Semantic and motor processes in infant perception of object-directed and tool-mediated action

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Declaration

This thesis is my own work and no portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification at this or any other institute of learning.

Áine Ní Choisdealbha 19th February 2016

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Abstract

Actions are the translation of internal states such as intentions into overt gestures and goals. Actions are communicative, because by observing another's overt behaviour we can infer that person's internal states. Infants' abilities to execute actions are limited by developing motor processes. Their capacity to make inferences from others' behaviour is hindered by their inability to engage in perspective-taking and other advanced social cognitive processes. Nonetheless, extensive evidence shows that infants perceive actions as goal-directed sequences that are meaningful, and that they respond to observed actions with motor resonance. The aims of this thesis were to determine how semantic and motor processing of observed action develop in infancy, whether these processes develop separately or in conjunction with one another, and how infants' abilities to execute and plan actions affects ability to detect semantic and motor differences between actions. These aims were achieved by studying how infants processed grasping actions that varied on different dimensions. In Chapter 1, the literature on infant action perception from social, motor and semantic perspectives is reviewed and the objectives of the thesis are described. In Chapter 2, the ability of 16-month-olds to discriminate between the uses of a novel tool when motor simulation processes are uninformative was investigated. In Chapter 3, the attentional and semantic neural correlates of processing of observed grasps were measured in 9-month-olds, 11.5-month-olds, and adults. In Chapter 4, motor activation in 10-month-old infants in response to motorically similar but semantically distinct grasping actions was related to infants' action planning skills. The results of these experiments show that there is a complex interplay between motor and semantic constituents of the action processing system, and that this interplay is developmentally dynamic. The implications of the results for understanding action processing in development are considered in Chapter 5.

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Chapter 1: General Introduction

Literature Review

The developmental cognitive neuroscience of action: semantics, motor resonance and social processing.

Text as it appears in Ní Choisdealbha, Á., & Reid, V. (2014). The developmental cognitive neuroscience of action: semantics, motor resonance and social processing. *Experimental Brain Research*, *232*(6), 1585-1597. Given Springer journal regulations, APA citation style is not used in this text.

Abstract

The widespread use of EEG methods and the introduction of new brain imaging methods such as near infrared spectroscopy have made cognitive neuroscience research with infants more feasible, resulting in an explosion of new findings. Among the long-established study of the neural correlates of face and speech perception in infancy, there has been an abundance of recent research on infant perception and production of action and concomitant neurocognitive development. In this review, three significant strands of developmental action research are discussed. The first strand focuses on the relationship of diverse social cognitive processes, including the perception of goals and animacy, and the development of precursors to theory of mind, to action perception. The second investigates the role of motor resonance and mirror systems in early action development. The third strand focuses on the extraction of meaning from action by infants and discusses how semantic processing of action emerges early in life. Although these strands of research are pursued separately, many of the findings from each strand inform all three theoretical frameworks. This review will evaluate the evidence for a synthesised account of infant action development.

1.1 Introduction

Human infants are born at an earlier stage of motor and brain development than might be expected when compared with the newborns of other primate species (Bard et al. 2011; Miller et al. 2012) and consequently are dependent on their caregivers to fulfil their needs and wants. Actions are a means of forming an interface between those needs and wants and the external world. Although neonates and very young infants appear unable to act except reflexively, it is probable that some volition underlies their behaviour (Meltzoff and Moore 1997; van der Meer et al. 1995; Rochat and Hespos 1997; von Hofsten and Fazel-Zandy 1984) and by 3 months of age they will act with intent, for example, to reproduce a salient outcome (Hayne and Rovee-Collier 1995). By 6 months, infants perceive actions as goal-directed (Woodward 1998). There has been a raft of recent research exploring how infants perceive and engage in intentional interaction with the external world. By examining how the ability to act is acquired and improved in its earliest stages, developmental action research is changing not only how we approach early social and cognitive development but also how action is conceptualised across the lifespan.

Actions are distinct from reflexive movements. They are purposeful and internally generated (von Hofsten 2004). It is commonly known that pronounced motor developments such as the acquisition of walking, crawling and pincer grasps occur during infancy, but motor proficiency is not the sole component of action. Action production and perception involve cognitive and higher-order perceptual processes in the forms of object recognition (Hunnius and Bekkering 2010), goal maintenance (Csibra et al. 1999; Luo and Baillargeon 2005), and problem solving (Barrett et al. 2007; Elsner and Pauen 2007). There is also some evidence that competence in motor planning and execution is beneficial for both perception and production of action (Daum et al. 2011; Loucks and Sommerville 2012; van Elk et al. 2008b). The goal of developmental action research is to understand how infants develop the ability to perceive and produce purposeful actions of different levels of complexity, how other processes affect action development, and how action development might be related to the emergence of other processes, such as language (Brooks and Meltzoff 2005; Oudgeneog-Paz et al. 2012; Reid et al. 2009) or visuo-spatial reasoning (Johnson 2010; Soska et al. 2010).

The cognitive neuroscience approach to action development predominantly adopts one of three distinct but related theoretical perspectives. One approach comes from the social cognitive tradition (Striano and Reid 2006), which emphasises the impact of social cues and observation on learning. There has already been much research investigating infant neural responses to social stimuli, including social action stimuli (Grossmann and Johnson, 2007). A second approach derives from work investigating the ontogeny of the mirror system. As a known correlate of action perception, changes in the infant's EEG response to observed action can be used as a marker of action perception (Nyström et al. 2011). Furthermore, the known similarities in the EEG representation of performed and observed actions can be used to understand how the ability to perform an action influences the perception of that action (van Elk et al. 2008b). Finally, action is also viewed an element of the world that is interpreted via semantic information processing, with a focus on how actions are processed in this way during development (Cummings et al. 2008; Pace et al. 2013; Reid and Striano 2008; Reid et al. 2009) and how the emergence of action perception may be linked to the emergence of other forms of semantic processing (Brooks and Meltzoff 2005).

The insights into action development gleaned from research using neuroscience methods and through adopting one of the three outlined perspectives will be discussed in this review. More crucially, the overlaps between the perspectives will be identified, along with contradictions. These perspectives are not mutually exclusive yet they are not treated as such in extant literature. This is potentially because of the novelty of these approaches. Behavioural research has shown that infants make inferences about ongoing actions, that they anticipate goals, and that movements without goals are not perceived as purposeful actions (Csibra et al 2003; Woodward 1999). The adoption of EEG methods has uncovered the processes that underlie this goal-oriented perception of action. For example, EEG frequency analyses in the mu band have shown that the motoric representation of viewed actions is elicited only when the action is discernibly goal-directed (Nyström et al. 2011; Southgate et al. 2010). Similarly, the presence of an N400 response to actions in 9-month-olds (Reid et al. 2009) indicates that infants' inferences about action are based in an early developing semantic framework, which goes beyond infants' pairing of objects and outcomes simply because they always appear simultaneously. This review proposes a framework in which social, motor resonance and semantic views on action development are integrated.

1.2 Social cognition

The social cognitive perspective is becoming increasingly prevalent in neuroscience research as it becomes evident that specific brain regions and neurophysiological processes are particularly responsive to social stimuli such as faces, voices and bodies (e.g. Kanwisher et al. 1997; Lloyd-Fox et al. 2011; Vuilleumier et al. 2001). An infant is dependent on others, and therefore, the early environment is highly social. It is well established that infants have an innate or early emerging preference for faces, voices and movements (Bertenthal et al. 1987; Blasi et al. 2011; Morton and Johnson 1991). Consequently much of infant development is influenced by the presence of social stimuli (e.g. Pascalis et al. 2002).

One means of studying action development from a social cognitive neuroscience perspective is to look at how established social cognitive processes influence action perception in infancy. Eye gaze is often studied in this regard, using event-related potentials (ERPs). Neonates discriminate between direct and averted gaze, and by at least 4 months of age, this discrimination is reflected in the N170 component of the response to human faces, which has a higher amplitude for direct than averted gaze (Farroni et al. 2002). Sensitivity to gaze is an important aspect of early action development, as it allows infants to detect what others are paying attention to (Reid and Striano 2007; Striano and Reid 2006), facilitating learning about the external environment. Presented with a scene with two objects, 4-month-olds will direct their attention to the object an adult is gazing at (Reid and Striano 2005). In the same paradigm, the infant Nc and positive slow wave (PSW) ERPs, which index attention and memory encoding, respectively, differ in morphology for objects previously cued and uncued by an adult’s gaze (Hoehl et al. 2008). The Nc component of the infant’s evoked response to an object is also of greater amplitude in joint attention contexts, when a live adult engages the infant in mutual gaze and then uses her own gaze to cue the infant to the object, than when the infant views the object with no preceding joint attention interaction (Striano et al. 2006). This shows that infants’ attention to objects in their environment is facilitated and enhanced by social interaction. It also shows that infants are sensitive to the relationships between other people and objects in the environment, which may be a precursor to action perception. Social cues other than gaze have been shown, behaviourally, to contribute to the development of action perception. A number of studies show that infant preference for looking at objects and acting on objects is influenced by adults’ emotional responses to those objects (Repacholi 2009; Repacholi and Meltzoff 2007; Flom and Johnson 2011). The neural correlates of infant responses to adult emotional action cues are open for investigation but existing research suggests that infants can use social cues to learn about actions and outcomes.

Another social cognitive approach is to investigate action in the same manner that faces, bodies and voices have been studied in the past and to find if there is something “special” about viewing actions as performed by a conspecific, or if the perception of actions performed by others is just one application of a more domain-general cognitive ability (e.g. making probabilistic inferences about outcomes based on outcomes often previously seen; Gopnik et al. 2004; Paulus et al. 2011b). Woodward (1998) showed that 5- and 6-month-olds perceive reaching as an object-directed action. Infants of this age also perceive the difference between non-purposeful contact (contact with the back of the hand) and intentional contact (grasping) with an object (Woodward 1999). Hunnius and Bekkering (2010) used eye-tracking techniques to show that from 6 months, infants predicted how an actor would use a familiar object. For example, the infant looked to an actor’s ear when an actor picked up a phone. Processing of goals is often taken to mean that some form of social cognition is occurring, though there is also the possibility that a more general form of probabilistic or associative learning is taking place.

There are additional challenges to and findings in favour of action perception as a specifically social cognitive process. One favourable finding is that infants below one year of age do not expect a mechanical claw to keep grasping the same object unless they know that a human actor operates the claw (Hofer et al. 2005). There are also studies with results that challenge the idea that goals are attributed to conspecifics. However, these studies differ on how “human” a non-human object has to be for 5- to 7-month-olds to perceive it as acting in a goal-directed manner. Kamewari et al. (2005) showed that humanoid robots but not boxes are perceived to have goals, whereas Luo and Baillargeon’s (2005) infants did attribute a goal to a moving box. An early negative ERP in 8-month-olds discriminates between point-light walkers with normative and abnormal human body configurations, while a late positive ERP discriminates between biomechanically possible and impossible actions (Reid et al. 2008). This further suggests that an action can be perceived and processed by infants even if the observed organism is not human.

Perception of agency may be contextual, as Pauen and Träuble (2009) found that 7-month-olds attribute self-propelled movement to a ball when it is presented alone but not when it is presented with an animal-like object. Kaduk et al. (2013) found that infants show a larger Nc response in the visual ERP to scenes in which a ball moves without animacy (i.e. it is stopped by obstacles) than scenes in which the ball moves with animacy (i.e. it stops and jumps over obstacles). This shows again that infants make a distinction between movement from an organism and incidental movement that is based on nuanced, contextual cues and not on the “humanity” of the actor.

In spite of inconsistencies, these behavioural and ERP results indicate that infants by 12 months have well-developed abilities to predict the actions of certain types of agent and can perceive animacy on the basis of motion and context. Such results are not definitive, however, as they do not show whether the predictions are really social-cognitive inferences about goals or whether they arise from domain-general processes used to predict outcomes. By studying action prediction at a neural level, it may be possible to identify specific brain regions or ERPs involved in the perception of action as performed by agents. In this way, the social-cognitive aspects of action might be dissociated from domain-general factors.

Actions are the infant's first exposure to the intentions of others. It has been proposed that this is a social cognitive process – that the infant perceives similarities in another's actions and their own, and is able to attribute a goal to the other actor based on their own experience (Meltzoff 2007). Action experience promotes social cognitive processing of action, as 3-month-old infants with experience of reaching are more capable of detecting the goal of another's reaching action than those with no such experience (Sommerville et al. 2005). Infants' attention to goal-directed action (Woodward 1999), and their tendency to imitate an actor's goals but not his means (Gergely et al. 2002), suggests that some form of social cognitive inference is being made by infants during action observation. Recent work suggests that by predicting actors' goals, infants may be engaging in implicit reasoning about beliefs, which is a precursor to theory of mind (Sodian 2011; Thoermer et al 2012). Engaging the gaze of an adult while observing an unusual action at 20 months predicts theory of mind ability at 44 months (Charman et al. 2000), showing clear links between action understanding and theory of mind.

False-belief reasoning has been associated with a late slow wave ERP that differs between children who can and cannot perform false belief tasks (Meinhardt et al. 2011), and between adults and children (Liu et al. 2009). This component distinguishes between trials in which an actor holds a true versus a false belief, and is observed in adults as they passively observe stimuli (Geangu et al. 2013). Using this passive paradigm, the development of social cognitive action understanding and theory of mind precursors can be investigated in infants. Studies like those of Meinhardt et al. (2011) and Geangu et al. (2013) illustrate one of the benefits of using neuroscience methods with infants. It is difficult to elicit overt behaviour from preverbal children that shows whether or not they understand an actor's false belief. However, the presence (or absence) of an ERP similar in morphology to the ERP elicited in adults by false belief tasks could allow us to infer the ability of an infant or toddler to engage in false belief reasoning. Similarly, changes in the morphology of that ERP could be linked to changes in behaviours related to false belief understanding occurring in a similar timeframe.

There remain many questions about action processing as a social cognitive process. For example, it is still unclear whether the processing of human action differs from the processing of non-human action. Hopper and colleagues (2010) showed 3- to 5-year-old children a task performed on a novel object. Children who were given a demonstration performed by an actor were more successful at performing the task than children who were shown the novel object moving in the same way, but without an actor causing the movement. This shows that social modelling of action is of benefit for learning about action in childhood and infancy (e.g. Hofer, Hauf & Aschersleben, 2005). However, it remains unclear whether infants' predictions of adult actions are the result of social cognitive inferences and if the ability to make such predictions is a precursor to theory of mind. Beyond this context, findings from infancy research can be used to address questions such as whether action perception is a specifically social or a domain-general process.

