp objects; touch pointed end of crayon not flat end to cardboard
		NAIL CLIPPERS Open lever of nail clippers; insert fingernail into clipping end; depress lever to clip fingernail; close lever	Fingernail is cut	Use hand not foot to grasp; use fingers not toes to open; cut fingernail using clippers not biting/picking; use fingers not toes to close (no points for rotating lever; basic affordance of object)
	Non-tool use	SURGERY MASK Unfold mask using hands; hold the mask flat in front of self; put over face; put strings behind ears	Mask is open; mask is oriented toward body; mask is on body (specifically, on face); strings behind ears	Use hands not feet to manipulate mask
		BONNET Unfold bonnet using hands; put bonnet on head	Bonnet is open; bonnet is oriented toward body; bonnet is on body (specifically, on head)	Use hands not feet to manipulate
		GLOVE Hold glove with fingers oriented down; insert hand; put fingers of hand into fingers of glove	Hand inside glove; fingers of hand inside fingers of glove	Use hands not feet to manipulate; hold glove with fingers oriented down

Table 4.1-2. Chimpanzee behavior in test of means/ends copying

Faye – received no special training on copying behavior

TRIAL			Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
NOVEL ACTIONS *(no points if target action occurs in baseline)*	**Tool use**	TONGS AND GRAPE	Tried to use end of tongs to scoop up grapes.	Reached toward grapes with fingers; did not use tongs.	0	0	0.5
		PASTA SPOON AND GRAPE	Tried to pull spoon through cage mesh; banged spoon on platform.	Oriented spoon toward grapes correctly and extended spoon outwards but didn't "trap" grapes.	0.5	0.5	0.5
		POKER STICK AND BANANA	Used poker to scoot food pieces toward cage mesh, ate several.	Nudged banana with poker several times but did not get banana.	0	0	1
		BACK SCRATCHER BRUSH	Repeatedly returned brush; tried to break it.	Occasionally held the brush but did not use it, then put it down and ignored it.	0	0	0
	Non-tool use	PIPE RATTLE	Repeatedly returned objects.	*Video lost*	*Not scored*		
		PINWHEEL	Stuck lips through cage mesh in front of pinwheel and "pouted" them out; extruded tongue; blew a "raspberry" at the pinwheel.	Same but less frequent.	0	0	-N/A-
		CARABINEER	Depressed lever several times and returned repeatedly.	*Video lost*	*Not scored*		
TOTAL POINTS					.5	.5	2
POSSIBLE POINTS					5	5	4
SCORE					.1	.1	.5

Table 4.1-2 (continued). Chimpanzee behavior in test of means/ends copying

Faye (continued) – received no special training on copying behavior

TRIAL			Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
FAMILIAR ACTIONS *(Points for target action in baseline)*	**Tool use**	LOCK AND KEY	Tried to open lock to adjoining cage, did not direct key at given lock.	Ignored/returned objects.	0.5	0.5	0.5
		CRAYON AND CARDBOARD	Touched crayon lightly to cardboard a few times and "drew" but didn't press down hard. Broke crayon, mostly just shredded cardboard.	*Video lost*	*Not scored*		
		NAIL CLIPPERS	Rotated lever away but did not clip nails, tried to insert into cage lock.	Rotated lever away but did not clip nails. Mainly repeatedly returned them to experimenters.	0	0	0
	Non-tool use	SURGERY MASK	Returned through cage mesh.	Did not pick up by strings or place toward face.	0	0	-N/A-
		BONNET	Repeatedly returned.	*Video lost*	*Not scored*		
		GLOVE	Picked up with fingers oriented down, looked inside, started to put fingers inside but didn't fully.	Didn't look inside or put fingers inside.	0	0.5	-N/A-
TOTAL POINTS					.5	1	.5
POSSIBLE POINTS					4	4	2
SCORE					.125	.25	.25

TOTAL FOR BOTH NOVEL AND FAMILIAR ACTIONS			
TOTAL POINTS	1	1.5	2.5
POSSIBLE POINTS	9	9	6
SCORE	0.11	0.17	0.42

Table 4.1-2 (continued). Chimpanzee behavior in test of means/ends copying

Katrina – received "do as I do" training in 1995 study

TRIAL			Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
NOVEL ACTIONS *(no points if target action occurs in baseline)*	**Tool use**	TONGS AND GRAPE	Played with/destroyed tongs.	Used wrong end of tongs to prod fruit toward cage but did not successfully obtain it.	0	0.5	0.5
		PASTA SPOON AND GRAPE	Tried to get grape with spoon (unsuccessfully); did not flip the spoon over.	Tried to get grape with spoon but never flipped it over the right way.	0	0	0.5
		POKER STICK AND BANANA	Used poker to nudge food toward cage.	One unsuccessful spearing action, then went back to nudging.	0.5	1	1
		BACK SCRATCHER BRUSH	Interacted with brush but no scratching.	Ignored/returned to experimenters.	0	0	0
	Non-tool use	PIPE RATTLE	Ate banana balls, tried to open pipe unsuccessfully.	Ate banana balls, returned pipe through ceiling.	0	0	-N/A-
		PINWHEEL	Looked at object, reached towards it.	Puckered lips at pinwheel.	0.5	0.5	-N/A-
		CARABINEER	Interacted with carabineer but did not depress lever.	Minimal interaction.	0	0	-N/A-
TOTAL POINTS					1	2	2
POSSIBLE POINTS					7	7	4
SCORE					.14	.29	.50

Table 4.1-2 (continued). Chimpanzee behavior in test of means/ends copying

Katrina (continued) – received "do as I do" training in 1995 study

TRIAL			Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
FAMILIAR ACTIONS *(Points for target action in baseline)*	**Tool use**	LOCK AND KEY	Directed key at given lock, successfully unlocked, then tried to use key to open door/cage locks.	Same.	1	1	1
		CRAYON AND CARDBOARD	Ate them both.	Immediately drew on cardboard, then ate items, then drew again after 2nd demo.	1	1	1
		NAIL CLIPPERS	Spun end around, examined closely, scratched with fingernail.	Examined with mouth/hands.	0	0	0
	Non-tool use	SURGERY MASK	Picked apart.	*Video lost.*	*Not scored*		
		BONNET	Picked apart.	Little interest.	0	0	-N/A-
		GLOVE	Ignored object.	Ignored object.	0	0	-N/A-
TOTAL POINTS					2	2	2
POSSIBLE POINTS					5	5	3
SCORE					.4	.4	.67

TOTAL FOR BOTH NOVEL AND FAMILIAR ACTIONS			
TOTAL POINTS	3	4	4
POSSIBLE POINTS	12	12	7
SCORE	.25	.33	.57

Table 4.1-2 (continued). Chimpanzee behavior in test of means/ends copying

Patrick – received no special training on copying behavior

TRIAL			Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
NOVEL ACTIONS *(no points if target action occurs in baseline)*	**Tool use**	TONGS AND GRAPE	Tossed around the cage.	Pushed through cage mesh.	0	0	0
		PASTA SPOON AND GRAPE	Banged spoon on platform, food-begged at experimenters, reached toward grape with hand, directed spoon at grapes but did not obtain any.	Thrust spoon toward grapes but more of a "smashing" than "trapping" movement; knocked some grapes into reach of hand.	0	0	1
		POKER STICK AND BANANA	Poked at banana; stabbed at it until it flipped into grabbing distance.	Flailed and stabbed at banana.	0	0	1
		BACK SCRATCHER BRUSH	Played with, returned, and ignored brush.	Touched bristles to the top of his head.	0	0.5	0.5
	Non-tool use	PIPE RATTLE	Smashed banana balls, tore up cup, dragged pipe across mesh, stood on pipe, hit pipe on floor.	Smashed pipe on ground a few times, poured out banana balls.	0	0	-N/A-
		PINWHEEL	Looked at object, reached towards it.	Looked at object, reached towards it.	0	0	-N/A-
		CARABINEER	Swatted it a few times.	Touched a few times, then ignored it.	0	0	-N/A-
TOTAL POINTS					0	0.5	2.5
POSSIBLE POINTS					7	7	4
SCORE					0	.07	.63

Table 4.1-2 (continued). Chimpanzee behavior in test of means/ends copying

Patrick (continued) – received no special training on copying behavior

		TRIAL	Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
FAMILIAR ACTIONS *(Points for target action in baseline)*	**Tool use**	LOCK AND KEY	Ignored/returned.	Ignored/returned.	0	0	0
		CRAYON AND CARDBOARD	Little interaction.	Little interaction.	0	0	0
		NAIL CLIPPERS	Some interaction (tossed around, spun open lever).	Little interaction.	0	0	0
	Non-tool use	SURGERY MASK	Very little interaction.	Very little interaction.	0	0	-N/A-
		BONNET	Mostly just returned it to me. Tossed up in air once, examined once.	*Video lost*	*Not scored*		
		GLOVE	Opened glove and inserted fingers partially.	*Video lost*	*Not scored*		
TOTAL POINTS					0	0	0
POSSIBLE POINTS					4	4	3
SCORE					0	0	0

TOTAL FOR BOTH NOVEL AND FAMILIAR ACTIONS			
TOTAL POINTS	0	0.5	2.5
POSSIBLE POINTS	11	11	7
SCORE	0	0.05	0.36

Table 4.1-2 (continued). Chimpanzee behavior in test of means/ends copying

Scott – received "do as I do" training in 1995 study

TRIAL			Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
NOVEL ACTIONS *(no points if target action occurs in baseline)*	**Tool use**	TONGS AND GRAPE	Tried to pull apart; bit end; held and "clapped" the ends together correctly; oriented toward grape.	Poked tongs toward box with grapes.	0.5	0.5	0.5
		PASTA SPOON AND GRAPE	Manipulated rake in vicinity of grape.	Manipulated rake in vicinity of grape.	0.5	0.5	0.5
		POKER STICK AND BANANA	Manipulated poker in vicinity of banana.	Poked a piece of primate chow and then speared the banana.	1	1	1
		BACK SCRATCHER BRUSH	Bit the brush, wedged it into corner, then ignored.	Scratched self with hands repeatedly.	0	1	0
	Non-tool use	PIPE RATTLE	Ate banana balls, tried to open pipe, hit on ground.	Dragged pipe along cage mesh.	0	0	-N/A-
		PINWHEEL	Stared intently and tried to touch.	Puckered lips at pinwheel.	0.5	0.5	-N/A-
		CARABINEER	Pulled and bit carabineer, fingered lock, wound chain around mesh.	Manipulated and examined carabineer but did not depress lever.	0	0	-N/A-
TOTAL POINTS					2.5	3.5	2
POSSIBLE POINTS					7	7	4
SCORE					.36	.5	.5

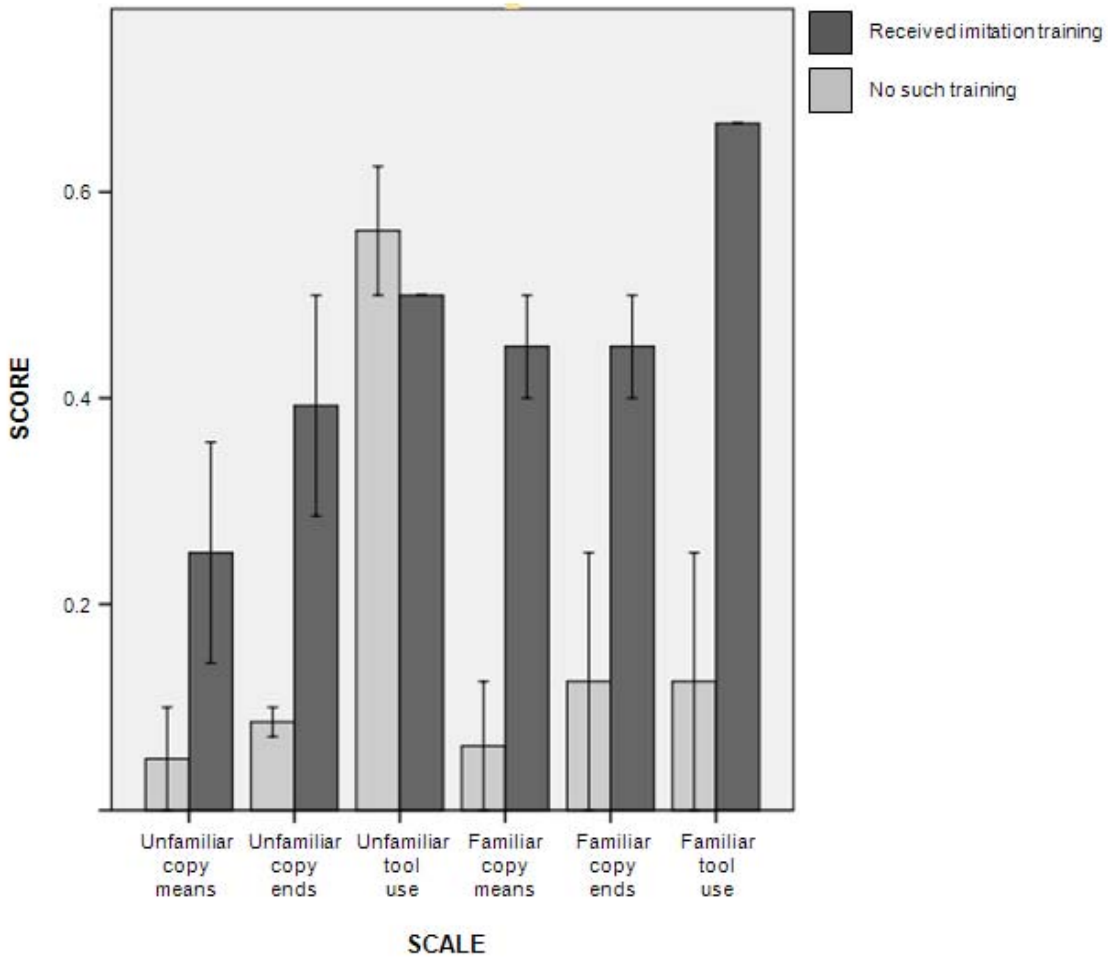
Table 4.1-2 (continued). Chimpanzee behavior in test of means/ends copying

Scott (continued) – received "do as I do" training in 1995 study

TRIAL			Summary of behavior in baseline trial	Summary of behavior in demonstration trials	Copying Means	Copying Ends	Tool Use
FAMILIAR ACTIONS *(Points for target action in baseline)*	**Tool use**	LOCK AND KEY	Successfully unlocked, and tried to unlock adjoining cage.	Successfully unlocked.	1	1	1
		CRAYON AND CARDBOARD	Drew on the cardboard immediately.	Drew lines in a circular pattern.	1	1	1
		NAIL CLIPPERS	Fiddled with cage locks.	Spun the handle around but didn't clip nails.	0	0	0
	Non-tool use	SURGERY MASK	Put on erection.	Held near face (did not place on erection).	0.5	0.5	-N/A-
		BONNET	Put on erection.	Put on erection again, but this time unfolded the bonnet like the demonstrator did.	0.5	0.5	-N/A-
		GLOVE	Did not interact.	Did not interact.	0	0	-N/A-
TOTAL POINTS					3	3	2
POSSIBLE POINTS					6	6	3
SCORE					.5	.5	.67

TOTAL FOR BOTH NOVEL AND FAMILIAR ACTIONS			
TOTAL POINTS	5.5	6.5	4
POSSIBLE POINTS	13	13	7
SCORE	.42	.5	.57

Figure 4.1-3. Scores on test of means/ends copying



Mean score of imitation-trained and non-imitation-trained chimpanzees for copying means, copying ends, and tool use in unfamiliar and familiar demonstrated actions.