Conceptualising action understanding in infancy as a social cognitive process is a logical step, given the huge contribution of social cues and context to many other forms of perceptual and cognitive development (Grossmann and Johnson 2007). Action perception by definition involves more varied information than the perception of emotion or of direct eye gaze. It appears that these social cues contribute to action understanding (Repacholi and Meltzoff 2007) and that action perception in turn contributes to making social cognitive inferences (Meltzoff 2007). The more fundamental, automatic processes underlying action processing will be discussed in the remainder of this review.

1.3 Motor Resonance

A recent focus on motor resonance has occurred due to the rise of mirror system research in adult and infant populations. The mirror system refers to human brain responses that are similar for the performance of actions and for the perception of the same actions as performed by others (Gallese et al.

2004). Although activation of the mirror system is elicited by the actions of others and may in some senses be “social”, it is also elicited by stimuli in which objects move but no actor is present (Southgate and Begus, 2013). Two markers of this activity in humans are the mu or sensorimotor alpha and beta rhythms, distinctive oscillatory rhythms within infant EEG from 4 to 10 Hz and 12 to 25 Hz. Four to 10 Hz is a lower frequency than adult mu, but the topography and function of this range in infants justify its characterisation (Marshall and Meltzoff 2011), and infant EEG frequencies are lower than adults’ across all bands. These rhythms index motor activation by becoming desynchronised during action performance and perception. The desynchronization or decrease in alpha power in infants is generally smaller than of that of adults by a factor of 5 or 6, depending on the stimulus (Marshall and Meltzoff 2011). ERPs and changes in blood oxygenation in motor areas (as captured by near-infrared spectroscopy or NIRS) can also be used as markers of mirror system activity. *Motor resonance* is a more broad term than *mirror system* (Uithol et al. 2011), referring to motor activation elicited by any percept, such as a tool, hand or word (Chao and Martin 2000; de Lange et al. 2006; Yang and Shu 2011). Mirror system activity is distinctive because it is thought to involve semantic processing of the action as well as motor simulation (Uithol et al. 2011).

The relationship between the perception of action and the acquisition of new motor abilities can be addressed by determining whether the neural correlates of action performance and perception in infancy are similar, and by studying how these correlates change as new actions are acquired. Marshall and Meltzoff (2011) have identified some of the theoretical and practical questions that must be addressed, such as whether the desynchronization found during action perception and production arises from the same neural source. Findings indicate that the infant brain is discriminately responsive to actions over non-action motion and that much of this activity originates from primary motor cortex. For example, using NIRS, Shimada and Hiraki (2006) found a significantly larger response in the sensorimotor area of 6- and 7-month-olds to an adult directly manipulating a toy than the toy being moved with no visible manipulation. Nyström (2008) showed infants stimuli depicting static and moving dots, and goal-directed and non-goal-directed human action, and found a late positive ERP (about 700ms after stimulus onset) that was significantly larger for the goal-directed action than all other stimuli.

Nyström's (2008) study found motor desynchronization during action observation in adults but not infants. Power changes in the mu and beta rhythms of infant EEG have been found in action studies with older infants. Marshall et al. (2011) found mu desynchronization in 14-month-olds during execution and perception of the same action. In 8-month-olds, Nyström and colleagues (2011) found desynchronization of the mu rhythm in premotor cortex in response to observed action, with greater power decreases found in response to goal-directed action when contrasted with non-goal-directed action. The presence of a desynchronization effect in 8- but not 6-month-old infants suggests that the mirror system is not fully functional at birth but develops over time. In support of this interpretation, it has been shown that adults exhibit a larger mu rhythm power decrease than infants in response to the same stimuli (Marshall et al. 2011). It must be noted that differences in the power of infant and adult EEG or in the morphology of infant and adult ERPs do not relate only to functional differences. The large scale of neural development occurring in infancy means that infants tend to show more interindividual variability in their EEG activity and ERPs than adults (Hoehl and Wahl 2012). Their EEG activity is quite different overall from adults'. Delta and theta activity, seen only in adults in deep sleep, is seen in infants' waking EEG. With these limitations borne in mind, there is still much that can be inferred from differences in infant EEG activity and ERPs across development.

Nyström et al. (2011) found mu desynchronization in 8-month-olds' EEG activity in response to goal-directed action, but not in response to a stimulus with the same outcome but without a goal-directed action. Although this kind of specific, goal-detecting response might suggest that some kind of social, intention-detecting process is being undertaken, it is possible that the process is related to a prediction of outcomes that is not necessarily social in nature. Behavioural research has shown that infants are proficient at predicting the goals of familiar actions (Hunnius and Bekkering 2010). This predictive ability is reflected in mirror system function. In 9-month-olds, mu desynchronization in response to goal-directed grasps is seen before the grasp is completed (Southgate et al. 2009b). The same effect is found for the ERP component identified by Nyström (2008). The 9-month-old's mirror system is responsive only to action with an outcome that the infant can predict – hands in non-grasping postures and hands that reach for empty space do not elicit mu desynchronization whereas hands reaching to grasp a goal object do, even if the goal object is hidden (Southgate et al. 2010). It has also been shown that the goal-directed action does not need to be performed by an agent to elicit mu desynchronization – 9-month-olds show this response to an object being picked up and moved, even if no visible actor performs the action (Southgate and Begus 2013).

These results affirm that the mirror system is driven by goal-directed behaviour, likely because actions with goals are easy to predict and simulate. While mu desynchronization indexes the processing of predictable actions, actions that are goal-directed but violate predictions elicit even greater power decreases in the mu rhythm. Stapel and colleagues (2010) found greater mu desynchronization in 12-month-olds when they were shown unusual actions versus ordinary actions (e.g. bringing a cup to the ear versus bringing it to the mouth). The authors propose that when a prediction about an action turns out to be untrue, the motor cortex is increasingly recruited in order to simulate the new stages of the action. This relates to Kilner et al.'s (2007) conceptualisation of the mirror system as a predictive coding system, wherein frontal predictions about how an action will proceed are fed back to subordinate levels, which then identify prediction errors and signal these back to frontal cortex. The non-grasping gestures in Southgate and colleagues' work (2010) did not elicit this kind of escalated mirror system activity, perhaps due to the movement being perceived as incidental, rather than as an action with an unpredictable outcome.

The conceptualization of mirror system function as a predictive rather than a social process is not entirely straightforward. Shimada and Hiraki (2006) showed that infants process live actions differently to video action, and that motor cortex activity discriminated between stimuli in which an object was moved by an actor, and stimuli in which it moved alone, suggesting that by 6 months of age, the mirror system is more responsive to actions with a visible actor. Perhaps this is due to an early preference for attending to social stimuli, or alternatively it is because the outcome of the action used by Shimada and Hiraki was less salient than the outcome used by Southgate and Begus (2013), and was less obviously goal-directed in the absence of an actor. The mirror system of 4-month-olds has recently been shown to respond to the actions of robots with a humanoid body structure (Grossmann et al. 2013). Given that actions must be goal-directed to elicit mirror system activity, this suggests [like Kamewari et al.'s (2005) work] that infants can attribute agency to non-human actors. The precise relationship between mirror system activity and the agency or "humanness" of the observed actor is currently unknown.

The mirror system's implicit simulation of others' actions could have implications for social cognitive perspectives on action. If infants learn about others' intentions by relating their own actions to actions they observe (Meltzoff 2007) the mirror system may at least provide the basic framework for this ability. Supporting this notion, prior work has indicated that joint action is a social cognitive process in which mirror system activity is also involved. Activation in brain regions associated with the human mirror system is stronger when performing an action in collaboration with others than when performing an action alone (Newman-Norlund et al. 2008). Research with young children has replicated this with mirror system activity being stronger in 4-year-old children during observation of an action performed by another person when the child is participating in that action than when she is not (Meyer et al. 2011). In the same study, mirror system activation while watching a partner's action was associated with successful performance of the task. Behavioural research has shown that 10- and 14-month-olds are more likely to perceive that both actors in an observed joint action share a goal if the infant has previously participated in a similar joint action. If not, they attribute the goal only to the actor who directly interacts with the goal object (Henderson et al. 2013; Henderson and Woodward 2011). Saby et al. (2012) found that mu desynchronization in 14-month-olds is stronger during observation of an action the infant has recently performed, again suggesting that the motor experience influences mirror system responses to others' actions. These results suggest that infants' imitation and perspective-taking are influenced by motor simulation. On the basis of these data, it is clear that social cognition and motor resonance processes interact with one another.

The question of how motor experience influences motor resonance and action processing extends beyond research on joint action. A substantial amount of motor development occurs in the first two years of life, including the acquisition of pincer grips (Sacrey et al. 2012). The ability to perform a pincer grip and use it to grasp objects predicts the ability to discriminate between pincer and power grasps in functional terms (Loucks and Sommerville 2012) and to predict the form of an object for which a hand in a grasping posture is reaching (Daum, Prinz and Aschersleben 2011). The results of these studies provide support for the hypothesis that perception of an action is influenced by production of that action, and that motor resonance and mirror system activity play a role in this process. Van Elk et al. (2008b) showed 14- and 16-month-olds videos of infants walking and crawling across a screen. The authors found that experience with these forms of locomotion affected mu and beta desynchronization in response to these stimuli, as infants with more crawling experience exhibited greater desynchronization, and all infants showed greater beta desynchronization in response to the crawling than walking videos. Motor experience and activation have been shown to facilitate other forms of development, such as spatial reasoning. Soska et al. (2010) found that infants' experience of sitting unaided and exploring objects visually and manually predicted ability to mentally rotate 3D objects. Research with adults has shown that this form of mental rotation elicits activity in adult premotor and supplementary motor areas (Richter et al. 2000), suggesting that motor activation underlies the effects found by Soska et al. (2010).

Although performance and perception of motor abilities are linked behaviourally and in brain activity (Daum et al. 2011; van Elk et al. 2008b), action performance is not crucial for action perception. Meyer et al. (2013) conducted a study with 8-month-olds, none of whom could reliably perform a pincer grasp. The infants were shown an adult hand succeeding or failing to perform a pincer grasp on a small object. Greater mu desynchronization was elicited during observation of the correct than the failed action. The authors propose that while the infants attempt to simulate the novel grasp when the outcome is successful, the combination of an unsuccessful outcome and a novel grasp is too complex for them to process in any meaningful way. They propose a U-shaped function, in which motor resonance is strongest when viewing correct actions in which one is not proficient and incorrect actions in which one is proficient, and weaker for actions that one can perform but not with high proficiency. It is also likely that semantic congruence affects this function, as incongruent actions elicit stronger mirror system activity than congruent actions (Stapel et al. 2010).

There is other, behavioural research that has shown that semantic processing may account for how infants understand actions despite not being able to perform them yet. It has been shown that 12- and 15-month-olds categorize novel objects on the basis of semantic elements, such as the function and causal effects of the object, even if they cannot perform the planning and manipulations needed to use those objects (Elsner and Pauen 2007). This suggests that semantic processes can be used to process action if the action cannot be mapped onto a motor representation gained through experience. A long tradition of research with adults has shown that action is processed semantically (e.g. Chainay and Humphreys 2002). More recent research has shown that the semantic congruence of an action in adults is reflected in desynchronization of activity over the motor cortex (van Elk et al 2010). By investigating semantic representations of action in the infant mirror system using neuroscience methods, it could be possible to determine whether the developmental changes in one process for understanding action (e.g. the emergence of an N400 ERP) affects the development of another (e.g. changes in the mirror system response to actions, driven by differences in action congruence).

Infant mirror system research has the potential to show how new actions become incorporated into the motor repertoire. Motor resonance research in adults has been used to understand how new sequences of actions are learned (Cross et al. 2009). However, most adults already possess the motor ability to perform the components of these new sequences but have not attempted these sequences before. For example, research on adults' learning of novel motor sequences, through observation or performance, uses stimuli such as dance movements (Cross et al. 2009; Cross, Hamilton and Grafton 2006). These stimuli may be novel as entire sequences but composed of individual movements that adults have the ability to perform, and comprehend as a dancing movement. For infants, actions that cannot be performed proficiently are often neither simulated nor perceived functionally (Daum et al. 2011; van Elk et al. 2008b). Infancy therefore presents a unique time to study action, as the ability to simulate many kinds of action (e.g. those requiring pincer grasps) is emergent. Consequently, changes in the neural representation of action during and after the acquisition of entirely new motor abilities can be studied. This kind of research may lead to a more parsimonious understanding of action learning throughout the lifespan. It also has implications beyond developmental research, for example for the rehabilitation of adults who have suffered neurological damage rendering them unable to execute or control certain actions, or who need to learn to control prosthetic limbs and digits. An additional implication of this kind of research is the importance of the “humanness” of the actor. Research with adults has shown that it is possible to learn new actions via observation of others (Cross et al., 2009). Determining whether infant mirror system-mediated learning of action is facilitated by watching conspecifics only versus any kind of humanoid actor could have implications for the training of athletes, dancers, military personnel or medical personnel via computer simulations and robotics.

Within developmental research, studying the function of the mirror system in infancy has implications beyond discovering how new actions are learned and represented in the motor cortex. In terms of social cognition, this research could inform how infants come to attribute agency to different kinds of actor, from mirror system responses driven by human action alone at 6 months (Shimada and Hiraki 2006) to a later ability to infer goal-directed action even in the absence of an actor (Southgate and Begus 2013). It could also illustrate, through joint action research, how motor abilities influence the development of social cognitive processes such as perspective-taking. In relation to semantic processing of action, the response of the mirror system to actions the infant cannot perform but can predict may show whether these systems for action processing develop separately or in tandem, and whether they are separable or linked systems.

1.4 Semantics

EEG research with infants has shown that the mirror system is engaged during action processing from an early age. ERP research has shown that action perception in infancy is also a semantic process. There is long-standing evidence in adults for these two forms of action processing. Neuropsychological dissociations between different kinds of impairment show that actions can be processed in two different ways, semantically or via a direct vision-to-action pathway. For example, some patients imitate demonstrated gestures but cannot produce an appropriate gesture in response to an object (Chainay and Humphreys 2002). Further support for action perception and production as semantic processes comes from research showing that an N400 ERP is elicited in response to visually-presented sequences of actions with unexpected or inappropriate outcomes, tools or gestures (Kutas and Federmeier, 2011; Sitnikova et al. 2008).