Figure 4.1-4. Training X activation effects

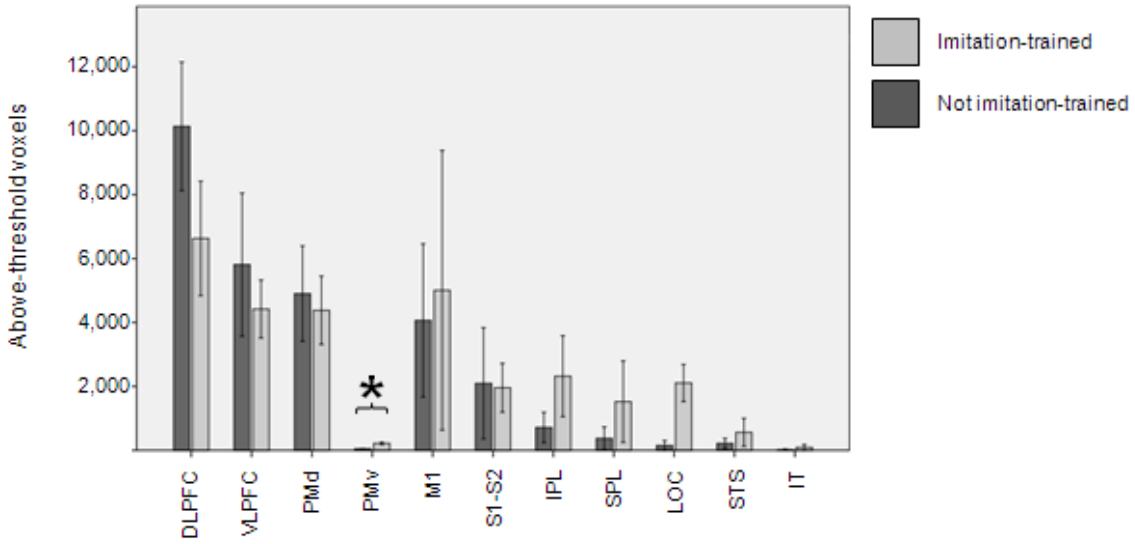
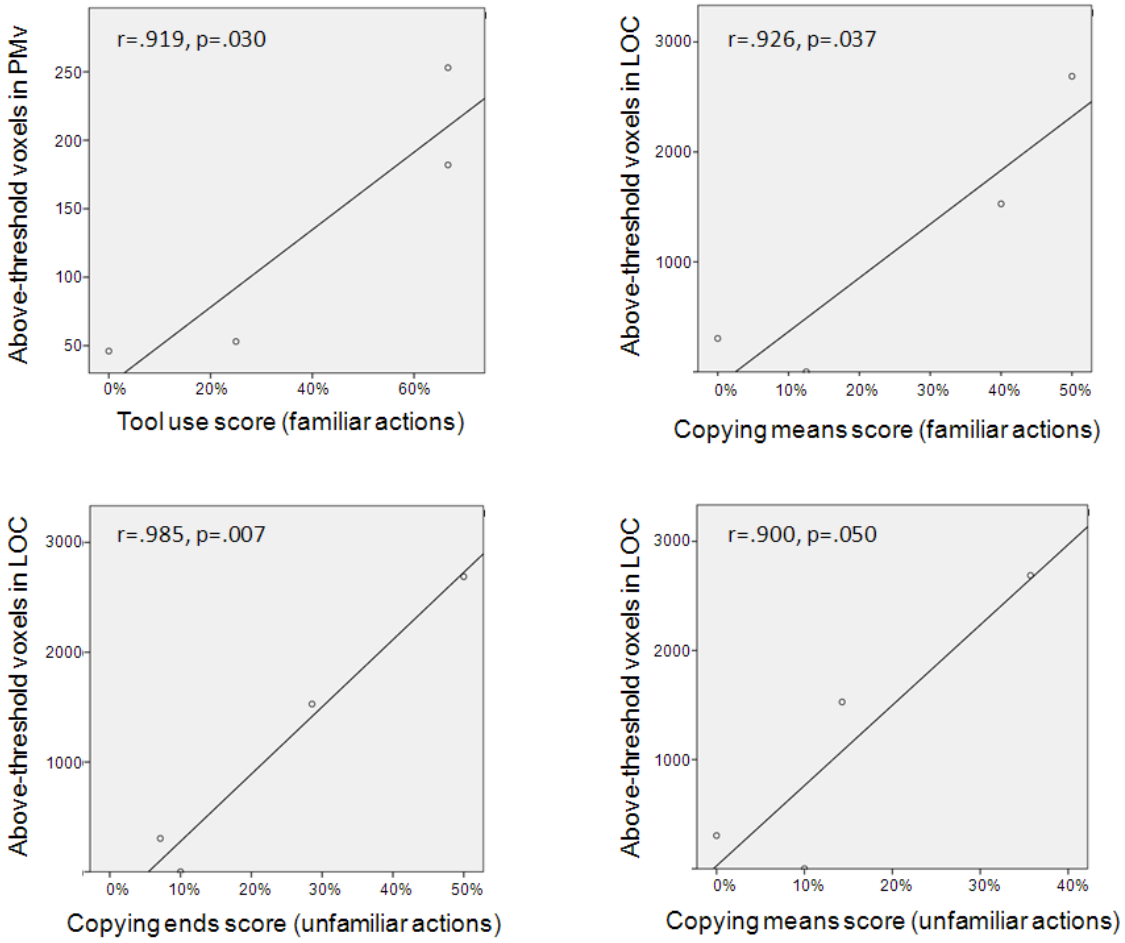


Figure 4.1-5. Correlations between activation and behavior



Chapter 5:

Conclusions

5.1. Summary of results

The goal of this dissertation was to investigate neural adaptations for social learning in primate evolution, specifically adaptations underlying humans' unique capacity to copy not only the ends or outcomes of observed actions but also their means or movement details. The general hypothesis was that differences in the component processes that occur when a chimpanzee versus a human views another individual's action translate to differences in the way in which chimpanzees versus humans replicate that observed action. In other words, we hypothesized that species differences in social learning are due to species differences in the neural networks that process observed actions. This general hypothesis was applied to known information about the neural bases of action observation and social learning to formulate a set of studies on the connectivity of the mirror system, activations during action execution and observation, and social learning behavior. Major findings are summarized and discussed below.

The structural connectivity of the action observation network differs between macaques, chimpanzees, and humans. In macaques and chimpanzees, the preponderance of this circuitry consists of frontal-temporal connections via the extreme/external capsules. In contrast, humans have more substantial temporal-parietal and frontal-parietal connections via the middle/inferior longitudinal fasciculi and the third branch of the superior longitudinal fasciculus. In chimpanzees and humans but not macaques, this circuitry includes connections with inferior temporal cortex. In humans alone, connections with superior parietal cortex were also detected. We interpreted these results in light of the different functions associated with each of these regions. Since parietal cortex is associated with organizing the spatial aspects of movements, the macaque-chimpanzee-human gradient in connectivity here may be

related to the macaque-chimpanzee-human gradient in proficiency for copying movement details. Since inferotemporal cortex is associated with object and tool recognition, as well as tool concepts, chimpanzees' and humans' increased connectivity between this region and frontoparietal mirror regions may be related to the fact that chimpanzees and humans but not macaques naturally acquire tool use through social learning. Finally, since superior parietal cortex is associated with spatial awareness and attention, one possible function of humans' greater connectivity here may be related to greater awareness or attention to the spatial details of others' actions.

Chimpanzees have a frontoparietal mirror system similar to humans and macaques. This is not surprising, given that chimpanzees are phylogenetically intermediate to humans and macaques.

The chimpanzee mirror system responds to intransitive action. This supports the theory that the aspects of an observed action that are "mirrored" in the brain, determine which aspects of the observed action can be behaviorally copied. This idea would explain why macaques don't imitate: macaques copy action results but not movements (emulate but do not imitate) because their mirror systems respond to action results (transitive actions) but not movements (intransitive actions). Similarly, perhaps chimpanzees and humans are both capable of copying both action results and movements (emulating and imitating) because both species' mirror systems respond to both action results (transitive actions) and movements (intransitive actions). This suggests that the ability to copy action movements (imitate), as well as the responsiveness of the mirror system to intransitive action, emerged sometime between the macaque-chimpanzee divergence (~25-27 million years ago) and the chimpanzee-human divergence (~5-6 million years ago). If this idea is true, then other primate

species that can imitate (e.g., marmosets (Voelkl and Huber 2000)) should have mirror system activation to observed intransitive action.

The chimpanzee frontal mirror region is more active than the parietal mirror region during action observation. This may explain why although chimpanzees are *capable* of imitation, they typically emulate instead. A preponderance of activation in frontal vs. parietal cortex may be related to greater attention to or processing of observed actions' goals, results, or meaning in a broader context rather than their spatial movement details or kinematics. Anatomically, this may be related to the fact that most of the connections we tracked from lateral temporal visual regions went directly to the frontal mirror region without passing through the parietal mirror region.

Compared to chimpanzees, humans have more activation in ventral premotor cortex, inferior parietal cortex, and inferior temporal cortex. Chimpanzees have more activation in ventrolateral prefrontal cortex. This may reflect more top-down processing or a higher-level more abstract representation of observed action, which could explain their behavioral tendency toward copying action results/outcomes rather than movement details. Humans' increased occipitotemporal and parietal activation may reflect more bottom-up processing or more attention to the lower-level features of observed action, which could explain humans' behavioral tendency toward copying movement details. Humans' increased inferior parietal and inferotemporal activations could be due to their increased connectivity in these same regions.

Variation in chimpanzee social learning behavior may be related to variation in brain activation during action observation. In line with previously published research, chimpanzees were better at copying the ends than the means of demonstrated actions. This was expected and validated the methodological approach. Chimpanzees who participated in a 1995 imitation-training study were better at copying means and successfully using tools in familiar actions. These chimpanzees also had more activation in ventral premotor cortex and lateral occipital cortex while observing object-directed grasping actions. In the transitive action observation PET scans, activation in ventral premotor cortex was correlated with chimpanzees' ability to use tools. Activation in lateral occipital cortex was correlated with the ability to copy demonstrated actions' means and ends. The bulk of previous research on the roles of ventral premotor and lateral occipital cortex would suggest that imitation-trained chimpanzees' greater PMv activation during action observation is related to their increased proficiency at copying means and ends, and that their greater LOC activation is related to their increased proficiency at tool use. However, actual ROI-behavior correlations were opposite. The results support the hypothesis that individual differences in social learning are related to individual differences in neural responses to observed action, but suggest that the neural representation of observed action may be more distributed than is typically assumed, and that a conceptual framework that attempts to localize specific aspects of observed action to discrete regions may be overly simplistic. The study's small sample size warrants replication in a larger group.

An ultimate explanation?

The results reported here offer a potential proximate explanation for species differences in social learning – anatomical and functional adaptations to the brain. An ultimate

explanation, though, must take into account selection pressures over the course of primate evolution, and offer some rationale for *why* it is more advantageous for humans to imitate rather than emulate. Of course, such explanations are highly speculative, but may still be useful for structuring future thought about this topic.

To start, why *don't* macaque monkeys imitate? This dissertation postulates a proximal explanation – their mirror systems respond only to results, not movements, so they can only *copy* results, not movements. One interpretation is that the macaque mirror system "boils actions down to their results," representing only relatively higher-order information about others' behavior, like what the behavior accomplishes (Lyons, Santos et al. 2006). This may be useful for understanding the personally relevant aspects of others' actions. In other words, jumping straight to "What is that other monkey trying to accomplish?" without processing issues like "What methods is he using to do it?" might facilitate a quick understanding of "How does it affect me?"

Similarly, it has been suggested that chimpanzees emulate rather than imitate because this is the more adaptive strategy for their socioecological niche (Horner and Whiten 2005). A focus on the involved objects in an action, along with the general outcome that the action accomplishes, may allow chimpanzees to learn about means-ends dependencies in a way that supports adapting that information to new situations that might not be exactly similar. This might be especially important for socially learned actions for which understanding means-ends dependencies are crucial to successfully completing the action – e.g., tool use.

Along the same lines, humans must imitate rather than emulate because it is the most adaptive strategy for *our* socioecological niche. It might be advantageous for socially

learned actions where kinematics are very important – e.g., shooting a bow or flinting an arrowhead. This could also be advantageous for socially learned actions for which understanding means-ends dependencies may be difficult – e.g., procedures for treating illness or preserving food. Chimpanzees imitate rather than emulate in Horner and Whiten's puzzle box experiment when the box is opaque and the means-ends dependencies are impossible to extract (Horner and Whiten 2005). In a sense, many of the socially learned actions in modern human society are like this – they are so complex that few people understand them. As humans were evolving, and the average individual human became more and more intelligent, more individuals would discover more ways to address the challenges of surviving.