Investigating action development from a semantic perspective may offer some clarification as to why infants rapidly learn about goals in action without assuming them to be proficient social thinkers. Csibra and Gergely (2007) characterise action perception as a teleological process, wherein infants and adults alike perceive action not in terms of its means but in terms of its goals. For example, 9-month-olds do not expect an agent to follow the same path to a goal when there is an obstacle present and when there is not (Csibra et al. 1999). This process may be separable from motor resonance, as 6- to 8-month-old infants are more surprised by inefficient but biomechanically possible reaches for a goal-object than efficient but impossible reaches (Southgate et al. 2008). Findings from this research effort can be understood as the infant making an association between a gesture, an object and an outcome. Violations of the learned association could elicit their interest much like a semantically unusual sentence might elicit surprise in adults (Ganis et al. 1996).

Baldwin et al. (2001) habituated 10- and 11-month-old infants to multi-step action sequences. Infants dishabituated to pauses in the action sequences only if the pause did not occur at a natural juncture in the action – for example, after a grasp had been completed. This shows that infants perceive actions as structured sequences with functional demarcations. Loucks and Meltzoff (2013) demonstrated a similar demarcation of action with toddlers. Three-year-olds shown two familiar, multi-step actions (e.g. putting a doll to bed and taking a doll for a drive) with the steps in the correct order but interspersed between the two actions, imitated the actions without interspersion. This suggests that toddlers' memory for a demonstrated familiar action sequence is dominated by their semantic representation of that action. The results of these behavioural studies are reflected in patterns of neural activity. Reid et al. (2007) presented 8-month-olds with action sequences that were suspended and reversed before completion, such as a video of an actor pouring water into a glass from a jug that ends prior to the liquid exiting the jug. Using EEG, it was found that bursts of synchronised gamma band activity over left frontal regions are more pronounced for incomplete than complete actions. This suggests that infants pay more attention to or are more surprised by incomplete actions. While surprise in response to goal violations may be attributed to social inference about actors' intentions, surprise in response to incomplete actions suggests less equivocally that infants have semantic representations of how actions ought to proceed and of the natural demarcations of actions.

In adults, an N400 ERP of greater magnitude indicates that an action has been perceived as unusual, unexpected or impossible (Kutas and Federmeier 2011; Reid and Striano 2008; van Elk et al. 2008a). The same effect is found in 9-month-old infants. Reid et al. (2009) showed infants sequences of images depicting actors picking food items up and placing them either in the mouth or on the head. An N400-like ERP was elicited about 700ms post-stimulus onset with a significantly larger amplitude for the incongruent than congruent actions. The same effect was not found in 7-month-olds. Given that younger infants can often determine the goal of an action (e.g. Daum et al. 2009a, b; Woodward 1998), this finding suggests that the efficient storage and retrieval of semantic representations of actions develops over time. Some differences are noted between the infant N400 and the adult N400 found in the Reid et al. (2009) study. No N400 component was seen in the waveform evoked in the 7-month-olds. In the 9-month-olds, the N400 component was seen. It was different in amplitude between conditions, indicating a response to stimulus congruence at this point. Compared to the adult N400, the infant response was later in latency and observed in more posterior locations. The difference in topology was attributed to a large, attentional fronto-central Nc component masking the N400 component over central electrodes. The difference in latency is common in developmental ERP studies (Hoehl and Wahl 2012), and may relate to the fact that myelination is complete in the adult brain, allowing rapid neural responses, but is an ongoing process in the infant brain (Picton and Taylor 2007). The fact that infant ERPs change in amplitude over the course of a standard testing session (Stets and Reid 2011) could also lead to differences in analysed infant and adult responses that might not reflect only the studied process – in this case, semantic processing of action.

In the above study, the congruence of the action was determined by whether the outcome of the action matched the function of the object held by the actor. Other aspects of an action can also alter the congruence of an action. For example, an actor may select an inappropriate tool to achieve their goal, or they may grasp or move that tool in an unusual way. During action observation, prior information determines how relevant a particular component of an action is to its semantic congruence. Southgate et al. (2009a) showed 18-month-olds a toy animal moving into a toy house. One group of infants were shown the action’s goal (i.e. the animal inside the house) before seeing the moving action. During the demonstration, the animal either hopped or slid into the house. The infants who had already been exposed to the action outcome were more likely to imitate the hopping or sliding than the group who did not see the outcome first, though all groups imitated the outcome of the action. This illustrates that older infants perceive outcomes or goals as the most important semantic component of an action, but can also process other aspects of the action semantically. A paradigm like Southgate et al.'s (2009a) could be used in an ERP study to determine whether prior knowledge of the actor's goal affects semantic processing of usual or unusual means of achieving that goal.

The existence of a direct vision-to-action pathway in adults (Chainay and Humphreys 2002) supports the possibility that motor simulation exists independently of the semantic storage of actions. This pathway may be present from birth and explain neonatal imitation of facial expressions (Meltzoff and Moore 1997). However, mirror system function and the semantic storage of action are not distinct processes (Uithol et al. 2011). Beta desynchronization is stronger when adults perform functionally incongruent than congruent grasps on familiar objects (e.g. grasping a water bottle over the lid versus around the body; van Elk et al. 2010). Mirror system activation is also responsive to the congruence of an actor's goals regardless of whether the observer attends to the goal (de Lange et al. 2008). These results show that semantic information about gestures, tools and goals are incorporated into the adult mirror system. It is possible that such representations are also present in the infant mirror system. For example, the fact that mu desynchronization is stronger for goal-directed than non-goal-directed actions from at least 8 months of age (Nyström et al. 2011) indicates that semantic representations of actions are incorporated into mirror system function at that time.

It is also possible to integrate the semantic and social cognitive perspectives on processing of action by infants. For example, 14-month-olds imitate an actor who uses her head instead of her hands to turn on a light switch only when her hands are unrestrained (Gergely et al. 2002; Zmyj et al. 2009). When her hands are restrained, they imitate the outcome but use their hands to accomplish it. This illustrates that while infants structure their imitation of adults' actions around the goal, they pay attention to social cues to clarify ambiguity and semantic violations, such as not using the hands to flip a switch. Evidence of a further interaction between semantic, social and motor resonance processing of action in infancy comes from another study using the head-touch paradigm (Paulus et al. 2011a). It was found that infants' imitation of the actor's head-touch was also influenced by whether or not the head-touch would be easy for the infant to represent motorically. The same principle of relying on multiple means of action processing might apply to findings from other studies. For example, even though the infant mirror system responds to actions with no visible agents (Southgate and Begus 2013), Hofer et al. (2005) found that younger infants are better at predicting the goal of a grasping claw when they know it is operated by a human, and Hopper et al. (2010) found that young children are better at imitating actions performed by humans than "ghost" actions. Thus, mirror system representations of action may facilitate its processing initially by detecting mismatches or incongruity in the action as usually performed and the action as observed (e.g. Stapel et al. 2010). At a later stage, the semantic processing of action may be facilitated by social information (e.g. the claw being operated by a human agent, the actor's hands being restrained), especially when the action is novel or ambiguous.

The relationship between the action N400 and the linguistic N400 may be found by studying the early development of these processes. Normative language development in toddlers is associated with an N400 of greater amplitude to nonsense versus real words at 19 months (Friedrich and Friederici 2006). If the N400 seen in 9-month-olds in response to action relates to general semantic development, it could therefore be used as a marker for risk of later language difficulties at an earlier stage. Actions communicate intentions, and because infants process the goals of actions early on in infancy, it is possible that action perception could be a precursor to the development of language. Indeed, attention to the direction of an adult's gaze at 10 and 11 months of age has been associated with language ability at 18 months (Brooks and Meltzoff, 2005), a finding that supports the possibility that early attention to and processing of goals is a precursor to language.

Early walkers are usually early talkers (Oudgeneog-Paz et al. 2012). They have greater opportunity to explore the environment, to discover and manipulate new objects, and to elicit new words from caregivers as a result (Oudgeneog-Paz et al. 2013). It has also been shown that 14-month-olds' use of gesture predicts their vocabulary size at 42 months of age (Rowe and Goldin-Meadow 2009; Rowe et al. 2008), suggesting another link between action production and language learning. Further developmental action research from a semantic perspective has the potential to clarify the precise relationship between action and language development. Given recent results showing that infants as young as 9 months exhibit an N400 congruency effect to visually presented objects following a label spoken by their mother (Parise and Csibra 2012), it is possible that language and action perception develop in tandem as semantic processes. In the clinical domain, the production of verbs by aphasic patients is aided by observation of human action (Marangolo et al. 2012), suggesting a link between mirror system function, semantics and language processing. A recent review comparing the morphologies of the action N400 and the linguistic N400 in adults suggested a common source for both (Amoruso et al. 2013). By expanding this work into developmental research, it is possible that future work will indicate whether these processes develop together or in isolation from each other.

Semantic processing of action is a specific application of a more general process for detecting when something we perceive does not match the predictions we have made based on the surrounding context. Within action processing specifically, mirror system responses to the action allow the outcome of that action to be predicted (Stapel et al. 2010). Social cognitive inference about the action may be facilitated by the mirror system response by allowing the infant to relate the actor’s intentions to their own experience (Meltzoff 2007), and can further be used to provide semantic context about whether the actor’s intention matches the action outcome (Reid et al. 2009). Action congruence is also represented within mirror system activity (van Elk et al. 2008a), which suggests that these processes work in tandem with one another, with higher-level predictions about actions influencing the mirror system response (Kilner et al. 2007). Table 1.1 lists some examples of action development research findings from each perspective, and offers an explanation of how these results can be accounted for in an integrated model. An aim for developmental research in the coming years is to discover how these systems develop in order to optimally function in conjunction with one another.

Table 1.1: *A timeline of infant action development accounted for by an integrated perspective.*

Age	***Action milestones***	***Integrated perspective***
6 to 8 months	***Social:*** Infants predict goals of simple actions (Hunnius and Bekkering 2010; Woodward 1998). ***Mirror system:*** Activity in motor cortex discriminates between human action and other movement (Nyström 2008; Shimada and Hiraki 2006) ***Semantic:*** Attentional Nc ERP component discriminates between congruent and incongruent action outcomes (Reid et al. 2009)	Infants attend more strongly to action outcomes that cannot be directly mapped onto their stored representations of action outcomes. Mirror system activity may facilitate this mapping.
8 to 10 months	***Social*:** Infants attribute goals to non-human actions if given prior knowledge that the action is caused by a human actor (Hofer, Hauf and Aschersleben 2005) ***Mirror system*:** Mu desynchronization is elicited only in response to actions that are discernibly goal-directed (Nyström et al. 2011; Southgate et al. 2010) even if no actor is present (Southgate and Begus 2013) ***Semantic*:** An N400 component is seen in response to action stimuli. This component discriminates between congruent and incongruent outcomes (Reid et al. 2009)	The mirror system facilitates simulation of action outcomes but social cues are still necessary for overt detection of goals. Goals that do not match prior representations are now processed semantically.

Age	***Action milestones***	***Integrated perspective***
10 to 16 months	***Social*: Infants imitate adults' goals without imitating their means (Zmyj, Daum and Aschersleben 2009) ***Mirror system*: Mu desynchronization is greater in response to action outcomes that are more difficult to predict (Stapel et al. 2010). ***Semantic*: Infants perceive actions as sequences of steps with clear junctures (Baldwin et al. 2001)	Mirror system representations of actions can be updated on-line, as sub-goals of actions are evaluated. The goal-driven nature of mirror system function and stored semantic representations of action goals facilitate more rational imitation.
Later infancy to childhood	***Social*: False belief reasoning is associated with a late ERP (Meinhardt et al. 2011) ***Mirror system*: Toddlers who exhibit stronger mirror system activity during observation of a partner's action are more likely to successfully perform joint actions (Meyer et al. 2011) ***Semantic*: Toddlers' memory for multi-step actions is strictly sequenced, even if demonstrations are performed out of order (Loucks and Meltzoff 2013)	The emergence of theory of mind may influence or be influenced by mirror system function. Complex, multi-step actions are represented semantically. Motor planning for imitation continues to be goal-driven and influenced by these semantic representations.

1.5 Conclusions

A decade ago, infant perception of actions and outcomes were characterised behaviourally and attributed to a number of processes such as probabilistic inference (Gopnik et al. 2004) or teleological reasoning (Csibra et al. 1999). While there is much evidence for these processes, it is with the use of neuroscience and particularly EEG methods in the past decade that the more fundamental modes of infant action processing that underlie these forms of reasoning have been explored. Research using these methods has shown that infant prediction of action is performed by the mirror system, that actions are processed semantically, and that semantic representations are incorporated into the mirror system. It has also shown that social cognition is influenced by mirror system function, and that social context and cues may inform semantic processing of action. Although research into infant action perception and production from each of these three perspectives is generally performed without reference to the other two, by synthesising the evidence from each of these perspectives it is clear that there is a substantial amount of overlap between them.

With the proliferation of new studies and new results in infant action research, many new questions have arisen. These include how mirror system activity discriminates between unfamiliar actions and actions the infant sees often but cannot perform, or whether the perception of actions performed by humans is distinct from the perception of actions performed by non-human agents. This review has identified some questions that relate to the potential overlap between the perspectives, including the issue of how semantic processing of action is incorporated into the mirror system, and of the mechanism by which mirror system function may facilitate social cognitive development. Investigation of this overlap is an important objective for infant researchers in the coming decade. Knowledge of how action processing emerges in infancy and how the diverse systems that contribute to it develop, whether in synchrony or apart from one another, has relevance beyond the infant context and could create a coherent picture of how action is performed and processed throughout the lifespan.

Thesis objectives

Are semantic and motor processes underlying action perception examples of a mutually dependent system in development?

Can the relationship between semantic and motor processes be disentangled by studying how infants perceive and process grasping?

The preceding literature review details some general means of characterising processing of actions by infants. It also highlights how these different means of conceptualising action processing may be targeting the same phenomenon at different levels of inquiry, and how semantic, motor and social means of action processing might influence one another. For example, an aspect of action processing considered to be linked to social perception is the perception of actions as goal-directed (Grossmann & Johnson, 2007). Early development of this kind of goal inference has been shown to be underwritten by motor experience (Sommerville, Woodward & Needham, 2005). Extending this assumption, the interpersonal aspects of motor activation (as described by Uithol and colleagues, 2011) that are evident in infancy might not only facilitate the kind of goal inference seen in many iconic studies in this field (e.g. Woodward, 1998). They might also be a representation of the same phenomenon at a different level of inquiry. Many studies of mirror system function in infancy (e.g. Nyström et al. 2011; Southgate et al., 2010) show that mirror activation occurs only when goal inference is possible. Part of the relationship between mirror system function and early social cognition may be a recognition of equivalences between what is seen and one's own actions (the "like-me" framework; Meltzoff, 2007). This allows for inference of another's goals by identifying that another's body is similar in posture and movement to one's own body, and that when one's own body is in such a position (motor resonance/mirror system) it is because one is performing a goal-directed (meaningful or semantically congruent) action, and therefore that the other person might have a goal (the same goal) too (social cognition).

We can refer to Table 1.1 to more comprehensively clarify differences between and overlaps in social cognition, motor processes (and especially mirror system function), and semantic processing. In some ways what the summarised studies show is that the operation of the three systems becomes more tightly linked in development. First, around six to eight months, goal prediction (Woodward, 1998) can be seen as a precursor to social cognition, as it allows infants to make inferences that are tied to the perception of agency in other people (although attribution of agency is flexible, e.g. Kamewari et al., 2005). Second, infants at this stage also show motor processing that differentiates between human and non-human motion (Nyström, 2008; Shimada & Hiraki, 2006). Finally, their encoding of action also refers to the function or "meaning" of the objects being used (Hunnius & Bekkering, 2010), though this may be based on familiarity rather than semantic processing (Reid et al., 2009). By eight to ten months, we can see how these three systems of means of action processing rely upon one another. Goals must be detected for mirror activation to occur (Nyström et al., 2011; Southgate et al., 2010), indicating that infants' understanding of action necessitates that actions are structured in a specific way and that a social entity that can have a goal is involved. Action conclusions that are incongruous or violate the typical structure elicit an N400 ERP (Reid et al., 2009), generally attributable to semantic processing (Kutas & Federmeier, 2011). However, the attribution of goals becomes more sophisticated. For example, the presence of unseen actors can be inferred from experience (Hofer, Hauf & Aschersleben, 2005). What this combination of findings suggests is that action understanding improves in the second half of the first post-natal year as a result of integrating different (social, motor, semantic) processes.

Perhaps goals that were initially detected via social processing lead to a hierarchical, sequential, semantic processing of action, which in turn means that infants try to detect such goals when mapping their own motor representations onto others' actions. Alternatively, repeated motor resonance in response to action in conjunction with a sensitivity to or interest in social stimuli (i.e. other people, Reid & Striano, 2007) may facilitate goal detection as the same action end-state is perceived and mapped repeatedly, eventually leading to a structured action prediction that is so entrenched that deviations are perceived as incongruous and violations of that structure. While much of the literature cited here points to overlaps between the systems, to date their relationships are not explicit, nor is the developmental structure well-elaborated in terms of which abilities are ontogenetic and self-sufficient in their emergence, and which abilities build upon others.

The goal of this thesis is to explore this integration of processes in infant action processing. The work is situated in the framework outlined in the literature review, being informed by the social cognitive perspective on action processing and addressing questions specifically targeted at disentangling the roles of semantics and motor resonance in action processing. This framework is not intended to be exhaustive. To revisit the broader framework of Chainay & Humphreys (2002), they conceptualise two primary routes to action processing, each of which has multiple sub-routes, steps, junctions and correspondences. One route is visual (or more broadly perceptual), and one is semantic. The work presented here is placed within the latter pathway and explores motor activation and motor processes via the mirror system, which is seen as a semantic system (Uithol et al., 2011), rather than via motor resonance more generally, which can be elicited by perceptual input without reference to a semantic processing system (Brass, Bekkering & Prinz, 2001). There is extensive evidence for a perceptual route to action processing in infancy. For example, Yang, Sidman and Bushnell (2010) and Perone and colleagues (2008) discuss infants' engagement in and processing of action as the perception of affordances. In the former work, this refers to "human" affordances and learning what actions can be executed by oneself via observation and imitation of others. In the latter work the authors emphasise the dorsal visual route, as it shows particular patterns of activation in infancy to small, graspable objects that are not seen in response to larger, non-graspable objects (Kaufman, Mareschal & Johnson, 2003), showing that at the level of visual perception, action-specific information is being encoded. While this visual and perceptual route is important, for example, in eliciting an initial motor response to an action (Brass, Bekkering & Prinz, 2001), the framework employed in this thesis relies on the semantic path in order to determine how infants determine whether an action is meaningful and how this relates to their ability to plan multi-step actions that require object affordances to be exploited via one of many possible means.

Neural evidence for semantic action processing (Reid et al., 2009) and mirror system activation (Nyström et al., 2011) is found from the latter half of the first post-natal year. Seven-month-olds do not exhibit the N400 semantic event-related potential (ERP) component in response to action sequences (Reid et al., 2009). Research using mu desynchronization as the measure of mirror system function in infants below nine months of age is sparsely published, and does not find significant mu desynchronization effects (Nyström, 2008). The paucity of research showing neural correlates of semantic and mirror system processing of action in younger infants may be due to inappropriateness of the paradigms used or a lack of sensitivity in the selected measures. It is by no means definitive evidence of the absence of mirroring processes before nine months. Motor measures other than mu desynchronization such as ERPs (Nyström, 2008) and blood oxygenation level dependent (BOLD) signals (Shimada & Hiraki, 2006) find potential evidence for mirror system function at younger ages. Further, research has shown that infant ERPs are changeable over the course of a testing session (Stets & Reid, 2011), allowing for speculation that fewer trials or reduced processing load may facilitate semantic action processing prior to nine months of age. Furthermore, the P400 ERP is sensitive to the directional congruence of pointing and grasping stimuli as early as six months (Bakker et al., 2014; Gredebäck, Melinder & Daum, 2010), suggesting that processing of action “meaning” may be emergent before the N400 is seen in the infant waveform. It cannot be definitively said that semantic and motor processing of action develop simultaneously with one another. What can be said is that these modes of action processing develop along a similar timeframe. It is possible that developmental changes in one have consequences for the other.

Leaving developmental chronology aside, there are two compelling reasons to believe that these means of action processing are linked. The first is that motor experience affects whether actions are processed as being novel or functional. For example, Loucks and Sommerville (2012) grouped 10-month-old infants into those who could use a pincer grip to retrieve a small object from a container, and those who could not. Participants were habituated to an actor grasping an upright bowl by the rim with a pincer grip, or grasping an inverted bowl by the base with a power grip, and moving the bowl across a table. In test trials, they were shown the bowl in the opposite orientation to habituation, and shown the actor executing both pincer and power grips on the bowl without moving it. The same grip used in habituation would be non-functional whereas the novel grip would be functional. Pincer grip users showed a different pattern of looking to infants who could not perform the pincer grip task[1]. Specifically, while less motorically adept infants simply dishabituated to a pincer or power grip that differed from the grip shown at habituation, pincer grippers looked equally long at the stimuli with the (functional) novel grips and the non-functional (previously habituated) grips. This shows that attention to the function of actions arises with motor experience. Much motor resonance or mirror system work with infants has shown that experience of performing a movement or action (van Elk et al., 2008) or experience of integrating visual and motor stimulation (de Klerk et al., 2015) affects activation in response to observed action. This is likely because generating a motor response to an observed action may be difficult if there is no previously held motor representation of that action. Research with adult dancers shows that motor activation during observation of action is modulated by the observer’s experience with and confidence in performing the action (Cross, Hamilton & Grafton, 2006), indicating that motor representations are affected by experience throughout the lifespan. Returning to the work of Loucks and Sommerville (2012), we see that having a motor representation of specific kinds of grip assists not just with representing that grip, as might be expected, but also with representing the function or semantics of the grasp. This makes implicit sense, as mirror responses are not just representations of specific movements but of meaningful, goal-directed actions (Gallese et al., 2009; Stapel et al., 2010).

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[1] Please note that for the remainder of the thesis, “grip” will be used to refer to the specific hand posture and “grasp” for the associated action of using said grip to apprehend an object.

What is novel about this inference is that it shows that infants might incorporate the means of performing actions, such as the grip employed, into their semantic representation of that action. Previous work emphasised the end-state or goal of the action only (e.g. Nyström et al., 2011; Reid et al., 2009; Southgate et al., 2010). In the thesis, this possibility is addressed in a number of ways. The presence of an N400 in infants in response to grasping actions is related to their own experience of grasping (Chapter 3). Similarly, differences in motor activation or mirror system function in response to semantically congruent and incongruent actions are measured and related not to infants' basic motor abilities, but to their ability to plan actions (i.e. their ability to represent action holistically; Chapter 4). In Chapter 2, older infants' ability to make semantic associations between novel tools and functions in the absence of information that facilitates motor mapping is studied. Thus one of the aims of the present work is to look at how semantic processing of action is affected by motor representations of action.

The other aim of the thesis is to look at how motor processing of action (mirror system function) is affected by semantic processes. The second existing compelling justification for looking at integration of motor and semantic processing of action is relevant here. Mirror system function has always been seen as a multi-stage neural process (e.g. Gallese & Goldman, 1998; Kilner, Friston & Frith, 2007), with involvement from parietal and superior temporal sulcus regions in addition to premotor activation. Taking into account the general functions of these regions, there is justification for believing that mirror activation in response to observed action has a semantic element. The parietal cortex occupies the main portion of what is called "association cortex" (Goldman-Rakic, 1988), facilitating the integration of multiple sensory-perceptual inputs. Along with the superior temporal sulcus, it is linked to the establishment of semantics or meaning (Vandenberghe et al., 1996). The superior temporal sulcus is also associated with shared attention (Materna, Dicke & Thier, 2008), processing of social stimuli (Redcay, 2008), and processing of intentionality in action (Pelphrey, Morris & McCarthy, 2004). The mirror system is therefore not just a motor system but incorporates social, semantic and perceptual processes as well.

Thus in the motor activation measured in studies of sensorimotor alpha or mu desynchronization there may be modulation of activity that originates from these other regions. While the presence of a conspecific performing the action is not necessary to elicit mu desynchronization in infants (Southgate and Begus, 2013), the rhythm is sensitive only to goal-directed action (Nyström et al., 2011). In order to infer the goal of an action, infants must perceive the actor as animate (Kaduk, Elsner & Reid, 2013; Kamewari et al., 2005; Luo & Baillargeon, 2005) or must perceive the "actor" as a tool controlled by a conspecific (Hofer, Hauf & Aschersleben, 2005). Mu desynchronization is therefore likely modulated by social aspects of the stimuli. Mu desynchronization is also likely to be modulated by semantic aspects of action stimuli. The work of Stapel and colleagues (2010) offers an example of this. There is little reason that the stimuli of a cup being brought to the ear or mouth shown in that study would elicit differential motor activation unless a previously held semantic representation of "drinking from a cup" was being recruited. More convincingly, the motorically identical stimuli of Southgate and colleagues (2010) modulated mu desynchronization differently depending on whether the action was meaningful (goal-directed) or not. Thus previous infant research suggests but does not explicitly show that semantic and motor processing of action are linked.

Adult research shows a strong link between semantic and motor components of tool-directed action. This is seen in the work of Creem and Proffitt (2001) in which an unrelated semantic task, but not a visuospatial task, interferes with execution of appropriate grasps on differently oriented handled tools. The intention of this thesis is to explore this link in infants. The question of how motor activation in response to observed actions is modulated by semantic components of the action is addressed specifically in Chapter 4. The underlying question of how the semantic system of action processing feeds into the mirror system is addressed in the other chapters as well. In Chapter 3, the semantic processing of grasp or motor components of action, as opposed to goal components, is studied. Thus it can be seen whether or not infants actually process different means of grasping objects as meaningful. In Chapter 2, the ability to represent the functions of a complex tool in the absence of motor information that might assist in distinguishing those functions is measured. This does not preclude mirror system function but illustrates how its semantic elements are active in late infancy.

The theoretical question of how semantic and motor processing of action is integrated in infancy is underwritten in this thesis by the concrete question of how infants perceive the relationships between hands and objects. The end state or inferred goal of an action gives meaning to that action (Proverbio & Riva, 2009). In adults, a larger N400 is elicited during preparation of actions that will have an incongruous end state (van Elk, van Schie & Bekkering, 2010), indicating that semantic processing of goals is not involved only in how we make sense of others' actions, but also in how self-executed actions are structured. However, the means by which we perform actions alters their meaning even if the implicated object (e.g. a claw hammer) has a strongly associated action (hammering). Depending on where on the handle the tool is grasped and in which orientation, it could be used for forceful hammering, precise hammering, or the removal of nails. In some cases, a means of holding an object that might preclude its use may have significance. A hammer might be held over the functional end so another person can take it by the handle. Research with adults has shown that elements of action performance are processed semantically, with a larger N400 elicited during observation of actions in which a tool is held in an incorrect orientation relative to the target (Bach et al., 2009). Motor responses differ between tools that are held in a standard manner and those held in a manner that prevents use of the tool, that is, held incongruently (van Elk et al., 2010). Thus is it reasonable to assume that the means of holding a tool alters the meaning of an action in many contexts. The empirical work in the present thesis explores how infants perceive hand-object relationships independent of (Chapter 3) or in relation to an ensuing action (Chapters 2, 4). This aim is an appropriate basis from which to investigate semantic-motor integration, given that changes in the relationship of a hand and object can render an action semantically congruous or incongruous without necessarily altering the motor aspects of the action (Chapters 2 and 4), or the intended goal of an action can remain unchanged despite motor differences in the hand-object interaction (Chapter 3).

In summary, the objective of the present thesis is twofold. In studying how infants perceive relationships between hands and objects in the context of motor activation, motor experience and semantic processing, it becomes possible to investigate the integration of multiple means of action processing. From a broader perspective, this investigation can tell us about the ontogenesis or origins in associative learning of the mirror system, a topic of recent interest and importance (Cook et al., 2014). Does motor processing of action depend on the ability to process action semantically, or vice versa, or are they two means of characterising the same underlying process? This kind of information can be important for harnessing the best means by which to scaffold infant learning about the world around them, whether through direct motor interaction or through demonstration. It is via action that infants impose their intentions and other aspects of inner life on the world. By investigating the development of tool use from its earliest stages, that translation from preverbal intention to overt action can be better understood and potentially facilitated via application of results to development of learning and communicative technologies in early education.