5.2. Conclusions and future directions

In summary, these experiments provided new information about neural adaptations in the action observation networks of macaques, chimpanzees, and humans that may underlie species differences in social learning. In particular, two specific findings have great potential explanatory power and could be further investigated with future research:

1) The ability to "mirror" intransitive action may reflect that observed actions are mapped onto the observer's motor system not only at the level of results/outcomes but also at the level of movements/methods. This ability seems to have evolved sometime after the macaque/chimpanzee divergence in primate evolution and may explain why chimpanzees and humans but not macaques are capable of copying movement details (imitating). This could be further investigated in the following ways:

- Other primate species that can imitate movements should mirror observed intransitive action. Other primate species that cannot imitate movements should not.
- In humans, individual variation in proficiency at copying intransitive action should correlate with individual variation in mirror responses to observed intransitive action.
- Neurological and psychiatric conditions that impair imitation should involve a reduced mirror response to observed intransitive action.

2) Beyond the *ability* to copy observed actions' movement details, individuals have to *choose* to actually do so. Humans do this with much greater frequency than chimpanzees. This bias may be related to the relative allocation of neural resources across the action observation network – humans' greater activation of parietal and occipitotemporal regions may reflect more detail-oriented, bottom-up processing, while chimpanzees' greater activation of prefrontal regions may reflect more conceptual, abstract, top-down processing. Interestingly, this contradicts the standard notion that human cognition and behavior are always more conceptually-driven than chimpanzee cognition and behavior. Because a bias toward copying movement details is thought to have been a crucial factor in the emergence of cumulative culture, these results may help explain why humans are so different from the rest of the animal kingdom. This could be further investigated in the following ways:
   - Individual variation in the bias toward copying movement details (over-imitation) should be related to individual variation in bottom-up vs. top-down processing of observed action.

- Experimental manipulations on the demand for top-down/outcome-oriented processing vs. bottom-up/movement detail-oriented processing should cause changes in the balance of prefrontal vs. parietal and occipitotemporal activation.
- The bias toward copying movement details appears to have evolved sometime after the chimpanzee/human divergence. If it is possible to identify cortical surface (endocast) or genetic correlates of this bias, then the emergence of these features should date to around the time that evidence for cumulative culture appears in the archaeological record.

Appendix

A-1. Comparisons between action execution/observation chimpanzee FDG-PET scans from the present dissertation and previously published chimpanzee resting state FDG-PET scans[11]

This appendix deals with some issues relevant to Chapter 3.1. The main findings of that chapter were that in action execution and observation activate a chimpanzee frontoparietal network similar to previously reported macaque and human frontoparietal networks, and that chimpanzee homologs of macaque frontal and parietal mirror neuron regions activate to observed intransitive action. An implicit assumption in these analyses is that the observed frontoparietal activations are causally related to the subjects' behavior during the uptake period (i.e., action execution or action observation). Ideally, a control condition with a lack of action execution or observation would show a lack of activation in these regions. Initial control analyses were carried out using the resting state FDG-PET scans from a previous study (Rilling, Barks et al. 2007), in which the author of this dissertation was not directly involved. Chimpanzee homologs to macaque frontal and parietal mirror neuron regions have above-threshold activation in greater percent of their volume during action execution, transitive observation, and intransitive observation than during rest (**Figure 3.1-19 A**). This supports the idea that these activations are causally related to the execution and observation of the object-directed grasping behavior under study. Additionally, after the dissertation defense, an additional set of analyses were carried out, involving SPM comparisons on scans with the cerebellum and brainstem masked out; these clearly show significant differences between the experimental conditions and rest in prefrontal, premotor, parietal, and occipitotemporal regions (**Figure 3.1-5** and **Figure 3.1-6).**

However, more in-depth analyses show that there is considerable activation of broader frontoparietal regions in the resting state scans. In the previous analyses of Chapter 3.1, "mirror activations" were identified as voxels active above the 1% threshold in both

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[11] *Rilling JK, Barks SK, Parr LA, Preuss TM, Faber TL, Pagnoni G, Bremner JD, Votaw JR. A comparison of resting-state brain activity in humans and chimpanzees. Proc Natl Acad Sci U S A. 2007 Oct 23;104(43):17146-51.*

action execution and observation (i.e., the execution/transitive observation overlap and the execution/intransitive observation overlap – **Figure 3.1-16** – **3.1-18**). Repeating these analyses to incorporate the resting state scans, we plotted voxels in the top 1% of the histogram of voxel values in both an [execution-rest] subtraction image and a [transitive observation-rest] subtraction image. The same was done for the overlap between [execution-rest] and [intransitive observation-rest]. Both of these analyses yield very little activity in cortex (**Figure A.1-1** and **Figure A.1-2**). Nonetheless, the volume of activation in the chimpanzee homologues of macaque frontal and parietal mirror regions is not different between the transitive vs. intransitive analyses (**Figure A.1-3**), in line with the results of Chapter 3.1 and supporting the interpretation that these chimpanzee mirror regions do not differ between observed transitive and intransitive action to the extent that the homologous macaque regions do.

Why is the overlap between [execution-rest] and [transitive observation-rest] or [intransitive observation-rest] so small? One possibility could be that the individual subtraction images, [execution-rest], [transitive observation-rest], and [intransitive observation-rest], each show a large volume of activated voxels but that these volumes do not overlap. This would mean that the regions of the chimpanzee brain that are more active during action execution than rest are *not* the same as the regions that are more active during observation than rest. This would run counter to the interpretation drawn from the results of Chapter 3.1, that chimpanzees "mirror" both observed transitive and intransitive action.

However, examination of the individual subtraction images shows that this is not the case (execution-rest: **Figure A.1-4**; intransitive observation-rest: **Figure A.1-5**; intransitive observation-rest: **Figure A.1-6**; all thresholded to show the top 1% of the histogram of voxel values). In fact, each of these individual subtraction images shows only a small volume of cortical voxels in all 3 sets of images. However, the volume of these small activations within the ROIs is not significantly different between execution, transitive observation, and intransitive observation (**Figure A.1-7**).

Again, why are these activations so small? The answer becomes apparent upon examination of the resting state scans with the same 1% threshold (**Figure A.1-8**). These scans involve frontoparietal activations which are quite similar to the action

execution and action observation scans. In fact, there were no differences in the volume of activation in rest versus action execution in any of the 11 frontal, parietal, and occipitotemporal ROIs studied in Chapter 3.2 (**Figure A.1-9**). This result could be due to one or more of the following: (a) these frontoparietal regions are part of the chimpanzee resting state (default-mode) network, and the experiments described in Chapter 3.1 activated them in this capacity (i.e., Chapter 3.1 reports chimpanzee resting state brain activations); (b) these frontoparietal regions are part of the chimpanzee action execution/observation network, and the experiments described in Rilling et al.'s previous study (Rilling, Barks et al. 2007) activated them in this capacity; (c) the FDG-PET methodology implemented in these studies was insufficient to detect differences between action execution/observation and rest. Each of these possibilities will now be discussed.

Did the experiments described in Chapter 3.1 activate the chimpanzee default network? It seems quite likely. The behavioral tasks used in the action execution, transitive observation, and intransitive observation conditions were incredibly simple, monotonously repetitive, and far from novel; subjects spent many hours training on these tasks prior to scanning. It often appeared to be difficult for chimpanzees to maintain attention and focus on these tasks, and indeed many scheduled PET scans were cancelled when subjects abandoned the task during the uptake period. Scans from the individual conditions (**Figure 3.1-18**) show activation of medial cortical areas, which are similar to the areas activated in resting state or default mode imaging studies in macaques and humans. This supports the idea that the behavioral tasks described in Chapter 3.1 were sufficiently "boring" for the chimpanzees to activate the default network.

But, were the *lateral, inferior frontoparietal* activations, which are the focus of this dissertation, activated in this action execution/observation study because they are part of the chimpanzee default network? This seems unlikely. The involvement of these frontoparietal regions in action execution and observation is incredibly well-established in macaques and humans by many studies using a variety of different methodologies and techniques – e.g., metanalyses of over 100 human imaging studies, e.g., (Caspers, Zilles et al. 2010, Molenberghs, Cunnington et al. 2012), human non-invasive electrophysiology, e.g., (Nishitani and Hari 2000, Muthukumaraswamy and Johnson

2004, Muthukumaraswamy, Johnson et al. 2004, Fadiga, Craighero et al. 2005, Pineda 2005, Hari 2006, Candidi, Urgesi et al. 2008, Cattaneo 2010, Koch, Versace et al. 2010), macaque single-cell recordings, e.g., (Gallese, Fadiga et al. 1996, Rizzolatti, Fadiga et al. 1996, Rizzolatti, Ferrari et al. 2006, Rozzi, Ferrari et al. 2008), and macaque imaging studies, e.g., (Raos, Evangeliou et al. 2004, Nelissen, Luppino et al. 2005, Raos, Evangeliou et al. 2007, Nelissen, Borra et al. 2011). The default mode/resting state network in both macaques and humans is conceived being directly contrasted against these lateral, task-related activations (Gusnard, Raichle et al. 2001, Raichle, MacLeod et al. 2001, Kojima, Onoe et al. 2009, Mantini, Gerits et al. 2011). Furthermore, the earlier study which produced these scans did not report activations in these lateral, action observation-related frontoparietal regions as part of the chimpanzee default network (Rilling, Barks et al. 2007).

Is it possible that these frontoparietal regions were activated by action execution and/or observation in the resting state scans? Videos of chimpanzee behavior during the FDG uptake period prior to the resting state PET scans could not be located, so it is not possible to directly measure the amount of time that subjects spent performing or observing movement. However, two pieces of evidence suggest that this interpretation may be true. First, M1 was *as active* in the resting state scans as in the action execution scans (**Figure A.1-9**). This strongly suggests the execution (or observation (Dushanova and Donoghue 2010)) of movement. Either performed or observed movement would also activate inferior frontal and inferior parietal regions. Second, although the videos could not be located, records of behavioral coding of these videos were located, and these records suggest that although chimpanzees' gross motor activity (e.g., locomotion) was very low, there may have been other, finer behaviors which would have been likely to activate the action execution/observation network. The ethogram (operational definitions of coded behaviors) and a summary of behavioral measurements are shown in **Figure A.1-11**, and the behavioral coding spreadsheets are reproduced in full in **Figure A.1-12**. For example, in the scans from the Rilling et al. (2007) study, subjects were not separated from their cagemates (this would likely have produced emotional arousal which would not be desirable given that study's goal of imaging the resting state or default mode network). Cagemate behavior was not coded in a detailed way, but it is common for chimpanzees to groom themselves or pick at objects in their environment when not engaged in another activity and it seems quite likely that the subjects may have

observed some of this grasping behavior. Also, "many vocalizations" and "banging" noises are noted coming from elsewhere in the chimpanzee housing area (**Figure A.1-12**). In the record for one subject's scan, 33 external stimuli are noted. In the records for other scans, 11.03% and 13.10% of the coded time blocks are recorded as involving any activity by the subject, including self-directed behaviors (grooming, scratching) and manipulating objects (**Figure A.1-12**). All of these types of stimuli activate macaque mirror neurons and human mirror regions.

These records are not as definitive as actual re-coding of the videos in light of the present dissertation's goals, and furthermore these records are incomplete – the record for Subject 4 (Faye) notes that the video cuts out 30 minutes prior to the end of the uptake period, and the records for all subjects note times when it is difficult to see what the subject and/or the cage mate is doing. Nonetheless, these records, combined with the degree of activation in M1, suggest that frontoparietal regions are activated in the resting state scans due to the execution and/or observation of manipulatory and communicative actions.

In sum, then, the most logical interpretation of these analyses seems to be that (a) the classical medial frontal-medial parietal default mode network was activated in the action execution and observation scans, consistent with these tasks' relatively low cognitive demands and repetitive nature, *and also* (b) the classical inferior frontal-inferior parietal action execution/observation network was activated in the resting state scans, consistent with the execution and observation of manipulatory and communicative actions reported in the video coding records. Furthermore, (c) since both networks were activated in both conditions, FDG-PET's limited statistical power and this study's small sample size limit our ability to disentangle these activations – although, importantly, SPM analyses of activation in the entire cerebrum identified significant differences between execution and observation vs. rest in the expected lateral inferior frontal and inferior parietal regions (**Figures 3.1-5** and **3.1-6**), and the volume of above-threshold activation was significantly different between the experimental conditions and rest in the mirror system ROIs (**Figure 3.1-19A**). If scans had been acquired with fMRI, we could simply discard epochs where chimpanzee behavior was off-target, but FDG-PET gives only one image for the entire uptake period so it is impossible to disentangle the effect of possible observed or executed manipulatory or communicative actions in the rest scans.

Furthermore, the fact that FDG-PET involves only one image per condition limits statistical power and also limits options for the types of statistical analyses that can be performed. However, this is the only method available for functional neuroimaging in awake, behaving chimpanzees, and the rarity of this data perhaps argues for reporting as many analyses as possible. Despite all of this, it is important to again underscore that significant differences between action execution and observation vs. rest were measured in the expected frontal and parietal regions (**Figure 3.1-5, 3.1-6,** and **3.1-19A)**.

Even accepting that the above interpretation is true – that there was a significant amount of executed and observed manipulatory and communicative action in the resting state scans – this should have been less than in the action execution and observation scans, which involved intensive, prolonged repetition of executed or observed manual actions. Thus, as one of the dissertation committee members (K.S.) suggested, a more liberal threshold might reveal regions of the action execution/observation network that are more active during the action execution and observation conditions than during the rest condition.