The thesis commences in the next chapter with a study that examines how 16-month-old infants form associations between complex, dual-function tools and their intended use when simulation of the associated action does not differentiate, on a motor level, the two functions. The results of this study illustrate that although semantic associations can be formed between the parts of a novel tool and its functions, the means in which a tool is held has importance for encoding those functions.

Chapter 2

Dissociating semantic and motor aspects of action understanding: Processing of dual-ended tools by 16-month-olds infants

Text as it appears in Ní Choisdealbha, Á., Westermann, G., Dunn, K., & Reid, V. (Early View). Dissociating associative and motor aspects of action understanding: Processing of dual-ended tools by 16-month-olds infants. *British Journal of Developmental Psychology.*

Abstract

When learning about the functions of novel tools, it is possible that infants may use associative and motoric processes. This study investigated the ability of 16-month-olds to associate the orientation in which an actor held a dual-function tool with the actor's prior demonstrated interest in one of two target objects, and their use of the tool on that target. The actors' hand posture did not differ between conditions. The infants were shown stimuli in which two actors acted upon novel objects with a novel tool, each actor employing a different function of the tool. Using an eye-tracker, infants' looking time at images depicting the actors holding the tool in an orientation congruent or incongruent with the actor's goal was measured. Infants preferred to look at the specific part of the tool that was incongruent with the actor's goal. Results show that the association formed involves the specific part of the tool, the actor, and the object the actor acted upon, but not the orientation of the tool. The capacity to form such associations is demonstrated in this study in the absence of motor information that would allow 16-month-olds to generate a specific representation of how the tool should be held for each action via mirroring processes.

2.1 Introduction

Many cues convey the outcome of a human action involving a tool. There may be prior knowledge about the actor's goals, knowledge about the implicated tool, or experience with the action. From six months, infants show a capability for using much of this information to predict others' actions. They form expectations about the target object of a reaching action from an actor's prior behaviour (Woodward, 1998). They anticipate action outcomes based on the object used (Hunnius & Bekkering, 2010). There are multiple perspectives on the processes recruited by the infant to facilitate this prediction (Ní Choisdealbha & Reid, 2014), and consequently on what kinds of action cue are essential for action prediction. One of the dominant ideas is that of the mirror system (Southgate, Johnson, El Karoui, & Csibra, 2010). Processing of action is also characterised independently of motor processes as associations between actions and outcomes. For example, 10-month-olds associate an observed action on an object with a particular outcome like a sound, and exhibit surprise when a new action elicits the same outcome (Perone, Madole & Oakes, 2011). These associations exist despite infants' inability to perform the implicated actions (Daum, Prinz & Aschersleben, 2009; Elsner & Pauen, 2007).

Semantic processing of action refers to the processing of actions as a series of steps or a grouping of action, object and outcome that has a particular meaning. For example, the presence of a cup elicits an expectation of drinking. If the cup is placed in a sink, a different expectation follows. This kind of action processing is well-established in the neuropsychological literature (Chainay & Humphreys, 2002). Although behaviourally difficult to disentangle from associative processing (and perhaps emergent from it), event-related potential research with infants (Reid et al., 2009) and toddlers (Pace, Carver & Friend, 2013) suggests that semantic action processing develops early in life. This study addresses whether motor and associative/semantic processes consistently co-occur in infant action processing (e.g. Daum, Prinz & Aschersleben, 2011) or if they are separable.

During action observation in infancy, motor representations of actions are recruited and activation differs between motorically similar actions with different outcomes (Nyström, Ljunghammar, Rosander & von Hofsten, 2011). Such activity is present for goal-directed actions even if the outcome is occluded from view (Southgate et al., 2010) and is greater in response to actions with unusual outcomes (Stapel, Hunnius, van Elk, & Bekkering, 2010). The fact that goal-directed structures of ongoing actions influence motor activation during observation suggests that there is a semantic element to mirror system function (Uithol, van Rooij, Bekkering & Haselager, 2011). For example, if the motor activation found in Stapel at al.'s research (2010) was not affected by an established representation of the familiar action's goal, it would be elicited near identically by the motorically similar familiar and unfamiliar actions performed by the actors.

One question arising from semantic-motoric processing of action is whether semantic processing of action relies on or can be dissociated from co-occurring motor activation. Links between action production and perception in infancy exist for reach-to-grasp actions (e.g. Daum et al., 2011). Dissociating semantic from motor activation is challenging given the strength of the link between production and perception across multiple age groups (Ambrosini et al., 2013). It may be possible in the context of tool use because tool use often requires manual skills that are beyond the abilities of infants, but produce outcomes that are salient and readily processed.

The findings described above apply to the perception of actions in which an object is directly apprehended by the actor, but do not generalize to tool-mediated actions. Such actions include those in which an external or goal/target object is acted on with a tool (e.g. hitting a nail with a hammer), as opposed to actions in which only one object is required to achieve the goal (e.g. reaching for and grasping a cup). There is evidence for learning of the function of novel tools from the beginning of the second year. Eleven- and 12-month-olds categorize novel tools on overall similarity without a demonstration of their function, and on functional part similarity following demonstration (Träuble & Pauen, 2007). Furthermore, functional categorization of these novel tools requires that their effects be causal rather than associative – that is, different objects that pull an elastic band are only categorized together if their demonstration showed a physical hooking of the band (Träuble and Pauen, 2011), not a “ghost” action in which hook and elastic band moved simultaneously. Thirteen-month-olds learn the function of tools if the causal part of the tool-mediated action is hidden but plausible (Hernik and Csibra, 2015).

These studies offer basis for a definition of infant understanding of tool function. It is an association made by the infant between a particular tool and one or more aspects of its relationship with a target object – whether the outcome produced on the target object by the tool (Hernik and Csibra, 2015) or the physical nature of the tool’s interaction with the object (Träuble and Pauen, 2011). These associations may be formed at a lower level, or semantically. Statistical factors and the contiguity and contingency of actions and effects (Elsner & Hommel, 2004) can partially explain asymmetries in how infants form action associations (Perone et al., 2011), or attribute actions to non-conspecifics (Kamewari, Kato, Kanda, Ishiguro & Hiraki, 2005). However, neurophysiological evidence shows that actions are processed semantically from late infancy (Reid et al., 2009); meaning that components of actions elicit expectancies in infants as to how the action will continue. While associations between tool and outcome may be formed at a lower level, it is simultaneously possible that semantic processing of the action linking them is occurring.

There is evidence for a disconnection between the ability to perform tool-mediated actions and associating effects with tools at 6 months (Daum et al., 2009). This disconnection persists for many months; 12- and 15-month-olds shown the functional relationship between tools and associated objects will bring such items together despite not using the tool competently (Elsner & Pauen, 2007). It is not suggested that mirror system activation is absent in tool-mediated actions. Infants may map motor representations of direct actions, such as grasping, onto tools (Southgate & Begus, 2013). It is possible that infants also learn the effects of novel tools from a semantic perspective, matching a tool to the effect produced. Previous novel tool work (e.g., Elsner & Pauen, 2007; Träuble & Pauen, 2007; 2011) employed two different kinds of tool for two different objects. When presented with one such object and both tools following a demonstration, 15-month-olds performed significantly more manipulations with the effective tool for a particular object than with the ineffective tool. Understanding an action-effect link might only require a motor representation of pushing or pulling on the target object, but does not account for the infants' tool choice, which must have resulted from associations between tool shape, target, and outcome. The results of Hernik and Csibra (2015) add further credence to the possibility of associative encoding or semantic processing of tool use, as that study featured two different tools acted upon identically, yet infants associated a specific outcome with each tool.

One- to 2-year-olds are capable of associating tools with specific effects on goal objects after a small number of demonstrations. Once learned, these associations are rigid. These infants grasp novel tools flexibly but familiar tools are held in the established manner even if it hinders the action they are trying to perform (Barrett, Davis & Needham, 2007). Thus, it may be difficult to attribute more than one effect to a single tool. Twenty- but not 14-month-olds exhibit anticipatory looking towards a target object on the basis of how a dual-function tool is held (Paulus, Hunnius & Bekkering, 2011). It is possible that a motor representation of the grasps on the tool allows the effects of the tool to be distinguished from one another. The 14-month-olds may not have shown this ability as they might not have been able to reproduce both grasps. In Loucks and Sommerville's (2012) work, 12-month-olds who could not yet perform pincer grasps failed to perceive a difference in contexts in which a functional grasp is a power versus a precision grasp. That is, the infants who had greater motor experience, whether due to a motor milestone (Loucks & Sommerville, 2012) or age (Paulus et al., 2011) could discriminate similar actions based on manual information.

Another source of information used by infants during action processing is prior behaviour. Infants anticipate that actors will repeat actions on specific target objects (Woodward, 1998), even if that action is a fixation and not a grasp (Johnson, Ok & Luo, 2007). Object-directed gaze creates an association between actor and object. Fourteen-month-olds shown an actor fixing her gaze on one of two objects will look longer to the fixated object during an action by the actor, but look longer at the other object in the actor's absence (Paulus, 2011). This indicates an association made between actor and object via her gaze. This association does not generalize to a new actor (Buresh & Woodward, 2007).

By the middle of the second year, infants integrate information from multiple sources to associate tools with specific outcomes. Although motor processes play a significant role in infants' processing of action (Daum et al., 2011; Nyström et al., 2011; Southgate et al., 2010), it is possible for them to associate tools with target objects and their effects on these in the absence of motor expertise (Elsner & Pauen, 2007). This associative knowledge about the tool gained from observing others' actions supersedes prior experience in performing the action oneself. However, a factor in understanding of tools at this age is failure to adjust the use of a tool to new actions (Barrett et al., 2007), possibly the result of failing to form associations between the tool and its new effects. Novel dual-function tools are therefore challenging. Twenty-month-olds are able to incorporate grasp information and use that information in predicting how an actor will use a tool. Fourteen month-olds cannot (Paulus et al., 2011). Although motor processes are not necessary for infants to understand the effects of tools (e.g. Träuble & Pauen, 2007), this research suggests that motor information can be used when possible to distinguish between tools' uses. In the absence of these kinds of grasp or motor cues, it is the semantic (Hernik & Csibra, 2015) and associative (Träuble & Pauen, 2007) processes that allow for differentiation between the functions of a novel tool.

The aim of this study was to establish whether infants distinguish the uses of a dual-function tool without distinguishing grasp information, placing the emphasis on associative, social and semantic processes, and minimizing mirror processes. A dual-function tool held identically for each function was created. Given that infants attribute different goals to different actors (Buresh & Woodward, 2007), two actors demonstrated each of the tool's uses. The association between a functional part of the tool and its matched object was contextualized to the presence of one of the actors. The infants' looking behaviour toward the tools would depend on their knowledge of the actors' individual goals, seen in prior research (Buresh & Woodward, 2007; Johnson et al., 2007). The challenge would come from understanding how the actor's means of holding the tool related to the object associated with the actor or her intention.

It was hypothesized that after familiarizing 16-month-old infants with each action they would prefer to look at an image of an actor holding the tool in an orientation congruent or incongruent with her goal. Such a result would show that in the absence of grasp information distinguishing the uses of a dual-function tool, an association can be made between the part of a tool oriented upward and the object it will be used on, in the context of the actor holding the tool. It would build on prior research showing that infants from one year of age make these associations with single-function tools. Infants would need to form multiple associations, not just between the specific tool part and the target object on which it is used, but also between tool orientation and actor. Positive results would also indicate that the differentiation of tool function by infants can proceed without inducing differential mirror system activation and that associations between tools and goal objects can be formed without corresponding motor competence.

EXPERIMENT 1

2.2 Methods

2.2.1 Participants

Forty-six infants were recruited from the research centre's participant pool. The eye-tracker failed to calibrate 12 infants. A further 9 infants were excluded because of insufficient eye-tracking data (*n* = 3) or insufficient trials (*n* = 6). The final sample contained 25 infants (17 male, nine female) aged between 15 months, 16 days and 16 months, 14 days (mean 15 months, 28 days; *SD* 7 days). Families received travel compensation and a baby book for participation.

2.2.2 Stimuli

Participants viewed pictures and videos of two female adult actors using a dual-function tool to act on two different ‘goal objects’. Both of the goal objects were painted grey wood. One consisted of a large and small post extended vertically from a flat base. A yellow loop hung from the larger post (Figure 2.1a). The other consisted of a large vertical post with two smaller posts extended horizontally from it. A red loop hung from the lower post (Figure 2.1b).

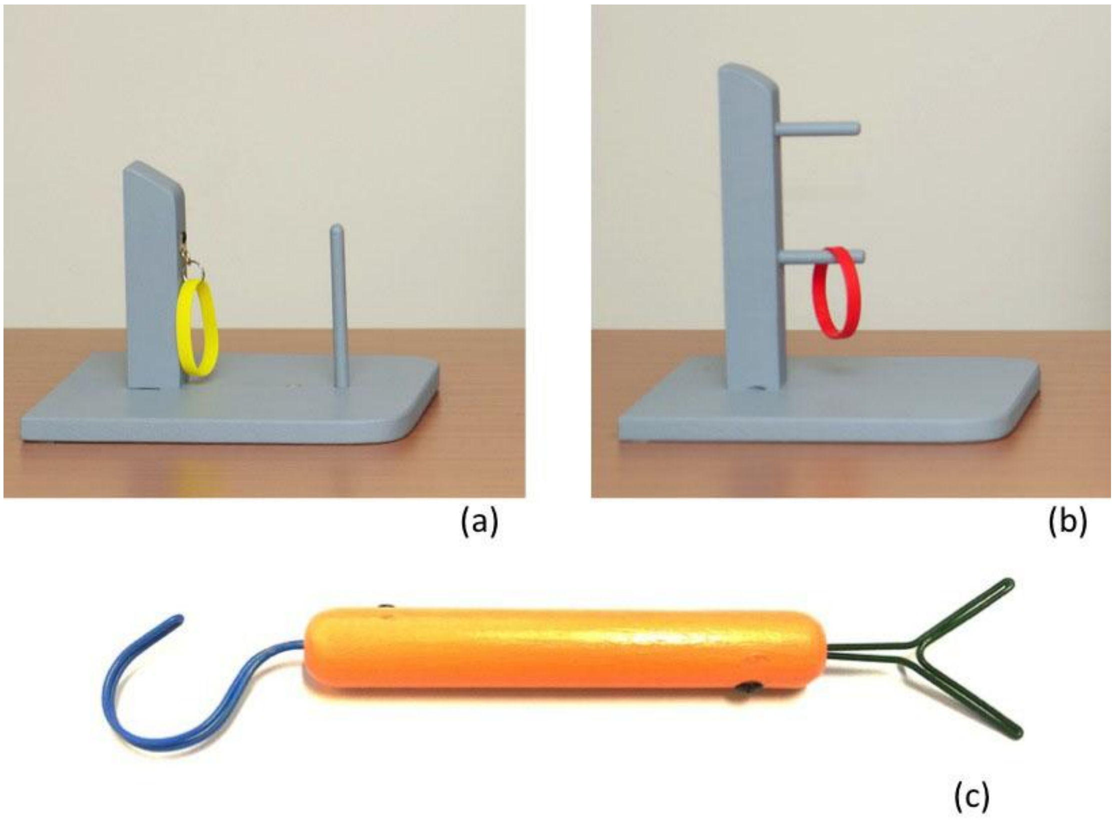

Figure 2.1: *Goal objects (a, b) and dual-function tool (c) used in video and photographic stimuli.*

The tool (Figure 2.1c) had an orange handle roughly 18 cm in length. On one end was a blue C-shaped effector; on the other a green V-shaped effector. The blue tool-end always pulled the yellow band. The green tool-end always lifted the red band from the lower to the upper horizontal post. Stimuli were designed to maintain similar perceptual salience across actions.