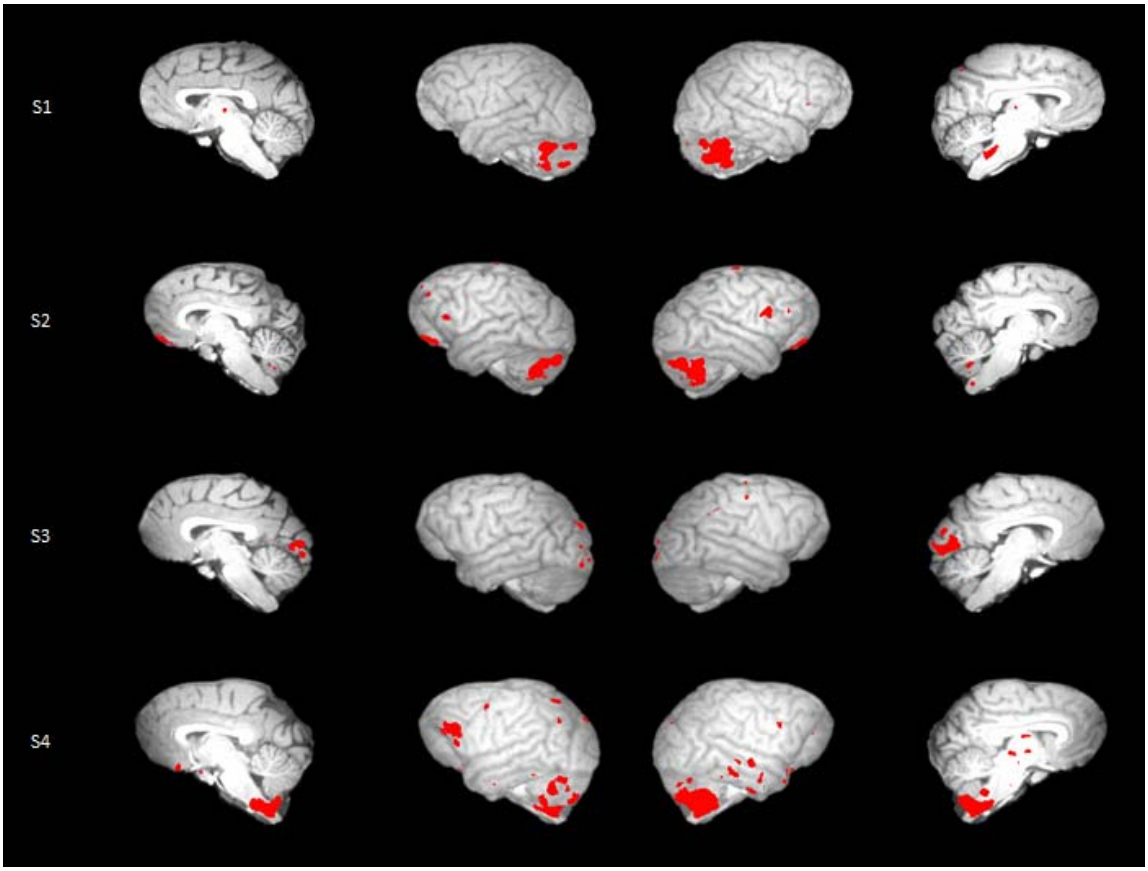
Therefore, we repeated all of the above analyses, as well as all of the analyses included in Chapter 3.1, using a more liberal threshold – the top 25% of the histogram of voxel values. **Figure A.1-13** shows the overlap between [execution-rest] and [transitive observation-rest] using this new more liberal threshold. **Figure A.1-14** shows the same for [execution-rest] and [intransitive observation-rest]. **Figure A.1-15** quantifies the volume of above-threshold activation in these overlap images in the mirror system ROIs used in Chapter 3.1; this graph is comparable to the original comparison in **Figure 3.1-19B**. **Figures A.1-16 – A.18** show the top 25% of voxels in each condition-rest. **Figure A.1-19** quantifies the volume of above-threshold activation in these individual condition-minus-rest subtractions in the mirror system ROIs used in Chapter 3.1; this graph is comparable to the original comparison in **Figure 3.1-19A**.

These analyses with the more liberal 25% threshold highlight a distributed frontoparietal network that is more involved in chimpanzee action execution and observation than rest, consistent with previous reports in macaques and humans (Gallese, Fadiga et al. 1996, Rizzolatti, Fadiga et al. 1996, Nishitani and Hari 2000, Muthukumaraswamy and Johnson 2004, Muthukumaraswamy, Johnson et al. 2004, Raos, Evangeliou et al.

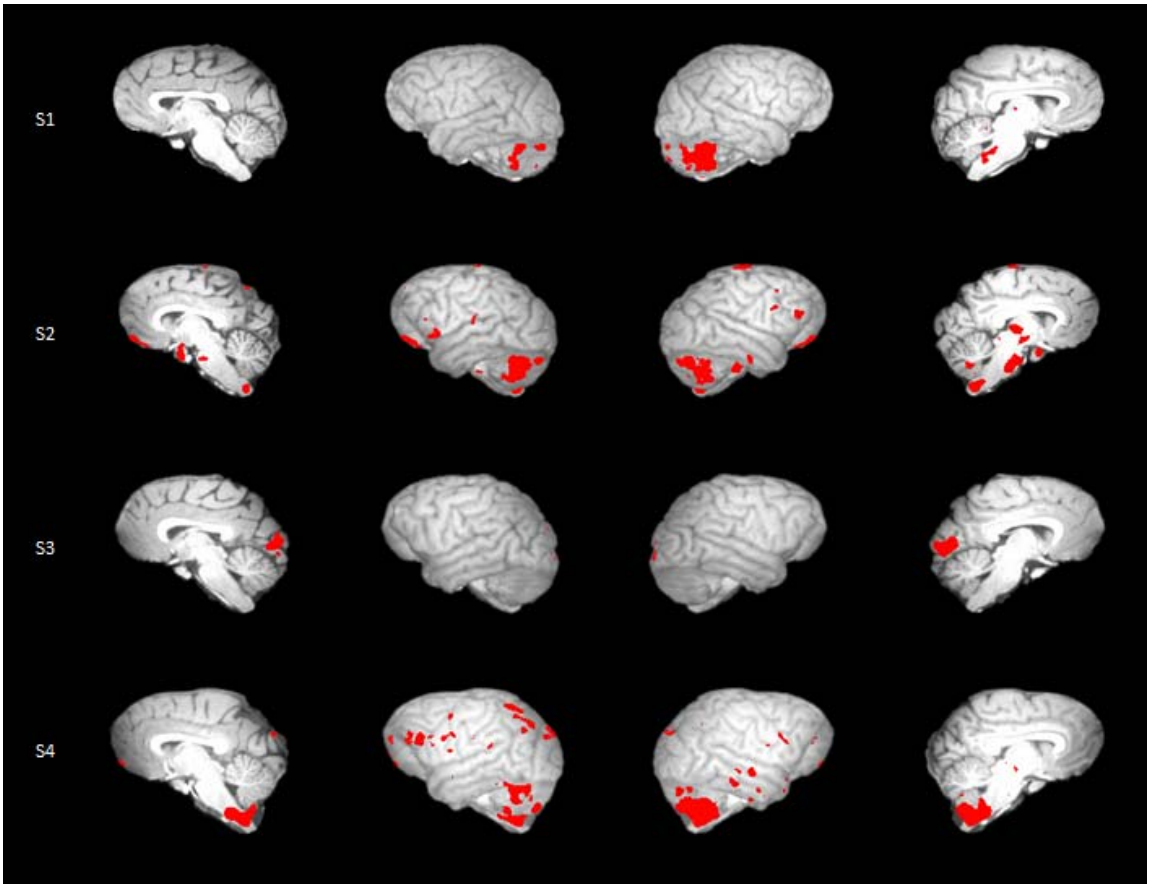
2004, Fadiga, Craighero et al. 2005, Nelissen, Luppino et al. 2005, Pineda 2005, Hari 2006, Rizzolatti, Ferrari et al. 2006, Raos, Evangeliou et al. 2007, Candidi, Urgesi et al. 2008, Rozzi, Ferrari et al. 2008, Caspers, Zilles et al. 2010, Cattaneo 2010, Koch, Versace et al. 2010, Nelissen, Borra et al. 2011, Molenberghs, Cunnington et al. 2012). These analyses do not reveal any differences between [transitive observation-rest] and [intransitive observation-rest], consistent with the conclusion of Chapter 3.1 that the chimpanzee brain is like the human brain and unlike the macaque brain in the sense that it responds to observed intransitive action in much the same was as observed intransitive action.

All of this being said, we do not want to imply that we are arguing that any of these regions are specifically, solely dedicated to action execution/observation. The homologues to macaque mirror regions have been implicated in a variety of other complex behaviors in humans as well as great apes and monkeys – for example, vocal and gestural communication and tool use (Stout and Chaminade 2012), or more broadly, hierarchical processing (IFGpo; (Petrides 2005, Koechlin and Jubault 2006, Badre and D'Esposito 2009)) and visuo-somato-motor transformations (IPL; (Fogassi and Luppino 2005, Jeannerod and Jacob 2005, Rizzolatti, Ferrari et al. 2006)). Furthermore, we certainly do not contend that the two ROIs studied here are the sole neural basis of action perception or action understanding. Understanding other individuals' behavior also involves other brain regions, including "mentalizing" regions which overlap with parts of the default mode/resting state network.

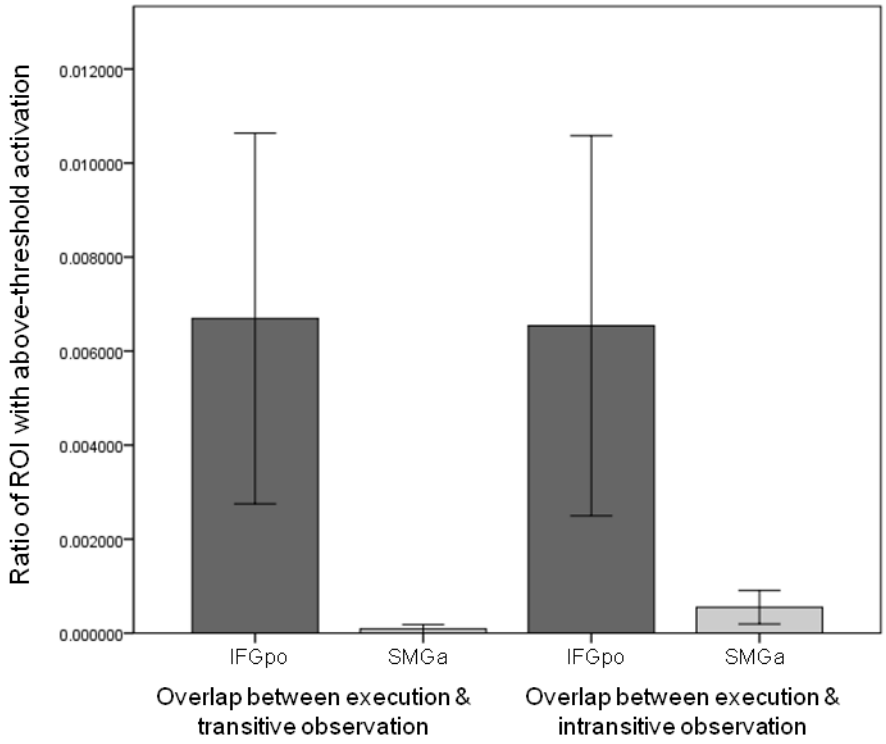
FigureA.1-1. Overlap between top 1% of voxels in execution-rest subtraction, and top 1% of voxels in transitive observation-rest subtraction (execution-rest thresholded at 99% U transitive observation-rest thresholded at 99%).



FigureA.1-2. Overlap between top 1% of voxels in execution-rest subtraction, and top 1% of voxels in intransitive observation-rest subtraction (execution-rest thresholded at 99% U intransitive observation-rest thresholded at 99%).



FigureA.1-3. Quantification of activations within ROIs in top 1% of voxels in execution-rest/transitive observation-rest overlap images, and execution-rest/intransitive observation-rest overlap images.



No effect of condition (df=1, F=.015, p=.909) or ROI (df=1, F=2.984, p=.183), repeated measures ANOVA. Error bars: +/- 1 SEM.

Figure A.1-4. Top 1% of voxels in execution-rest subtraction.

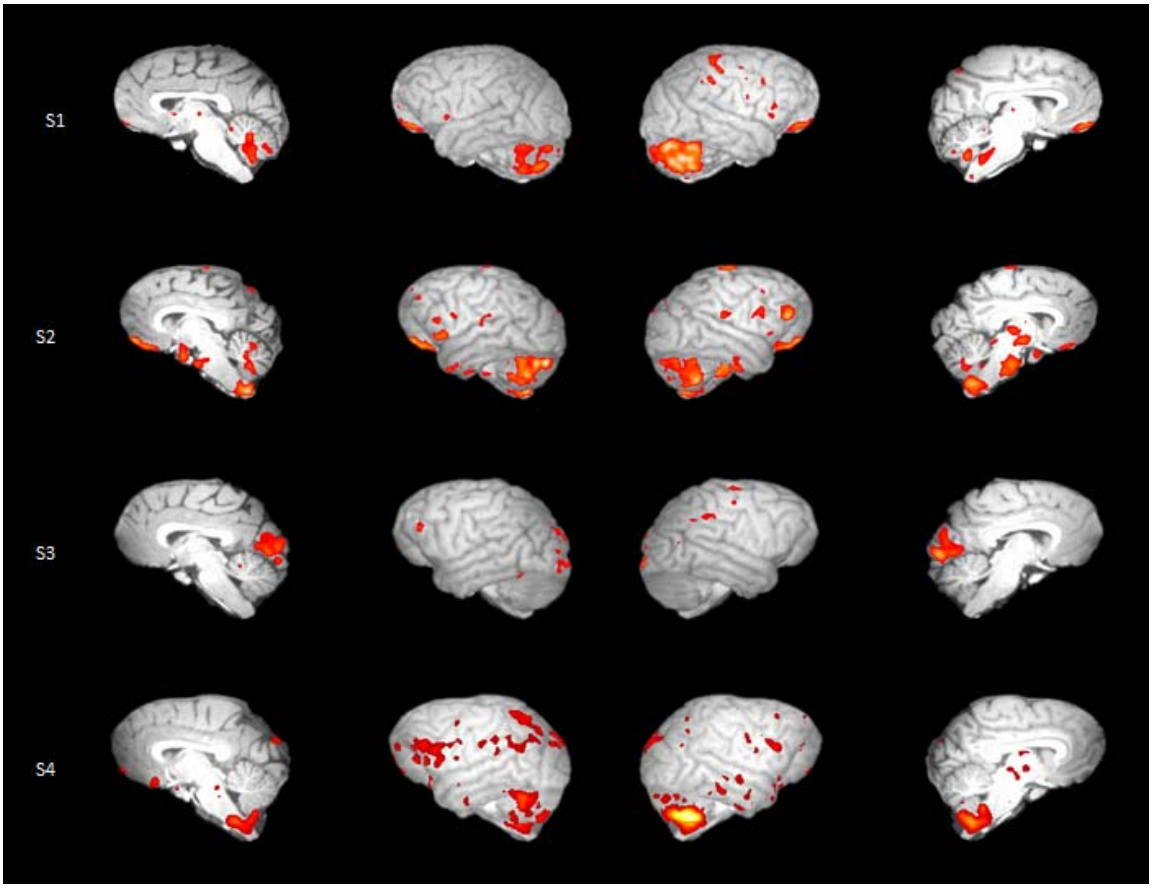


Figure A.1-5. Top 1% of voxels in transitive observation-rest subtraction.