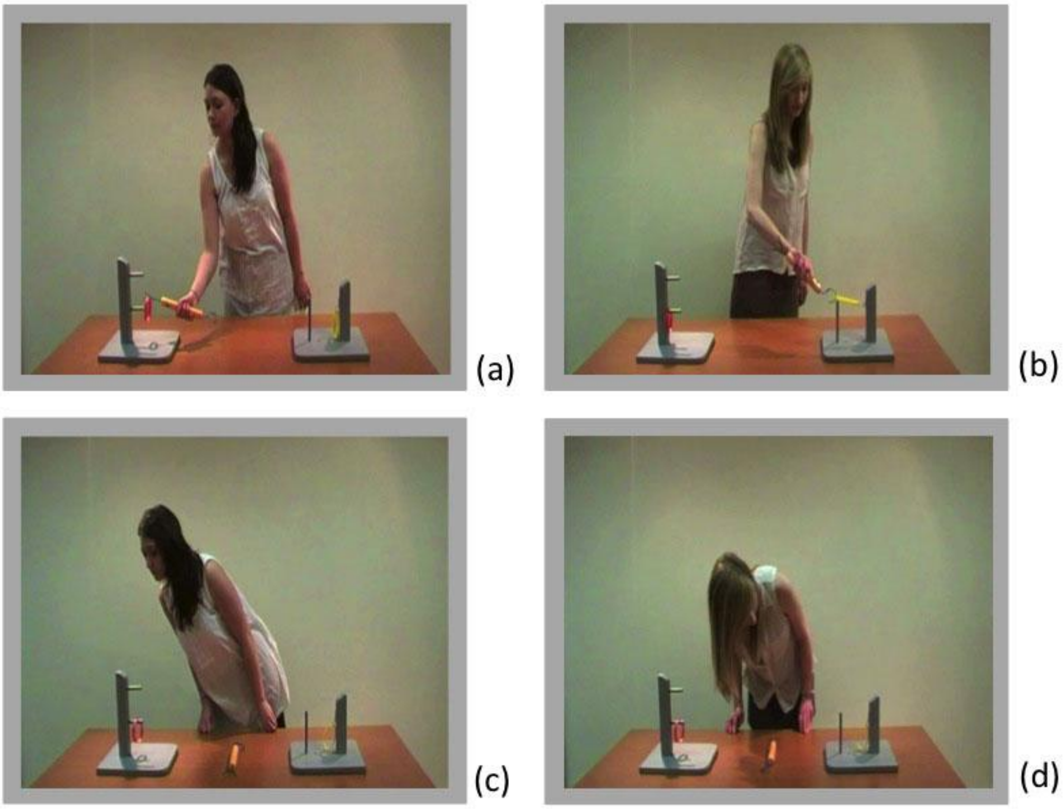

Figure 2.2: *Frames from the stimulus videos.*

The actors were shown in videos expressing preferences for one of the objects (‘liking’) and acting on it with the tool (‘demo’). All videos (Figure 2.2) depicted the actor standing behind a table, the tool at midline, an object on either side. Videos were created for each actor in all visual permutations (blue tool-end towards/away from actor, goal objects on left/right). Videos were silent except for a 1-s chirping/squeaking sound at the beginning to facilitate attention. Actors maintained neutral facial expressions throughout to avoid interfering effects of affect (e.g. Flom & Johnson, 2011). The ‘demo’ videos were 16-18 s in length. They began with the actor looking at the tool in front of her. She picked up and held the tool upright at her chest (appropriate tool-end for her action oriented upwards), making eye-contact with the camera. An identical whole-hand grip was used in all stimuli. She turned to the object matching the function of the upright tool-end, leaned toward it and performed the associated action. She withdrew the tool to her chest, made eye-contact with the camera again and replaced the tool on the table (Figure 2.2a, b). ‘Liking’ videos were 13-15 s in length. These began with the actor looking at the tool in front of her. She turned to one of the objects, leaned over it and looked intently at it from above for 2 s, then from the side for 2 s. She withdrew to an upright standing position, continuing to fixate on the object (Figure 2.2c, d). This pattern was based on Johnson et al. (2007).

Critical stimuli were images of the actors holding the tool, presented for 15 s (Figure 2.3). These were also accompanied by a 1-s sound. Two images of the same actor appeared side-by-side on a grey background. In one image, the blue tool-end pointed upwards; in the other, the green tool-end did. In the image in which the actor held the tool-end that matched her goal object upright, the orientation was congruent with her intended action. In the other, it was incongruent. Critical stimuli were created with the congruent and incongruent images appearing equally on each side of the screen. Each image subtended a visual angle of approximately 13° horizontally and 15.5° degrees vertically on a 22-inch screen (resolution 1350 x 1080 pixels).

Figure 2.3: *Example of a critical stimulus image shown to participants, depicting the same actor holding the dual-function tool in two different orientations.*

Each tool could be used to perform each action, moreso with the C-shaped than Y-shaped effector. However, each actor used her effector on only one of the goal-objects in the above-described manner. The congruence of her way of holding the tool was therefore related to her established goal, and not to the affordances of the goal objects. The paradigm was designed thus because there is evidence to show that when many action possibilities are available, infants assume that an actor will continue to behave in a previously demonstrated manner (e.g. Johnson et al.; Woodward, 1998).

2.2.3 Procedure

Infants were seated on the lap of their caregiver approximately 60 cm from the screen. Eye gaze was recorded using a Tobii X120 eye-tracker. Stimuli were presented using Tobii Studio (Tobii AB, Stockholm, Sweden). Calibration was performed using a 5-point procedure.

Following calibration, an attention grabber was played on the screen. Next, a series of videos was shown. The first was a ‘liking’ video of one actor followed by a ‘demo’ video of the same actor. Next were the ‘liking’ and ‘demo’ videos of the other actor. In each ‘liking’/‘demo’ pair, the position of the objects on the table and the orientation of the resting tool were the same.

Following this sequence, up to 12 trials were shown. In each, a ‘liking’ video was shown followed by the paired image stimulus. Alternate actors were shown in each trial. After the third and sixth trials, the ‘demo’ video that matched the preceding trial was shown. The non-critical features of each video (e.g. whether the blue end of the tool faced the actor or the infant) were counterbalanced for each presentation of these videos. The actor’s preferred object and consequently their means of using the tool was consistent throughout each experiment, but counterbalanced across participants.

2.2.4 Analysis

Identical areas of interest (AOIs) were defined on each of the critical images. These were the entire image, the actor’s face, the tool, the upper tool-end, and the lower tool-end. As the face and tool AOIs are subsets of the entire image AOI, and the upper and lower tool-ends are subsets of the tool AOI, two analyses were conducted to avoid comparing the same looks to one another under different categories. Data were extracted from Tobii Studio using an I-VT filter. For each pair of images shown, a trial was defined as the period following the end of the first look at either of the tool AOIs to the end of the trial. This definition was utilized because the images were decontextualized until the infant saw one of the tools. Prior to seeing one of the tools in either of the images, the infants saw the parts of the scene that were the same in both images – the actor's face and the background. By looking at the tool in either picture, the infant saw the specific orientation of the tool and could subsequently encode the meaning of the scene in relation to the tool being held and its orientation. The timing of infants' first look at the tool did not follow a uniform pattern and some trials (21%) were void as the infant did not look at the tool. All analyses used proportional total looking time.

2.3 Results

Trials were defined as 'congruent first' or 'incongruent first', depending on whether the infant's first tool look was at the congruent or the incongruent tool. Looking times to each of the congruent and incongruent images were similar, regardless of trial type (Figure 2.4).

A 2 x 2 x 2 ANOVA was conducted on looking time data with factors of trial type, image congruence and area of interest category. There were no main effects of trial type (F(1,24) = 3.214, p = 0.086, η^2_p = 0.118) or of image congruence (F(1,24) = 0.005, p = 0.942, η^2_p = 0). There was a main effect of AOI category; infants looked significantly longer at faces than at tools (F(1,24) = 6.626, p < 0.025, η^2_p = 0.216) (Figure 2.5). Infants spent an average of 26.38% (SE = 2.76%) of total looking time looking at each face AOI, versus 17.66% of total looking time (SE = 3.39%) looking at each tool AOI (Table 2.1). There were no interaction effects.

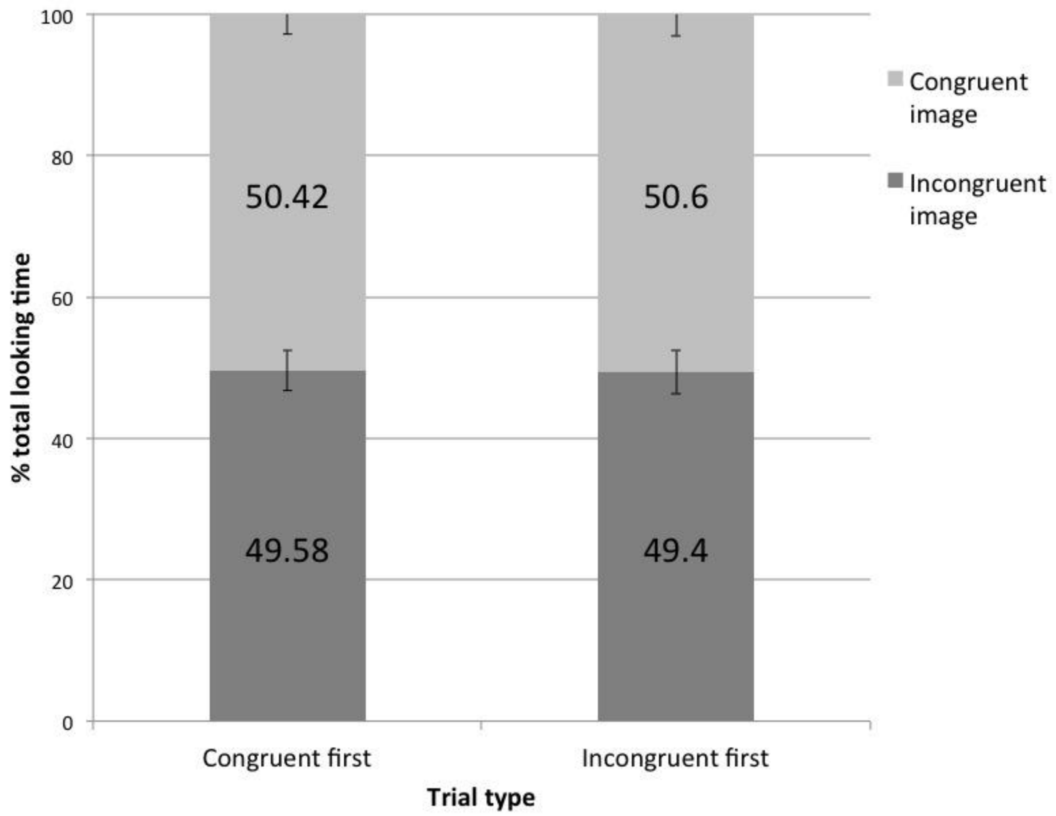

Figure 2.4: *Looking times to the overall congruent and incongruent images, Experiment 1.*

Overall, looking times to the incongruent tool-end were longer than those to the congruent tool-end (Congruent: M = 45.13%, SE = 6.6%; Incongruent: M = 54.87%, SE = 1.32%). A Bonferroni-corrected t-test (uncorrected p values, instead α was set to 0.0125 to account for four potential comparisons) was performed on looking times to each of the tool-ends within each image, and on looking times to each of the upper ends of the tools (Figure 2.6). In the case of the incongruent image, infants looked significantly longer at the incongruent tool-end ($p < 0.008$). No difference was present in looking times to the congruent image's tool-ends ($p = 0.135$). Infants did not spend a significantly longer proportion of time looking at the upper end of the incongruently-oriented tool versus the upper end of the congruently-oriented tool ($p = 0.038$).