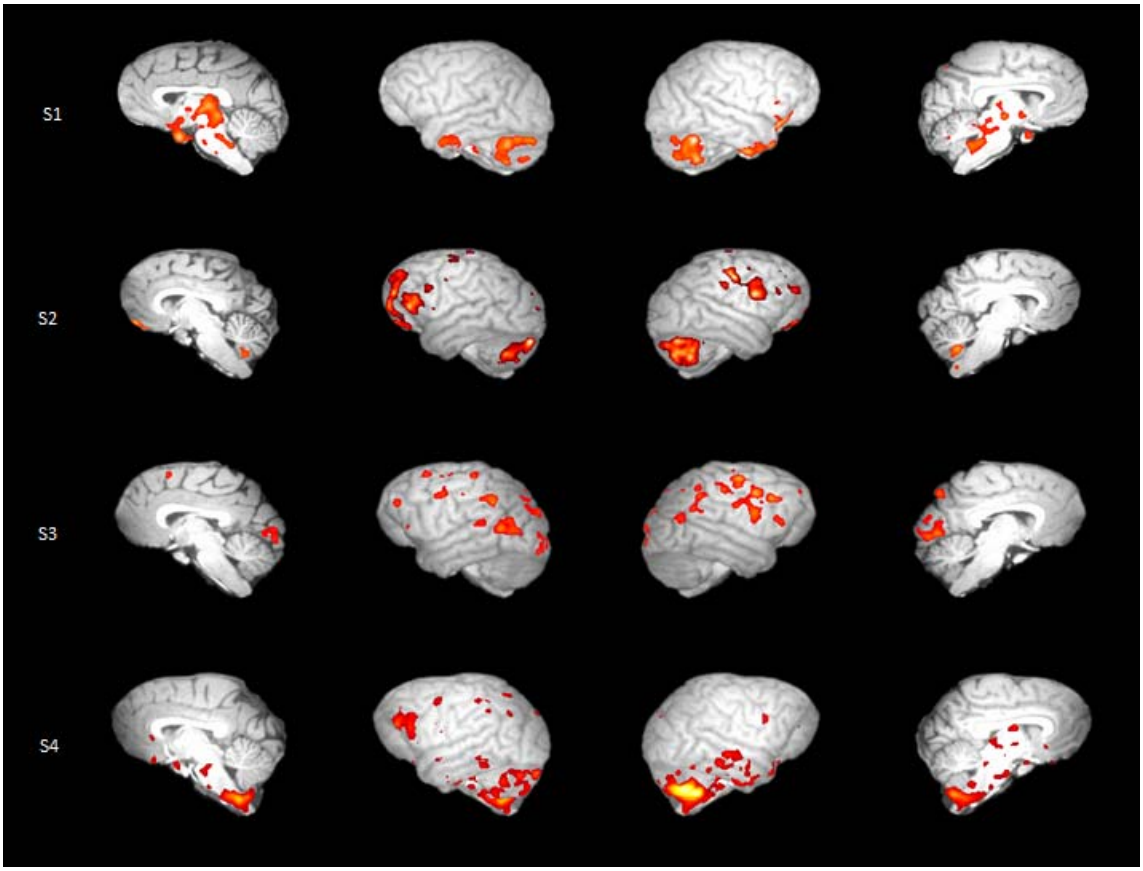


Figure A.1-6. Top 1% of voxels in intransitive observation-rest subtraction.

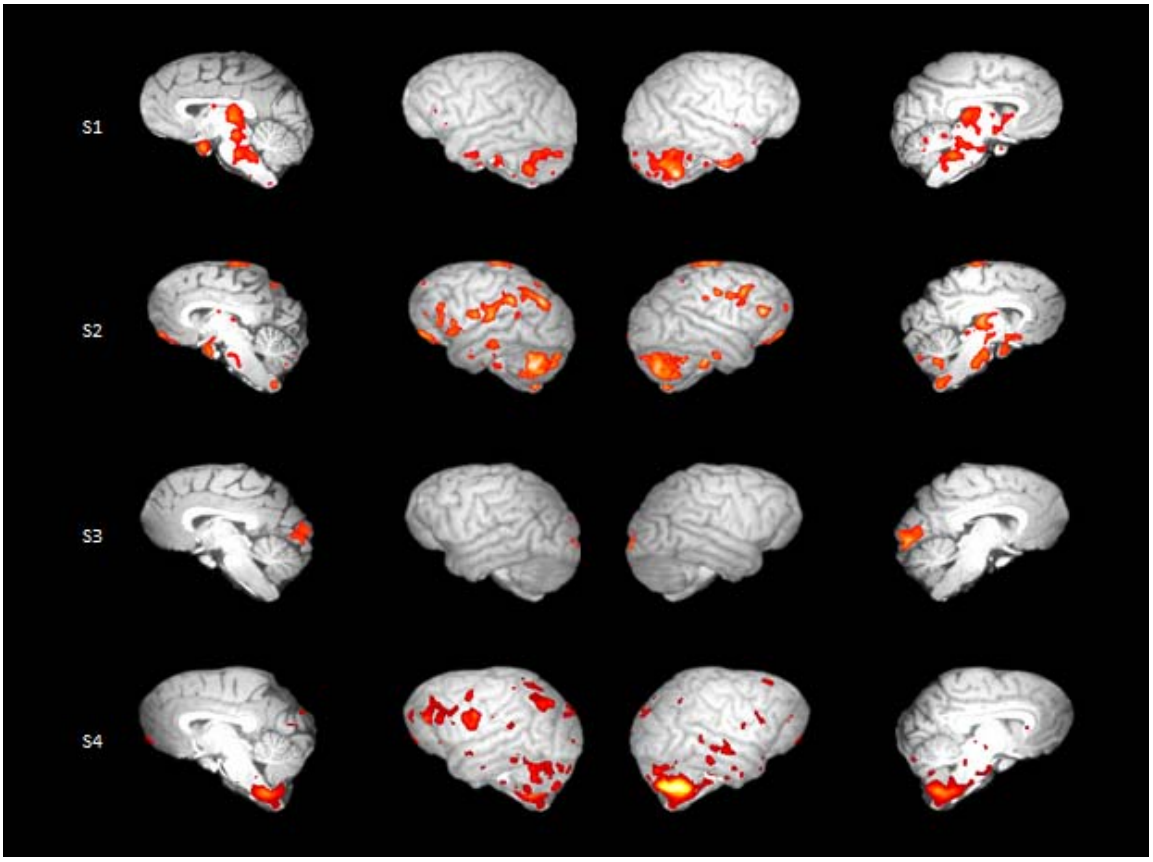
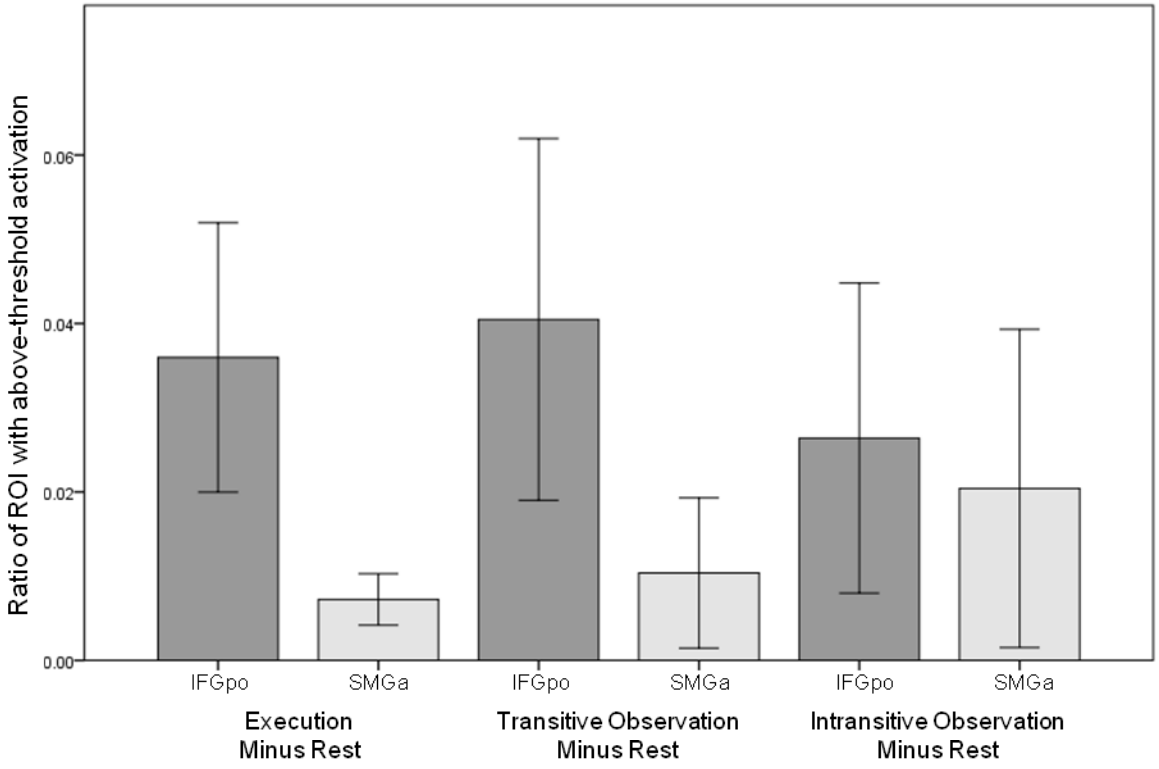


Figure A.1-7. Quantification of activations within ROIs in top 1% of voxels in execution-rest, transitive observation-rest, and intransitive observation-rest.



No effect of condition (df=2, F=.036, p=.965) or ROI (df=1, F=2.993, p=1.82), repeated measures ANOVA. Error bars: +/- 1 SEM.

Figure A.1-8. Top 1% of voxels in rest condition.

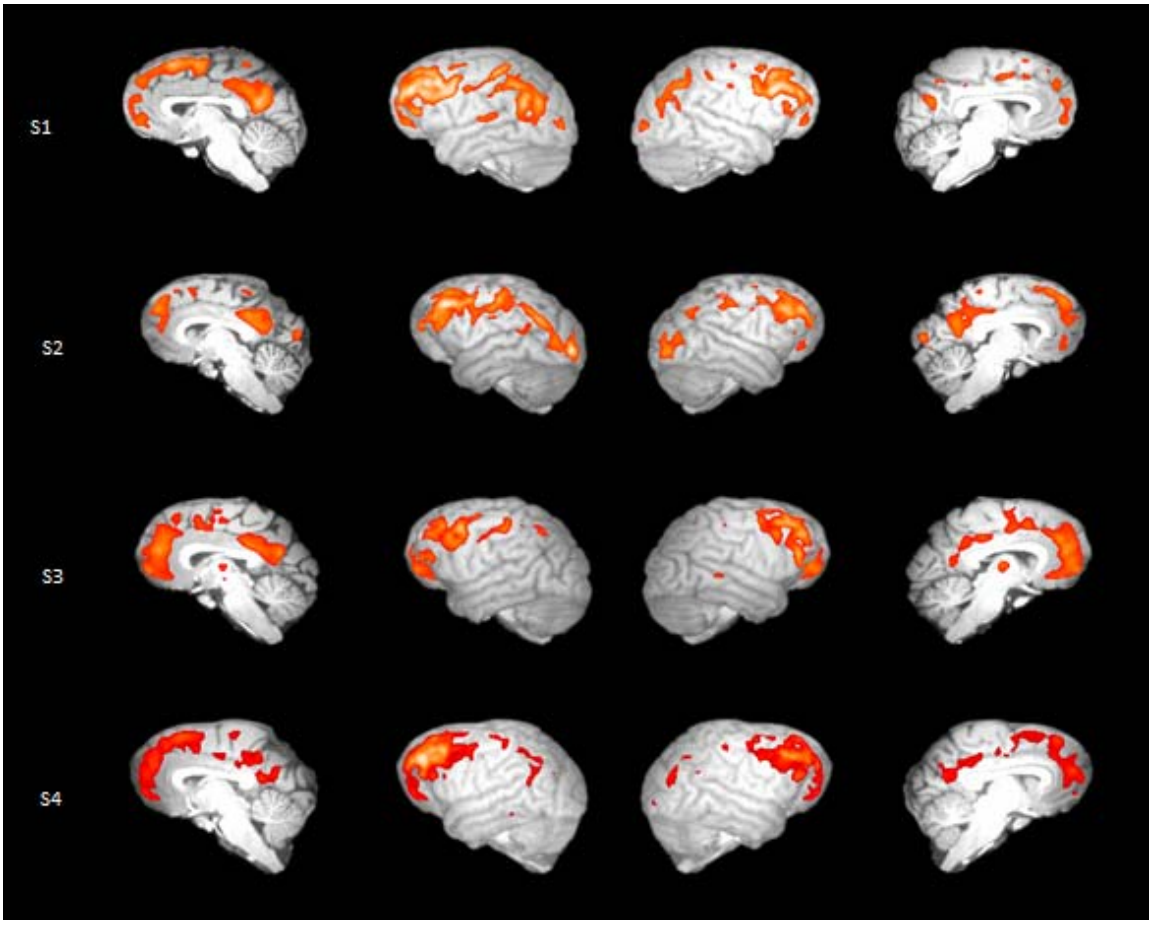
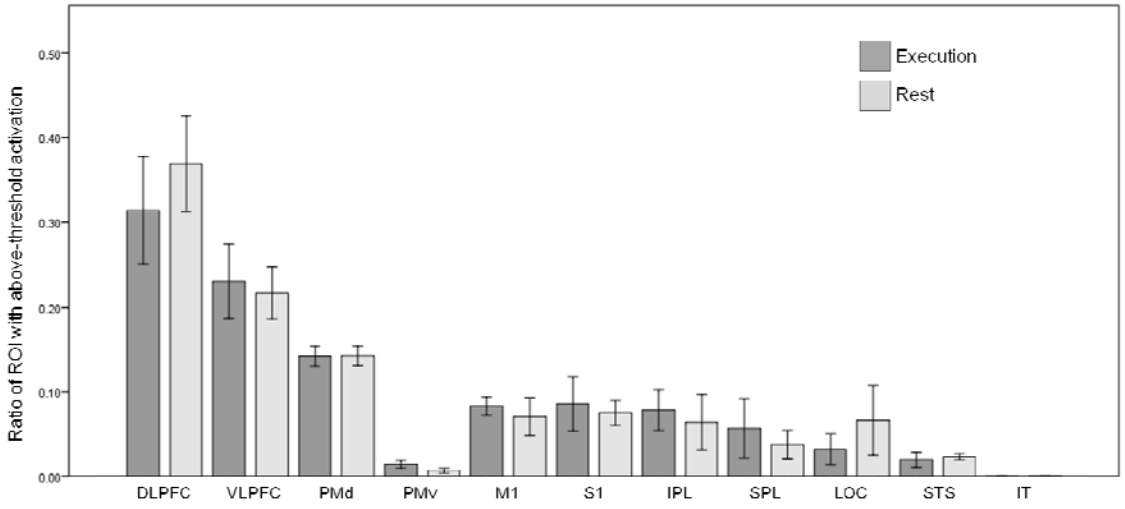


Figure A.1-9. Quantification of top 1% of voxels in execution and rest conditions in a broader set of frontal, parietal, and occipitotemporal ROIs.



No effect of condition (df=1, F=.051, p=.836). Error bars: +/- 1 SEM.

Figure A.1-10. Chimpanzee resting state study: analysis of video from each scanning session. Posture, location in cage, attention (watching something, generally alert, or neutral), and activity noted every 10 seconds. Measurements which may be relevant to the current study are highlighted.

Subject:	**Jarred**	**Scott SUBJECT 1**	**Katrina SUBJECT 2**	**Faye SUBJECT 4**	**Merv**
Posture:					
stand	2.70%	0.39%	0.51%	1.63%	1.52%
sit	24.27%	4.25%	21.63%	92.93%	0.76%
lie down	71.24%	95.37%	76.84%	13.59%	.
grasp cage	.	.	1.02%	.	.
upside down	.	.	.	.	0.19%
moving	.	.	.	.	3.43%
can't tell	.	.	.	.	94.10%
Location:					
front	61.80%	4.25%	10.95%	23.66%	1.14%
middle	.	0.39%	.	.	.
back	0.67%	95.37%	0.49%	1.08%	.
left side	.	.	.	2.69%	.
right side	.	.	.	3.76%	.
bench	35.51%	.	88.56%	68.82%	.
pass-thru	0.90%	.	.	.	0.38%
left cage	1.12%	.	.	.	.
outside	.	.	.	.	96.95%
outside/pass-thru	.	.	.	.	0.57%
moving	.	.	.	.	0.95%
Attention:					
watching	3.20%	1.94%	3.14%	13.07%	3.05%
alert	23.52%	2.33%	17.39%	27.14%	.
neutral	69.41%	8.14%	79.47%	59.80%	.
moving	.	.	.	.	2.86%
can't tell	3.88%	87.60%	.	.	94.10%
Any activity*:	20.22%	0.38%	11.03%	13.10%	5.52%
change location	14	2	13	8	7
walk around	.	.	.	.	7
change posture	19	2	7	1	2
self-directed behavior	25	.	21	.	1
play with or manipulate object	1	.	.	13	.
looking	15	.	4	1	9
yawn	6	.	.	1	.
grasp cage/door	1	1		1	3
drink water	2	.	.	.	.
urinate	6	.	.	.	.
External stimuli:	23	33	17	10	5
Responses to external stimuli:	3	0 to 9	5	1	3
Vocalizations:	1	0 to 6	0 or 1	0	0

*Percentage of 10-second time blocks that contained any activity.

Figure A.1-11. Ethogram and existing notes on videos from chimpanzee resting state scans.

W	**Watching**	
w3	intense watching	stay at cage front and look at monitor
w2	attentive	keeping eye on monitor but not up front
w1	periphal	infer watching
w0	avoid	move away, back turned, avoid monitor
D	**Display Activity / Aggitation**	
d0	sway, stagger	low intensity, usually with piloerection
d1	bluff display	
d2	bluff display with banging objects, fence	banging objects (bang mesh)
d3	specifically targeting computer or people	(spitting)
P	**Play type Behavior**	
p1	bob, head shake (bounce on all 4's)	
p2	slap mesh or ground w/ hand or foot	(playing with ball)
p3	play chase with another	
A	**Displacement type activities**	
a-	grooming self	
a1	rough scratch	
a2	gentle scratch	
a3	nose wipe	
a4	piloerection	
a5	yawning	
a6	stereotypical rocking (check d0's with notes)	
SI	**Solicit / Invitation**	
si1	to person	
si2	to computer	
si3	to another chimp (check with play behaviors or some displays)	
E	**External attention**	
e0	occurs	any external disturbance, no obvious response (can be cagemate)
e1	respond	external disturbance with immediate and obvious response (can be cagemate)
	ALL	
	vocalizations	barks, screams, pouts, grunts, hoots, pants, squeaks/yelps
	facial expressions	
O	**Orientation / Posture**	
o1	hang forward	(completely hanging anywhere in cage with face forward; both feet off ground or on mesh)
o2	hang away	(completely hanging anywhere in cage with face away; both feet off ground or on mesh)
o3	sit forward	(sit/stand/lie in front of cage with face forward; including hang with one foot on ground or barrel)
o4	rear forward	(sit/stand/lie in backof cage with face forward)
o5	rear away	(sit/stand/lie in back of cage with face away)
o6	moving most of the time (i.e. d0.d1.p3)	(changing location from any 1 to these to another if longer than 3 sec)
o7	at front of cage, face forward, but not looking at screen	

Subject 1 (Scott)

time	posture	location	attention	activity	external stim.	response	vocalization	notes
7:08								dosing not on the tape--?
:10					Matt on wing (& Lisa?)			Can hear Matt & Lisa talking but they are not on camera
:20								
:30								
:40	sit floor	front	watching	rattle door				Katrina on barrel at left side of cage
:50	"	"	"					
7:09	"	"	"					
:10	"	"	"					
:20	"	"	"					
:30	stand floor	middle	moving	walking/moving				
:40	sit floor	front	alert					
:50	"	"	"					
7:10	"	"	"		noise on wing	no		
:10	"	"	"					
:20	"	"	"		noise & voc on wing	no		
:30	"	"	"	adjust posture				
:40	moving	moving	moving	walk to back				
:50	sit/lie floor	back	can't tell					he is sitting or lying behind Katrina--can't see him--guessing he's not attending to anything but not sure
7:11	"	"	"					
:10	"	"	"		voices off wing	no		

:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:12	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:13	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:14	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:15	"	"	"	noise (water) on wing	no
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:16	"	"	"		
:10	"	"	"		

:20	"	"	"	noise on wing	no
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:17	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:18	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"	voc on wing	no
:40	"	"	"	"	"
:50	"	"	"		
7:19	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"	lots of voc on wing	no
:40	"	"	"		
:50	"	"	"	noise on wing	no
7:20	"	"	"	lots of voc on wing	no
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"	pant hoots on wing	no
:50	"	"	"		

7:21	"	"	"				
:10	"	"	"		lots of voc on wing	can't tell	he might be vocalizing but can't see him so not sure
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
7:22	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"		lots of voc/banging on wing	no	
:40	"	"	"				
:50	"	"	"				
7:23	"	"	"				
:10	"	"	"		lots of voc/pant hoots	can't tell	can't tell if any vocalizations come from S. or Katrina
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
7:24	"	"	"				
:10	"	"	"				
:20	"	"	"		pant hoots	can't tell	
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
7:25	"	"	"				

:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:26	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:27	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:28	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:29	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:30	"	"	"
:10	"	"	"

:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:31	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:32	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:33	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:34	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:35	"	"	"
:10	"	"	"
:20	"	"	"

:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:36	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:37	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:38	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:39	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
7:40	"	"	"	voc on wing	Katrina responds--hoots. Not sure about Scott.
:10	"	"	"		

:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
7:41	"	"	"		some voc & banging	no	
:10	"	"	"				
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
7:42	"	"	"		pant hoots	?	response vocalization is loud enough that it might be Scott, but can't tell
:10	"	"	"				
:20	"	"	"		chirps	?	"
:30	"	"	"		grunts	?	"
:40	"	"	"				
:50	"	"	"				
7:43	"	"	"				
:10	"	"	"				
:20	"	"	"		voices off wing	no	
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
7:44	"	"	"		voc (screams) on wing	no	
:10	"	"	"				
:20	"	"	"		pant hoots	no	

:30	"	"	"					
:40	"	"	"					
:50	"	"	"					
7:45	"	"	"					
:10	"	"	"					
:20	"	"	"		lots of voc on wing	?		
:30	"	"	"					
:40	"	"	"					
:50	"	"	"					
7:46	"	"	"		lots of voc on wing	?		
:10	"	"	"					
:20	"	"	"					
:30	"	"	"					
:40	"	"	"					
:50	"	"	"		lots of voc on wing	?		
7:47	"	"	"					
:10	"	"	"					
:20	"	"	"					
:30	"	"	"					
:40	"	"	"					
:50	"	"	"					
7:48	"	"	"					
:10	"	"	"		screams/banging	no		
:20	"	"	"					

:30	lie floor	back	neutral		lots of voc	no		Katrina moves to other side of cage--Scott is lying at the back by the door
:40	"	"	"					
:50	"	"	"		voc on wing (chirps)	no		
7:49	"	"	"					
:10	"	"	"					
:20	"	"	"					
:30	"	"	"					
:40	"	"	"		noise on wing	no		
:50	"	"	"					
7:50	"	"	"		voc on wing	no		Katrina responds--vocal
:10	"	"	"					
:20	"	"	"					
:30	"	"	"		radio & noise (where?)	no		Katrina at front of cage
:40	"	"	"					
:50	"	"	"					
7:51	"	"	"					
:10	"	"	"					
:20	"	"	"					
:30	"	"	"					
:40	"	"	"					
:50	"	"	"	adjust posture	noise on wing	no		
7:52								tape cuts out here

Subject 2 (Katrina)

time	posture	location	attention	activity	external stim.	response	vocalization	notes
5:52	sit floor	front	watching		Lisa dosing; voc on wing	yes	maybe her?	Dosing between 5:52:00 and 5:53:00. Lisa leaves 5:53:00. Scott & Kat both at front of cage, sitting; Scott on left.
:10								
:20								
:30								
:40								
:50								
5:53	sit floor	front	watching		Lisa dosing; voc on wing	yes	maybe her?	Dosing between 5:52:00 and 5:53:00. Lisa leaves 5:53:00. Scott & Kat both at front of cage, sitting; Scott on left.
:10	moving	back corner	watching	pacing	voc on wing	yes		still settling down
:20	standing	front	"					
:30	moving	front/bench	"	swing front to bench	voc on wing	yes		
:40	sit bench	bench	alert	rocking				
:50	"	"	"	gentle self-groom				
5:54	"	"	"	looking around				
:10	"	"	"					
:20	"	"	"					
:30	"	"	"					
:40	"	"	"	gentle self-groom	voc on wing	no		
:50	"	"	"	"				

5:55	"	"	"	"				
:10	moving	bench/front	watching	swing bench to front	voc on wing	yes		
:20	sit bench	bench	alert					Swing bench to front then back to bench within 10-second block
:30	"	"	"	gentle self-groom				
:40	"	"	"		voc on wing	yes	maybe her?	
:50	"	"	"		voc on wing	no		There is a vocalization that is either Scott, Kat, or a neighbor--can't tell
5:56	"	"	"					
:10	"	"	"					
:20	"	"	"	gentle self-groom				
:30	"	"	"	change posture				
:40	lie bench	"	neutral		voc on wing	no		
:50	"	"	"					
5:57	"	"	"		voc on wing	no		The voc might be Scott. At this time block it looks like it is, but in next I'm not so sure, and it's the same individual.
:10	"	"	"		"	no		
:20	"	"	"		"	no		
:30	"	"	"		"	no		
:40	"	"	"		"	no		
:50	"	"	"					
5:58	"	"	"		voc on wing	no		Probably Scott.
:10	"	"	"		"	no		Scott moves to back--first time he's moved.
:20	"	"	"					
:30	"	"	"					

:40	"	"	"				
:50	"	"	"				
5:59	"	"	"		noise on wing	no	
:10	"	"	"				
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				She is moving just enough that I don't think she's asleep.
:50	"	"	"				
6:00	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"	gentle self-groom			
:40	"	"	"				
:50	"	"	"				
6:01	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
6:02	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
6:03	"	"	"				
:10	"	"	"				
:20	"	"	"				

:30	"	"	"
:40	"	"	"
:50	"	"	"
6:04	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:05	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:06	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:07	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:08	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"

:40	"	"	"	
:50	"	"	"	
6:09	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:10	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:11	"	"	"	adjust posture
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	gentle self-groom
:50	"	"	"	
6:12	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:13	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	

:40	"	"	"	
:50	"	"	"	
6:14	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:15	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:16	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:17	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	adjust posture
6:18	"	"	alert	gentle self-groom
:10	"	"	"	
:20	"	"	"	

:30	"	"	"	gentle self-groom
:40	"	"	"	
:50	"	"	neutral	
6:19	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	nose wipe
:50	"	"	"	
6:20	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	alert	look around
:50	"	"	"	
6:21	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	look around
:40	"	"	neutral	
:50	"	"	"	
6:22	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:23	"	"	"	
:10	"	"	"	gentle self-groom

:20	"	"	"	
:30	"	"	"	
:40	"	"	"	gentle self-groom
:50	"	"	"	
6:24	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:25	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:26	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	gentle self-groom
6:27	"	"	"	"
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	adjust posture
:40	"	"	"	
:50	"	"	"	
6:28	"	"	"	

:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	"	"	"			
:50	"	"	"			
6:29	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	"	"	"			
:50	"	"	"			
6:30	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	"	"	"			
:50	"	"	"			
6:31	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	moving	bench/front	watching	move bench to top/front		Scott gets up from back and moves to front of cage, looks at something to the left--I didn't hear any noise. Katrina joins him.
:50	grasp front	front	watching			
6:32	"	"	"			
:10	moving	front	alert	swing to left side		Scott moves to the bench

:20	"	front/back	watching	move to back door
:30	stand floor	back	watching	look through door
:40	moving	front	alert	move to front
:50	sit floor	"	"	
6:33	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:34	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	neutral	
6:35	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:36	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:37	"	"	"	