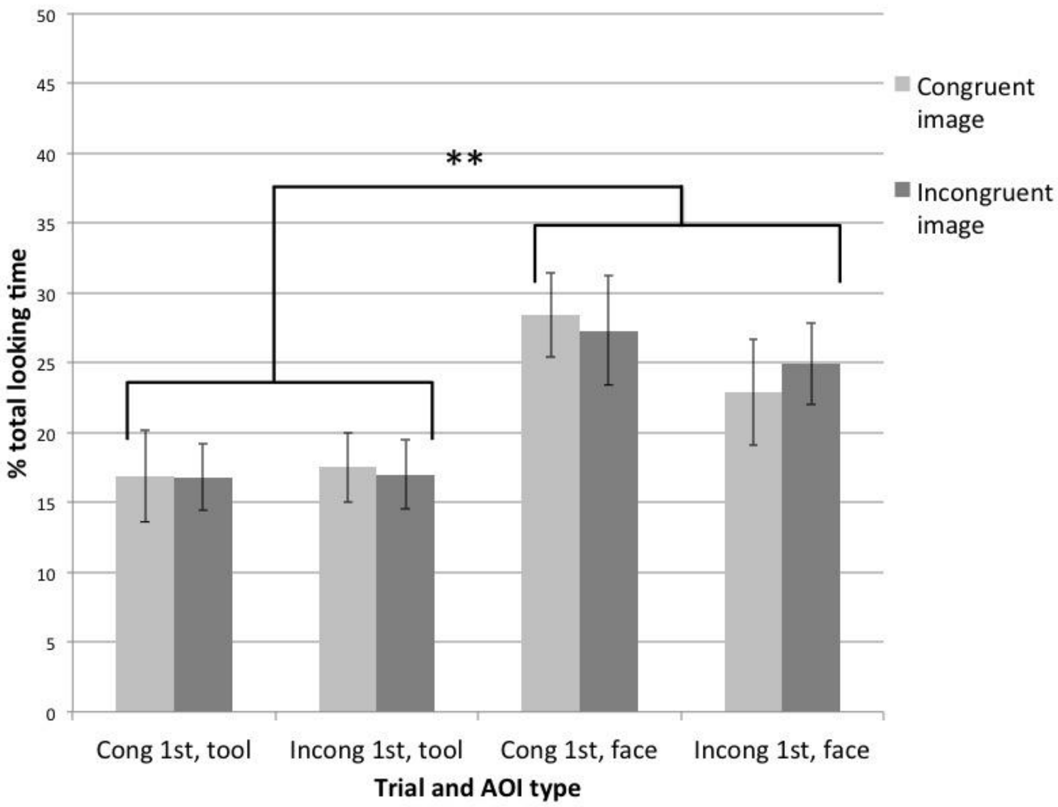

Figure 2.5: *Looking times to specific AOIs indicate an overall preference for looking at faces over tools, Experiment 1.*

Table 2.1: *Average percentage of looking time to each of the tool and face areas of interest in each trial type in Experiment 1.*

AOI / Trial *type*	*Congruent first, mean*	*Congruent first, SE*	*Incongruent first, mean*	*Incongruent first, SE*
Congruent image, face	29.05	3.04	23.36	3.79
Incongruent image, face	27.76	3.87	25.33	2.85
Congruent image, tool	17.22	3.26	18.09	2.55
Incongruent image, tool	17.23	2.48	18.09	2.83

An additional analysis was conducted to examine whether infants exhibited differences in looking times to the tool-ends within each tool AOI. In each image, the proportion of looking time spent looking at the tool-end congruent with the actor's goal versus the tool-end incongruent with the goal was compared. A 2 x 2 ANOVA with factors of tool orientation congruence and tool-end congruence was performed. Results revealed a main effect of tool-end congruence (F(1,24) = 54.834, $p < 0.05$, $\eta^2_p = 0.168$) and an interaction between orientation congruence and tool-end congruence (F(1,24) = 5.109, $p < 0.05$, $\eta^2_p = 0.225$).

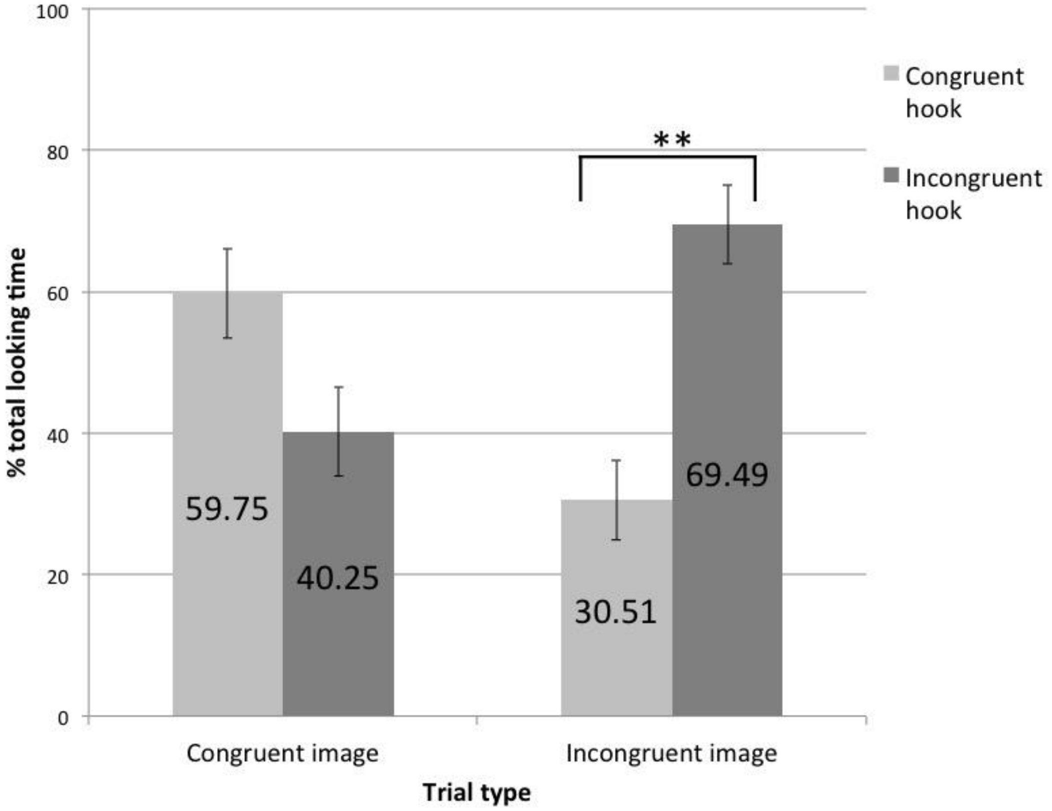

Figure 2.6: *Looking times to each tool-end in each image, Experiment 1.*

2.4 Discussion

The results of the first experiment suggest that 16-month-olds do not associate the orientation in which an actor is holding a dual-function tool with that particular actor (given the manner in which they previously held and used the tool in that manner) in the absence of motor information distinguishing the grasps used. However, looking patterns show that specific hooks were associated with the actor (and possibly, by inference, their intended use of the tool). Infants did not spend a significantly longer proportion of time looking at either of the upper-ends of the tool than the other, so the effect is seen solely in how they divided their looks between the two parts of the tool. The upper tool ends were potentially looked at more because they were close to the faces, which drew the infants' gaze. To explore the lower end of the tools would necessitate scanning past the upper end on the way down from the face. For the congruently-held tool, looking times to the upper end were diluted by looks at the incongruent hook, whereas for the incongruently-oriented tool, infants spent significantly longer looking at the upper, incongruent hook.

It is possible that the association between each actor and the specific hook she used (and resultant interest in the other hook when shown in the context of that specific actor) was semantic. Critical stimuli were removed from the demonstration context in which an association would have been formed. Looking behaviour driven by perceptual association would have entailed an overall preference for the image in which the tool orientation differed from the orientation during demonstration. Instead, looking preferences were driven by tool-parts rather than overall tool orientation, providing a semantic processing argument. Each end of the tool was visible when an actor demonstrated its function, so the association formed was contingent on the employment of the tool end on the target object, not its presence in relation to the actor. In the critical stimuli, the target object was absent but the association between the tool-part and the actor remained. This suggests that the association was based on encoding of the relationship between the tool part and the actor, in relation to the prior action on the target object. This kind of encoding may be semantic in nature because it refers to the "meaning" of the tool-part (it is used on the target object preferred by this actor).

In addition to this semantic explanation, there is also the possibility that the obtained results were the result of perceptual associations generated when the actor picked up the tool and held it at her chest while making direct eye-contact with the viewer during the demonstration videos. It is possible that the looking times to the incongruent tool end were based on similarities between the actor's pose in the demonstration video and in the critical stimuli. The infants may have looked longer at the incongruent end of the tool in the image in which the actor held the tool upside down because they expected the congruent hook to be in its place. A second experiment was conducted to rule out this possibility. It was identical to the first experiment, but the demonstration videos were shortened to show the use of the tool only. The infant therefore did not see the actor holding the tool in the manner of the critical stimulus images in any of the demonstration videos. A replication of the first experiment's results would suggest that the infants made an association between the hooks and their uses by each specific actor, and not between the position of the hooks in the demonstrations and the critical images.

EXPERIMENT 2

2.5 Methods

2.5.1 Participants

Nineteen infants were recruited from the research centre's participant pool. Six infants were excluded from the final sample – experimenter error (*n* = 1), insufficient trials (*n* = 4), and insufficient tracking (*n* = 1). The final sample comprised 13 infants (nine male, four female) aged between 15 months and 16 months, 16 days (mean 15 months, 26 days; *SD* 14.5 days). Families received travel compensation and a baby book following their visit.

2.5.2 Stimuli

Stimuli were identical to those used in Experiment 1 except that the actors were not shown picking up or replacing the tools in the demonstration videos. Each edited video was 4-5 s in length and began with the first second before the tool touched the object. The tool was oriented toward the goal object and in close proximity to it at the start of each video. The videos ended immediately after the intended action was complete. These shortened demonstration videos replaced the original demonstration videos at all times – in the initial learning phase and after the 3rd and 6th critical stimuli.

2.5.3 Procedure and analysis

The procedure and analysis were identical to those employed in Experiment 1. The unused trials, in which the infant did not look at either of the tools, amounted to 12.5% of all trials.

2.6 Results

Infants spent equally long looking at the congruent and incongruent images (2 x 2 ANOVA congruence by trial type, no significant main or interaction effects). The same 2 x 2 x 2 ANOVA as in Experiment 1 was conducted on looking time data with factors of trial type, image congruence and area of interest category. There were no main effects of trial type (F(1,12) = 0.662, p = 0.432, η^2_p = 0.052), image congruence (F(1,12) = 1.142, p = 0.306, η^2_p = 0.087), or AOI category (F(1,12) = 1.874, p = 0.196, η^2_p = 0.135). There were no interaction effects. Looking times to each of the AOIs are shown in Table 2.2.

Analysing looking times to the upper and lower ends of the tool, the primary result of Experiment 1 was reproduced (Figure 2.7). There was no main effect of hook congruence in this experiment (F(1,12) = 0.017, p = 0.9, η^2_p = 0.001) – infants did not spend more time looking at the incongruent hook overall. There was an interaction between orientation congruence and hook congruence (F(1,12) = 9.243, $p < 0.025$, η^2_p = 0.435). Bonferroni-corrected t-tests with the α level dropped to 0.0125 to account for four potential comparisons showed that infants' looking times to the two ends of the hook did not differ in the case of the tool held congruently, p = 0.086, but did differ in the case of the tool held incongruently, $p < 0.008$. As in Experiment 1, proportion of looking time to each of the upper hooks did not differ from one another, p = 0.508.

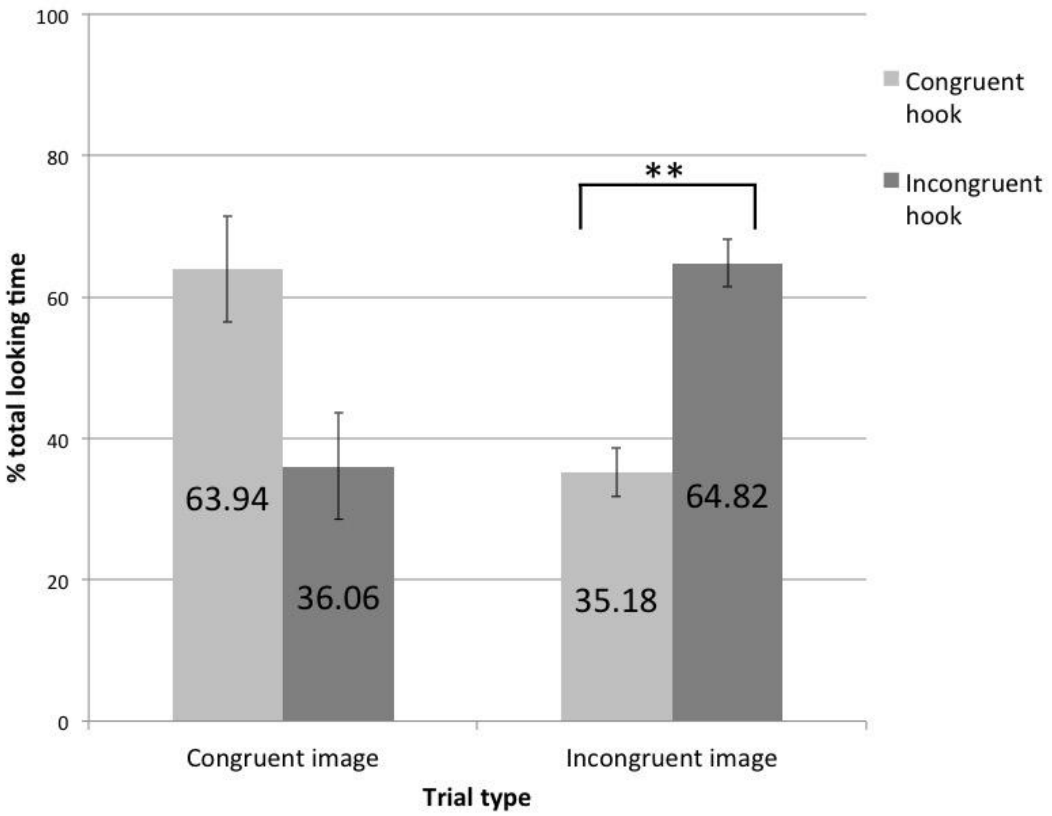

Figure 2.7: *Looking times to each tool-end in each image, Experiment 2.*

Table 2.2: *Average percentage of looking time to each of the tool and face areas of interest in each trial type in Experiment 2.*

AOI / *Trial type*	Congruent first, mean	Congruent first, SE	Incongruent first, mean	Incongruent first, SE
Congruent image, face	26.3	3.55	30.23	3.65
Incongruent image, face	27.32	3.45	22.3	4.41
Congruent image, tool	24.57	5.28	17.5	3.01
Incongruent image, tool	17.96	2.65	22.26	3.45

2.7 General Discussion

Although infants did not exhibit overall longer looking times to either critical image, looking behaviour did demonstrate learning about the relationship between each tool-end and the actor who used that tool-end. Overall interest in the upright end of the tool indicates interest in how the tool is being held for use, the upright tool-end always being used to perform the action. However, this enhanced interest in the upright tool-end was only present when the tool was held incongruently. This suggests a conflict between interest in the upright tool-end and interest in the tool-end unassociated with the actor (because it was not used by her). Infants were interested not (as hypothesized) in a dual-function tool which is oriented and held incongruently for the associated action, but in the feature of that tool that is incongruent with the actor's goal, regardless of how it is oriented. The increased looking time to the incongruent tool-end suggests that during action demonstration, the infants formed an association between the congruent tool-end and the actor's goal object. Consequently they were more interested in the incongruent tool-end, which they had not encoded in relation to the actor (via her use of said tool-end).