:10	"	"	"			
:20	"	"	"			
:30	"	"	"	gentle self-groom		
:40	"	"	"			
:50	"	"	"			
6:38	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	moving	front/bench	alert	swing front to bench		Scott swings bench to front (left); Kat ignores him at first, then swings to bench.
:40	sit bench	bench	"			
:50	lie bench	"	"			
6:39	"	"	neutral			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	"	"	"			
:50	"	"	"			
6:40	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	moving	bench/front	alert	swing bench to front		Two swings: bench to front left, then to front right. Grasping cage.
:50	moving	front/bench	"	swing front to bench		
6:41	sit bench	bench	"			
:10	"	"	"			
:20	"	"	"	scratch		

:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:42	"	"	neutral	gentle self-groom
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	alert	nose wipe
6:43	"	"	"	"
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:44	"	"	"	
:10	"	"	neutral	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:45	lie bench	"	"	change posture
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:46	"	"	"	
:10	"	"	"	

:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:47	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:48	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:49	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:50	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:51	"	"	"
:10	"	"	"

:20	moving	bench/front	alert	swing bench to front	noise on wing	yes
:30	grasp front	front	watching			
:40	"	"	"			
:50	moving	front/bench	alert	swing front to bench		
6:52	sit bench	bench	alert			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	"	"	"			
:50	"	"	"			
6:53	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	lie bench	"	neutral	change posture		
:40	"	"	"			
:50	"	"	"			
6:54	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	"	"	"			
:50	"	"	"			
6:55	"	"	"			
:10	"	"	"			
:20	"	"	"			
:30	"	"	"			
:40	"	"	"			

:50	"	"	"
6:56	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:57	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:58	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:59	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
7:00	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"

:50	moving	bench/front	watching	swing bench to front	noise on wing	yes	Sheila leaves testing room/enters wing
7:01	end of rest period						Sheila comes to separate

Subject 4 (Faye)

	posture	location	attention	activity	external stim.	response	vocalization	notes
5:43	sit floor	front	watching		Matt dosing w/Sarah watching			Dosing between 5:43:00 and 5:44:00. Faye and Lucas both at front of cage, Faye on left.
:10	"	"	"		"			
:20	"	"	"		"			
:30	"	"	"		"			
:40	"	"	"		"			
:50	"	"	"		"			
5:44	"	"	"		"			
:10	"	"	"		Matt & Sarah leaving			Lucas moves to bench
:20	moving	front/back	"	move front to back				
:30	"	moving	"	pacing cage				Still settling down
:40	"	"	"	"				
:50	"	"	"	"				
5:45	stand floor	back door	"	looking thru door				
:10	"	front/back	"					Still lots of moving around--pacing, checking back door, etc. Lucas is on bench.
:20	sit floor	front	"		screams nearby	no		
:30	"	"	"		"	no		
:40	"	"	alert		"	no		
:50	"	"	"		screams/chirps	no		
5:46	moving	back door	watching	move front to back				
:10	sit floor	right side	alert	move barrel				
:20	"	"	"	play with barrel				Lucas swings over her head; she ignores
:30	"	"	"	"				
:40	"	"	"	"				

:50	"	"	"					
5:47	"	"	"					
:10	"	"	"	play with barrel				Moves barrel to left side
:20	sit barrel	left side	"					
:30	"	"	"	grasp cage	banging on wing	no		
:40	"	"	"					
:50	"	"	"					
5:48	"	"	"		voc on wing	yes		Stands up to look down wing
:10	stand barrel	front	watching					
:20	sit barrel	front	"	play with lock				
:30	"	"	"	"				
:40	"	"	"	"				
:50	"	"	"	"				
5:49	"	"	"	"				
:10	"	"	"	"				
:20	"	"	"		voc on wing	no		voc might be Lucas--rocking
:30	"	"	alert					
:40	"	"	"					
:50	"	"	"					
5:50	"	"	"					
:10	"	"	"					
:20	"	"	"					
:30	"	"	"					
:40	"	"	"		voc on wing	no		
:50	"	"	"					
5:51	"	"	"	play with lock				
:10	"	"	"					
:20	"	"	"					
:30	"	"	"					
:40	"	"	"	play with lock				

:50	"	"	"				
5:52	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
5:53	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"	play with lock			
:40	"	"	"				
:50	"	"	"				
5:54	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	moving	front/bench	"	swing to bench			
:40	sit bench	bench	"	rocking			She and Lucas are together on bench--it doesn't look like they are interacting/grooming.
:50	"	"	"				
5:55	"	"	"				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"				
:40	"	"	"				
:50	"	"	"				
5:56	"	"	neutral				
:10	"	"	"				
:20	"	"	"				
:30	"	"	"		noise on wing	no	

:40	"	"	"	
:50	"	"	"	
5:57	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
5:58	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
5:59	"	"	"	
:10	"	"	"	
:20	"	"	"	yawn
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:00	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:01	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	

:50	"	"	"
6:02	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:03	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:04	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:05	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"
6:06	"	"	"
:10	"	"	"
:20	"	"	"
:30	"	"	"
:40	"	"	"
:50	"	"	"

6:07	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
6:08	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
6:09	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
6:10	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	"	"	"		
:50	"	"	"		
6:11	"	"	"		
:10	"	"	"		
:20	"	"	"		
:30	"	"	"		
:40	moving	bench	alert	move to other side of bench	F. and Lucas switch places (F. displaces)
:50	lie bench	"	neutral		

6:12	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:13	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:14	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
6:15	"	"	"	
:10	"	"	"	
:20	"	"	"	
:30	"	"	"	
:40	"	"	"	
:50	"	"	"	
				tape cuts out here--resumes 30 min. later for separation
6:46	end of rest period			Matt comes out to separate

Figure A.1-12. Overlap between top 25% of voxels in execution-rest subtraction, and top 25% of voxels in transitive observation-rest subtraction (execution-rest thresholded at 75% U transitive observation-rest thresholded at 75%).

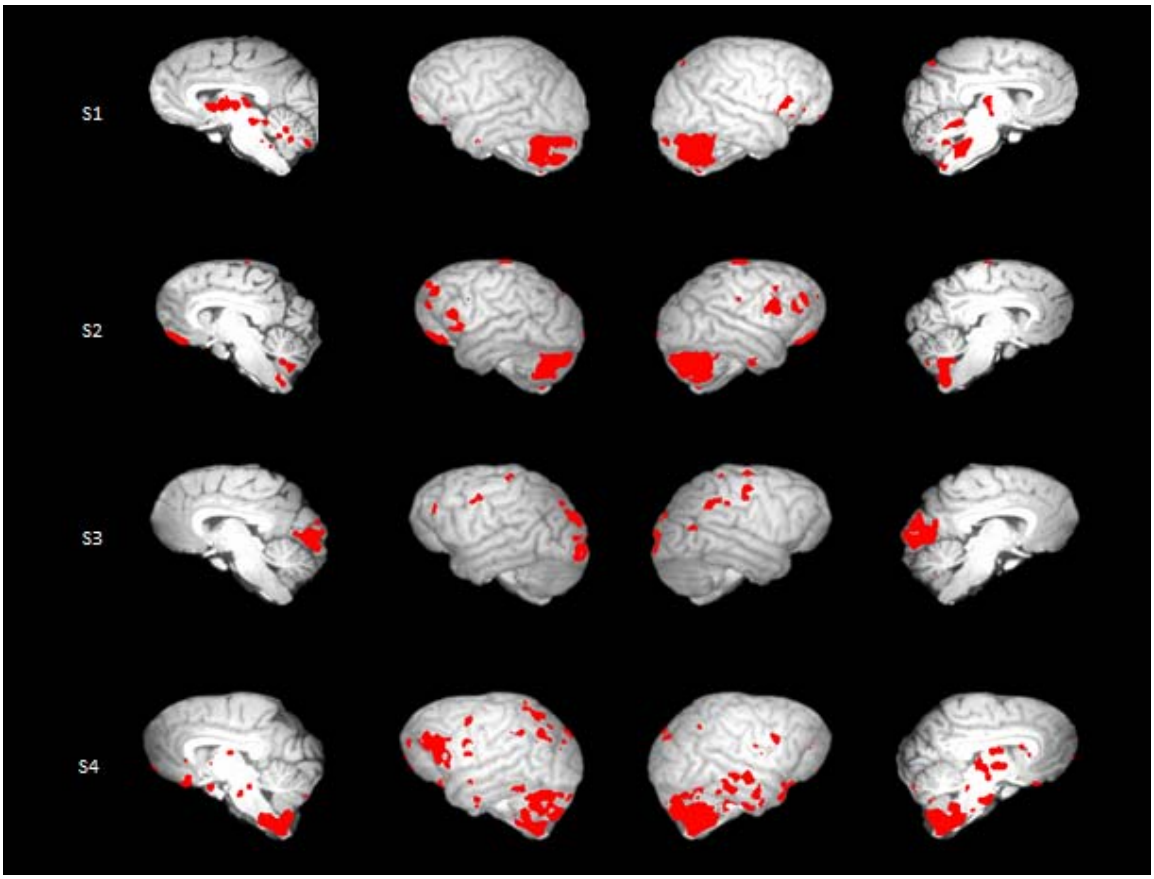


Figure A.1-13. Overlap between top 25% of voxels in execution-rest subtraction, and top 25% of voxels in intransitive observation-rest subtraction (execution-rest thresholded at 75% U intransitive observation-rest thresholded at 75%).

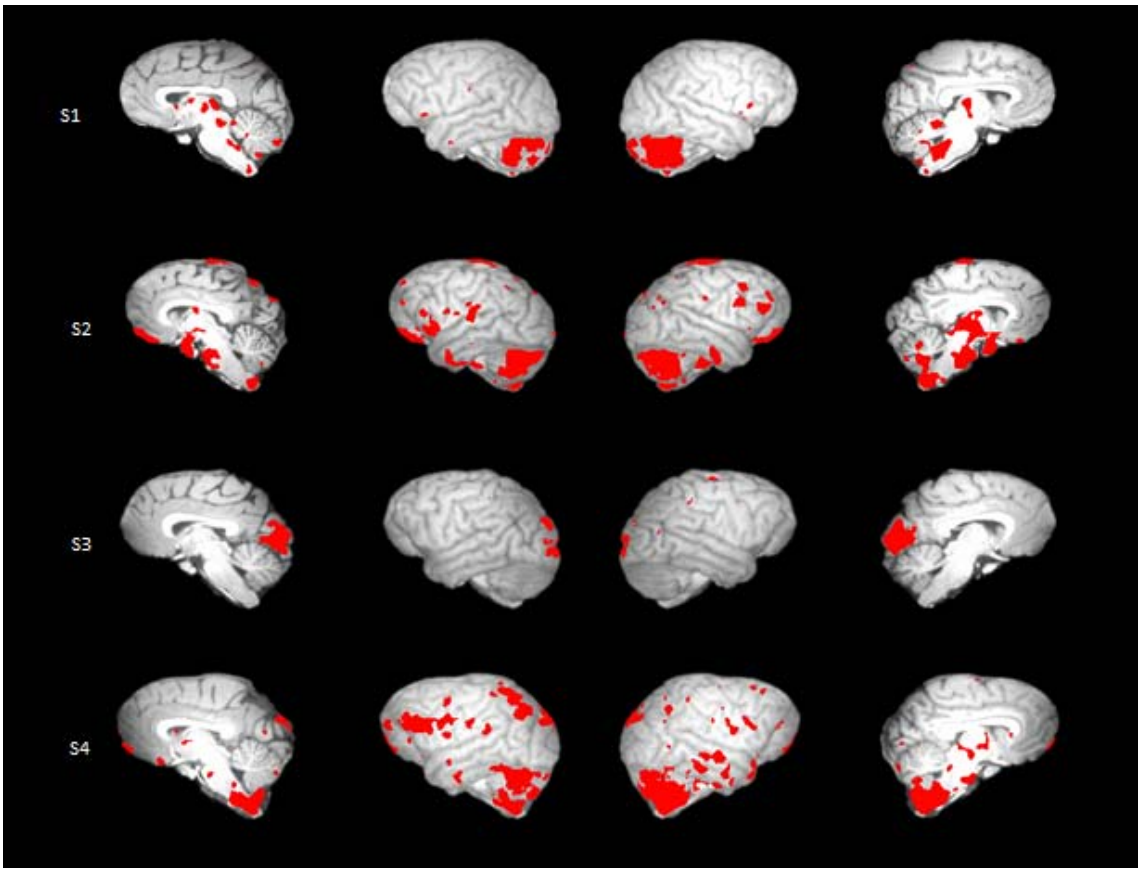
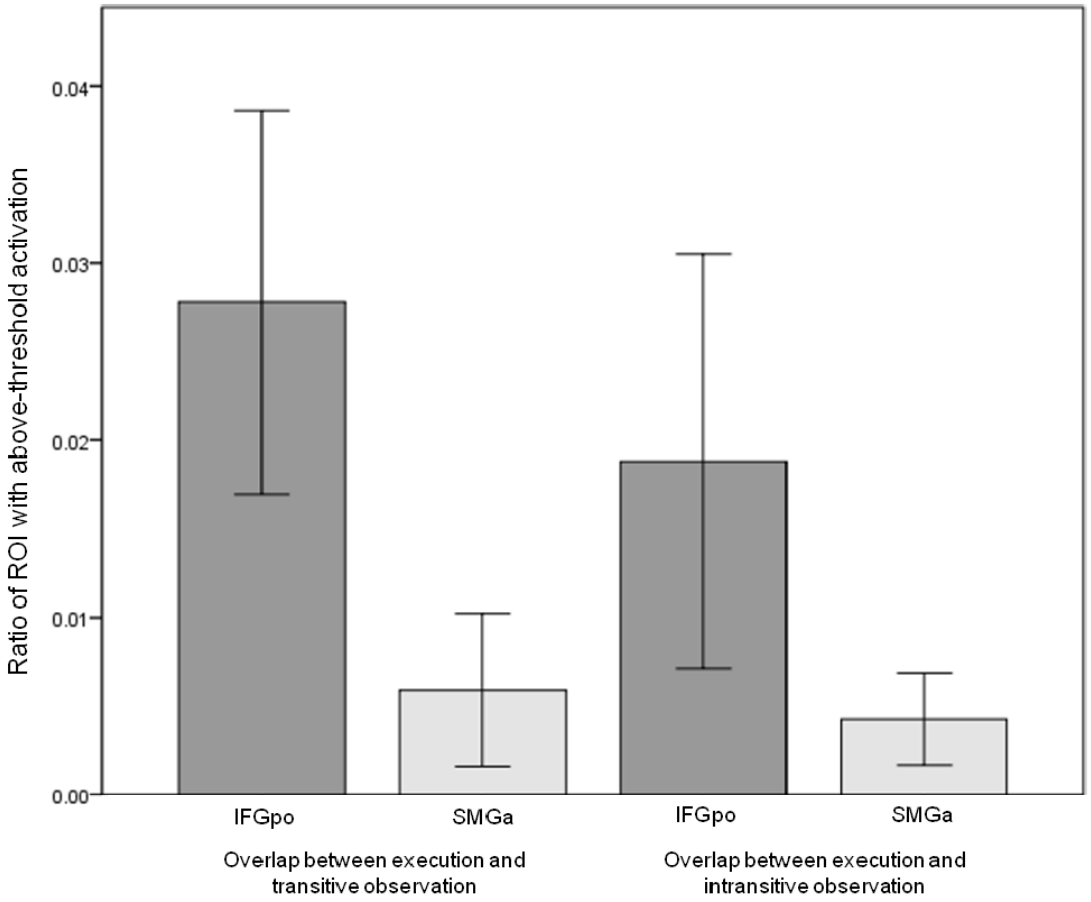


Figure A.1-14. Quantification activations within ROIs in top 25% of voxels in overlap analyses incorporating rest.



No effect of condition (df=1, F=2.984, p=.183) or ROI (df=1, F=2.529, p=.210), repeated measures ANOVA. Error bars: +/- 1 SEM.

Figure A.1-15. Top 25% of voxels in execution-rest subtraction.

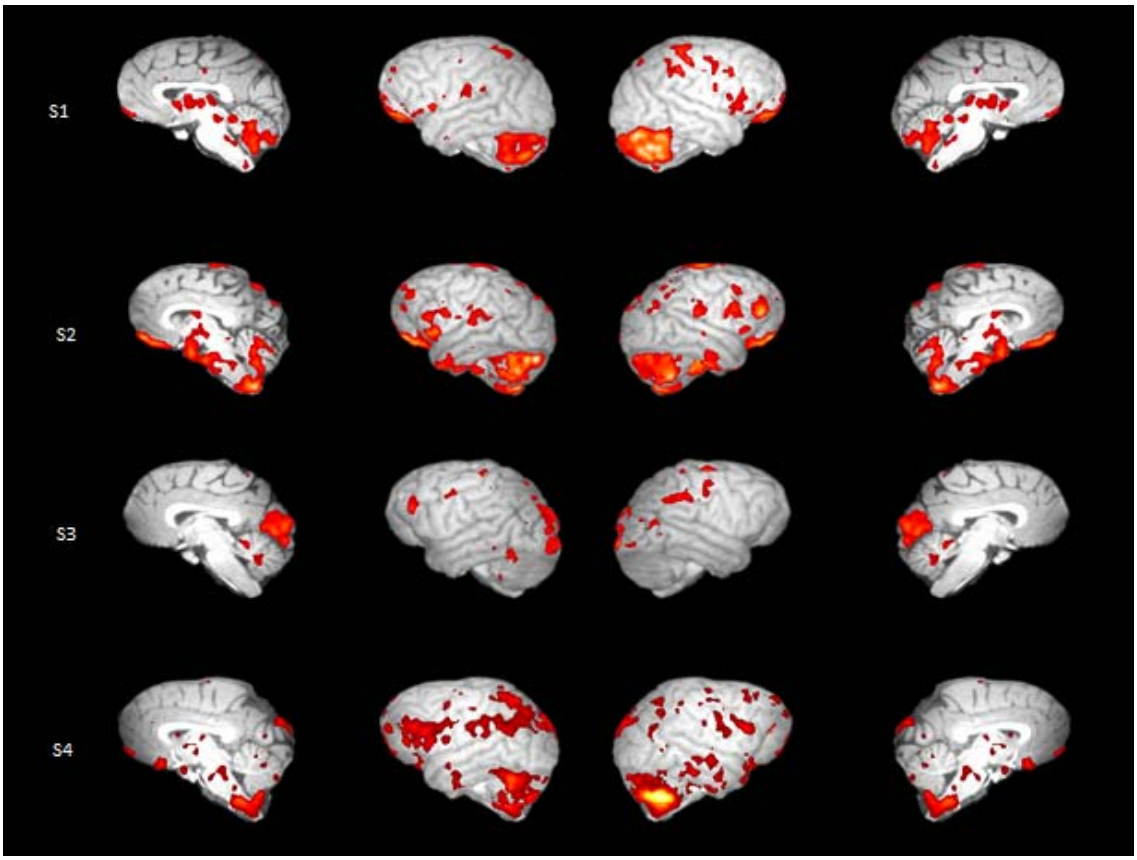


Figure A.1-16. Top 25% of voxels in transitive observation-rest subtraction.

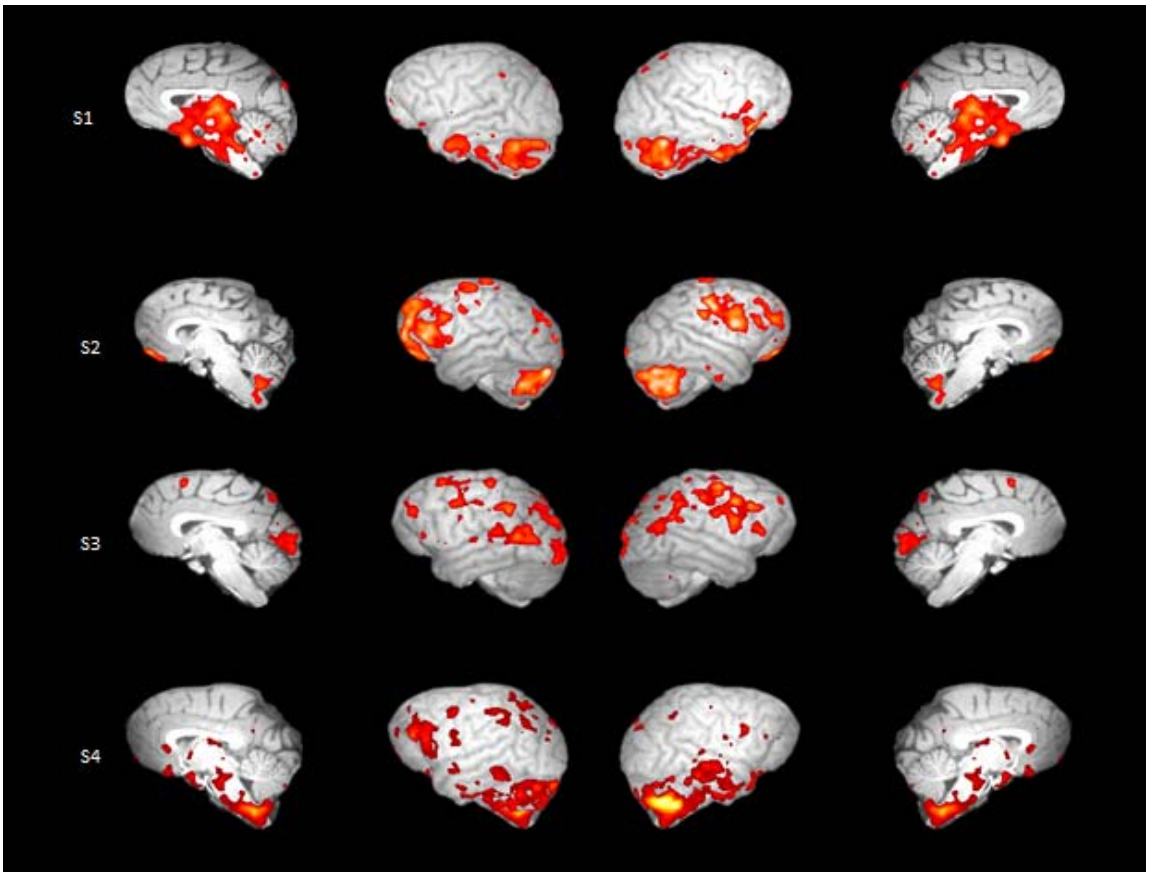


Figure A.1-17. Top 25% of voxels in intransitive observation-rest subtraction.

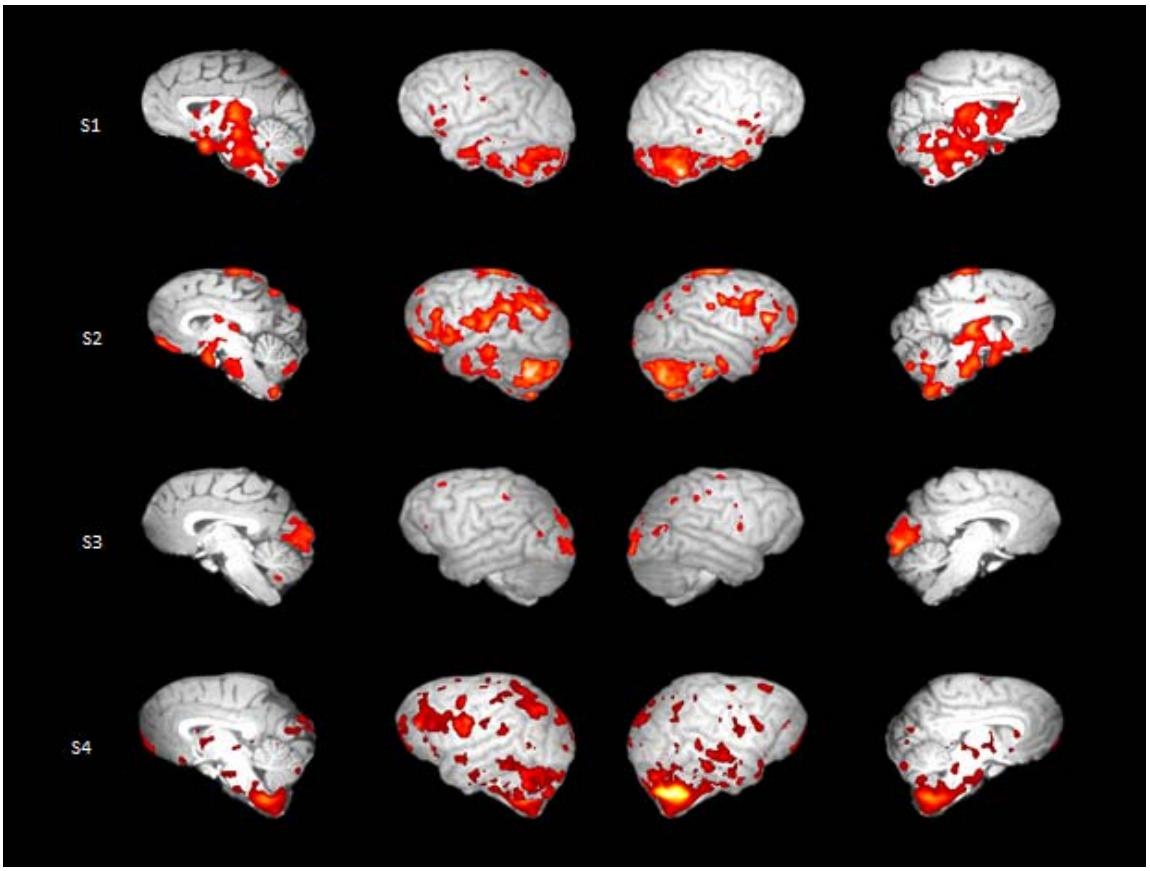
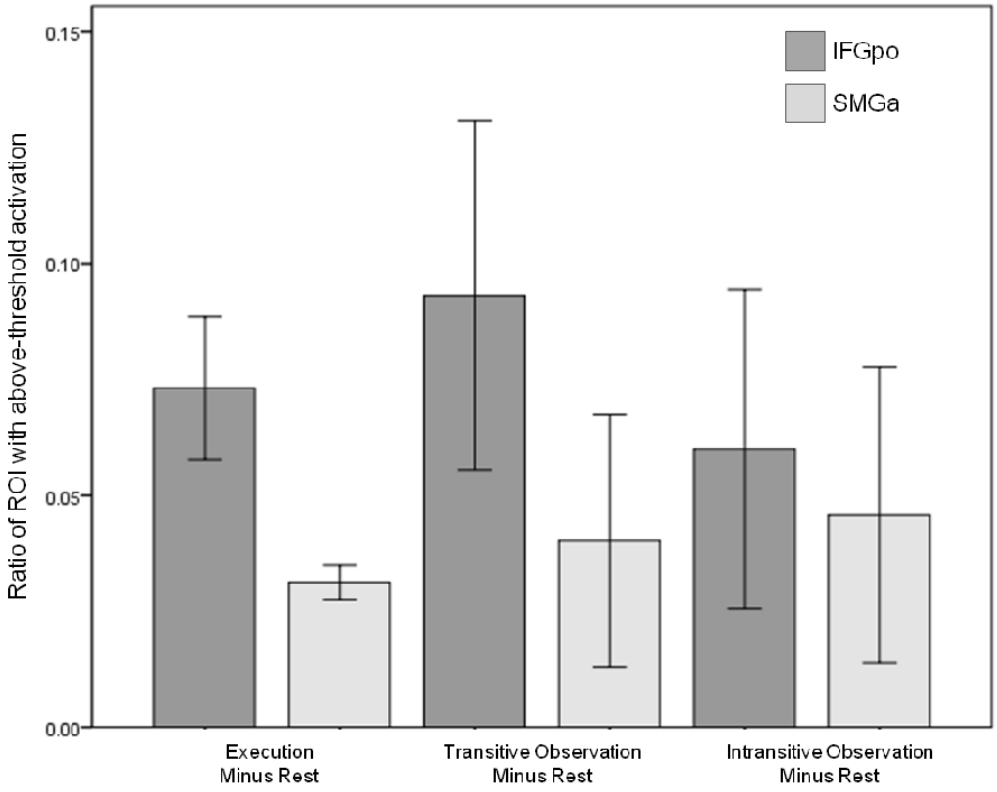


Figure A.1-18. Quantification activations within ROIs in top 25% of voxels in individual conditions-rest.



No effect of condition (df=2, F=.203, p=.822) or ROI (df=1, F=2.482, p=.213), repeated measures ANOVA. Error bars: +/- 1 SEM.

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