Results of Experiment 2 affirm the Experiment 1 interaction effect. Infants again looked longer at the incongruent than the congruent hook when the tool was held incongruently relative to the actor's goal (or simply her prior behaviour), but did not exhibit any difference in looking times to either end of the congruently-held tool. Preference for looking at the upright end of the tool emerged again despite there being no preference for looking at the faces. It is probable that the infants detected that the upright end of the tool was important (as the end likely to be used). Again the general preference for looking at the upper end was diluted in the case of the congruently-held tool by an interest in seeing the hook that did not match the actor's behaviour.

Unlike in Experiment 2, in Experiment 1 actors made direct eye contact with the camera during the demonstration videos. This may be why the infants attended to the faces in the critical stimuli. Infants show enhanced neural processing of direct gaze and use it to aid processing new stimuli (Baldwin, 1993; Farroni, Csibra, Simon, & Johnson, 2002; Reid & Striano, 2005). It is possible that they may have sought disambiguation about the tools from the actors' faces and gaze in Experiment 1 but not in Experiment 2. It is also possible that the result was also driven by similarity between the actors' pose during that part of the demonstration and in the critical images, because if they were using gaze as a social learning cue differences between conditions might have emerged. Consequently, no conclusions can be drawn about the nature of the face preference in Experiment 1 except that it was likely driven by the joint gaze during the demonstration videos.

It is possible that the infants' interest in the hook unassociated with the actor's behaviour was driven by the fact that they saw the other hook in the "upright" grip slightly more often (i.e. in the demonstration videos), or because it was held closer to the target object. These aspects of the action are necessary to it – common tools (phones, hairbrushes, spoons) are held in a radial grip and actions in which an effect is achieved despite distance between tool end and target are not understood as causal by infants (Träuble & Pauen, 2011). They do not rule out the possibility of higher level encoding. The infant saw one end of the tool placed next to one goal object as frequently as they saw the other end placed next to the other goal object. The associations made were contingent on the relationship between the target, tool and actor but persisted in the absence of the target. Looking behaviour did not suggest an overall association between the actor and how they held the tool, but suggested that it is the target object that grants meaning to the relationship between tool-end and actor – *this* actor prefers the object on which *this* tool-end is used.

A key difference between this and previous work (Paulus et al., 2011) was the absence of a 'canonical' grasp or means of grasping the tool that differed between functions. In previous work, 14-month-olds failed to predict the use of the object based on such a cue; 20-month-olds succeeded. The 16-month-old group studied here showed an ability to separately associate the ends of a dual-function tool with different actors and goals, even though mirroring the grasps in the critical images would not provide differential information about the intended action. Despite the lack of motor information, the infants differentiated the functions of the tool, albeit not on the basis of how it was held.

It is consequently unclear whether the ability to match tool-ends to the actors who utilise them (and potentially to the actors' goal-driven behaviour) emerges before or after the ability to predict tool use from grasp. Action experience can be useful for learning associations between objects and goals (Perone, Madole, Ross-Sheehy, Carey, & Oakes, 2008) just as it benefits mirroring during action observation (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). Ability to perform tool-mediated actions at 14 and at 16 months of age is similar (age from 12 to 18 months does not predict alteration of learned grasp; Barrett et al., 2007). Thus, it is plausible that 16-month-olds may, like 14-month-olds, fail to predict action based on tool grasps.

Results of the present study taken in conjunction with research on the mirror system in infancy suggest that although 16-month-old infants can represent motorically pulling or lifting outcomes of action (Southgate & Begus, 2013), they may be unable to mirror the means of holding the tool that performs that action. This is reflected in Elsner and Pauen (2007) –15-month-olds encoded the relationship between a tool and a target object but could not perform the target action accurately. In previous research on infants' spoons use (McCarty, Clifton & Collard, 2001), 14-month-olds often needed to adjust their grasp to use the spoon effectively. This illustrates a semantic match between the spoon and eating, but no semantic-motor representation of how to grasp the tool for that action.

In this study the functional part of the tool is held in a radial palmar grip in which the functional part protrudes from the grasp by the thumb and forefinger. Although the grasp itself is performed by infants from 6 months (Bakker, Daum, Handl & Gredebäck, 2014), any useful mirroring response to the critical images would need to incorporate the hand position relative to the functional tool-end. Although combined semantic-motoric representations are likely present by 16 months in relation to self-spoon-feeding (McCarty, Clifton and Collard, 2001), a similar representation could not be generated in response to this novel, dual-function tool. This could be because multiple representations need to be generated – the means via which the tool is used, the preferences of the actors, and the means of holding the tool for action. The results of the present study raise the possibility that mirroring processes required to understand tool-mediated actions with a dual function tool, in which orientation matters, develop after, or parallel with, processes which allow for semantic encoding of tool use. This differs from processing of tool-less object-directed actions, where motoric processes take primacy (e.g. Daum et al., 2011; Loucks & Sommerville, 2012; Perone et al., 2008).

2.8 Conclusions

Results suggest that 16-month-old infants can learn about tool-mediated actions through an associative and/or semantic processing system in which tools are matched to functions and actors' goals. Given the identical grasp employed for both uses of the tool, infants' mirroring processes did not allow them to distinguish between grasps and exhibit a preference for looking at the image with the tool congruently or incongruently oriented in relation to the actor's prior behaviour, as hypothesised. This suggests that when learning about the parts of dual function tools, 16-month-olds fail to utilize combined semantic-motor representations of how to grasp a tool in relation to the functional part to be used. As in the early use of other handled tools, infants form an association between the tool (or its parts) and its usage. In this case, that usage was tied to a specific actor and associations were formed in the context of learning about how different actors used the tool, though they each used the same grasp to do so. Thus, associating the parts of a dual-function tool with specific actors via those actors' prior behaviour is possible in the absence of action mirroring.

Prelude to Chapter 3

Does the means of holding a tool affect infants' perception of action?

The preceding work shows that although differentiating the functions of a dual-ended tool is challenging (Paulus, Hunnius & Bekkering, 2011) infants can separately associate specific ends of the tool with a particular actor in the context of that actor's demonstrated goal. Crucially, it did not matter in which manner the tool was held. That is to say, the 16-month-olds tested showed an elevated interest in the hook that did not match the actor's goal when it was held upward, and an anticipated interest in the upright-held hook in general was diluted by interest in the incongruent hook when it was held downward.

By using an identical, whole-hand grasp on the tool in all conditions, the aim was to show that these older infants can differentiate grasps on a dual-ended tool in the context of the tool's orientation without the need for differentiating grasps. Instead, results showed that at 16 months, infants do not care about the orientation in which a tool is held but associate functional ends with actors' goals. Previous work shows that predictions of how a dual-ended tool will be used, made on the basis of grasp information, arise in infants sometime between 14 and 20 months of age (Paulus, Hunnius and Bekkering, 2011). The current work shows that infants at 16 months of age don't discriminate between the orientations in which a dual-ended tool is held for use. In the integration of these findings, a number of additional questions arise.

One of these questions refers to what kinds of grip or grasp information are important for infant processing of action. "Grip information" and "grasp information" as used here relates to any aspect of hand posture or hand-object relationships, respectively. This could be a reach with a power or precision grip (Ambrosini et al., 2013), the size of the aperture between thumb and fingers (Daum et al., 2009), the function of the executed grasp in relation to the object (Loucks & Sommerville, 2012) or the grip used (Paulus, Hunnius & Bekkering, 2011), orientation of reaching hand to target object (Bakker et al., 2014), or the orientation of an object relative to the hand holding it (Ní

Choisdealbha et al., Early View; Chapter 2, this thesis). Already we have seen that the last of these is not important in 16-month-olds' encoding of a dual-ended tool's functions. However, all of the other kinds of grip or grasp information have been shown to be important at varying stages in infancy. Ambrosini and colleagues (2013) found that 8- and 10-month-olds but not 6-month-olds look toward a smaller rather than a larger object when an actor reaches with a precision (thumb-to-finger) grip. Daum and colleagues (2009) similarly found that 6- and 9-month-olds anticipate that a hand with a narrow aperture is reaching for a similarly narrow object. Loucks and Sommerville (2012) found that functional and non-functional power and precision grasps executed on objects are processed differently depending on the infant's grasping ability. Finally, Bakker and colleagues (2014) found that the P400 component of the infant ERP differentiates between reaching hands oriented toward and away from an object.

Another question is, in what contexts are of each of these aspects attended to by the infant and processed? If the teleological stance defines action perception in infancy (see p. 16), the grasp is important only when it presents a hindrance to the efficient completion of the action (Csibra, 2003). This certainly applies to the work listed above – a grip that is not the correct shape for the implicated object hinders grasping and possible subsequent use of that object. Of the work listed above, only Loucks and Sommerville (2012) suggest a difference in processing of grasps that do not prevent the completion of an action but are not appropriate for the implicated object. In this case, the effect is only present for infants with greater motor skill and is modulated by habituation to previous presentations of a power or pincer grip. It is also worth noting that in the many studies listed above, all actions presented to infants below 14 months were reach-to-grasp actions. There is nothing to indicate how these infants process grasps in the context of a longer, tool-mediated action and how goal prediction occurs when an object is grasped in a manner that would prevent action completion, such as bringing a cup to the mouth while holding that cup over the top. Motor activation research with adults indicates that representations of appropriate grasps for tool function exist in the developed brain (van Elk et al., 2010). When these representations develop is an extant question.

A final question is about the relative contributions of motor and semantic processes to perception of grasp. The studies showing how grip and grasp information affects infants' processing of action indicate that differentiation between wide and narrow hand apertures (Daum, Prinz & Aschersleben, 2011), differentiation of the goals of precision and whole-hand grips (Ambrosini et al., 2013), neural processing of grasping hands oriented toward and away from objects at 6 months (Bakker et al., 2014) and perception of the functionality of different grips (Loucks & Sommerville, 2012) are all mediated by the infant's own grasping ability. One inference to be made is that the ability to generate an accurate (or at least more complete) motor representation of an actor's grasping posture affects action processing. However, the relative influence of visual and motor representations on processing of seen hands is complex (Ní Choisdealbha, Brady & Maguinness, 2011). It may be the case that infants who can perform pincer or thumb-to-finger grips consequently receive more visual inputs of those grips and their relationships to objects of different sizes. This could result in a greater ability to predict the targets of different hand aperture sizes or grip types, or to determine whether certain hand-object relationships are functional or typical, or not.

The following chapter (Chapter 3) examines these questions. Power and pincer grips were presented to adults and 9- and 11.5-month-olds infants but what was measured was not the response to the grips themselves. Rather, we were interested in the relationship of the power or pincer grip to the shape of the object being held was encoded. The grips matched or did not match the structure of the objects. For example, in one case a handled cup was grasped with the whole-hand over the handle. None of the grips executed on the objects, whether congruent or incongruent with them, prevented execution of the associated goal, whether this was perceived to be a completed grasp or subsequent lifting and drinking from the cup. This means that goal inference from a teleological or efficiency perspective would not differ between conditions. Later work in this thesis (Chapter 4) discusses how infants process differences in grasp that lead to differences in action execution.

The measurements taken were neural. ERPs in response to congruent and incongruent grasps on familiar objects were measured with a particular focus on the N400 component. This component indexes semantic processing of both language and action (Amoruso et al., 2013) and emerges from about nine months of age (Reid et al., 2009). As adults, we perceive an action in which someone holds an object by the handle as meaningful, whereas accessing a representation of an action in which the functional end of the tool (e.g. a hammer's head, a spoon's bowl) is grasped may not present any immediate options for goal prediction. Work by Bach and colleagues (2009) found in adults that an N400 component is elicited, as expected, when the tool employed does not match the target in terms of overall goal (a screwdriver used on a lock rather than a screw). They also found that if the tool is held in the wrong orientation, a negative component in the typical N400 latency period is elicited. Thus we know that aspects of action other than goals modulate semantic processing and in the ensuing chapter, evidence is found that the grasp-object relationship is one of these aspects.

Differences in the N400 component in response to congruent and incongruent grasps in adults justified measurement of this component during early development. An N400 present in infancy in response to these stimuli would indicate that semantic processing of hand-object relationships is occurring at this developmental stage. A relationship with execution of pincer grips would then point toward a contribution of visual or motor experience to semantic processing of others' grasping actions. Positive results (i.e. the presence of an N400) would go some way to characterising the relationship between semantic and motor processing of action in development. They would show that not only do infants attend to whether a grasp matches or does not match the object it is executed upon, but that when infants encode actions and attribute meaning to them, they attend not only to the overall goal but to the means by which that goal is achieved. These hypotheses were not borne out by the data. Instead we see that neural processing of hand-object relationships and grasp appropriateness undergoes radical changes even in the short period between eight and twelve months of age. Again, we see evidence for the separate rather than dependent development of semantic and motor processing systems, as semantic processing of action goals appears to emerge before semantic processing of the motor components of actions.

Chapter 3

Neural encoding of hand-object relationships changes within infancy, and between infancy and adulthood.

Text in preparation for submission to *Developmental Science*.

Abstract

Actions are semantic entities – hierarchically structured sequences with components that generate expectancies about how the action will proceed. One such component is the means of apprehending tools. Even though semantic processing of action outcomes emerges in the first postnatal year, infants' limited motor skills may hinder their processing of differences in grasp. In the present work, three groups – adults, 9-month-olds, and 11.5-month-olds – were shown images of actors grasping cups via means that were congruent or incongruent with the shape of the cup. Participants' neural responses to the stimuli were measured using electroencephalography, and the N400 component of the event-related potential was computed for each age group. The presence of the component in adults and its modulation by stimulus congruence indicates that stimuli were processed semantically. Results from the infant samples indicate a multi-stage developmental trajectory of this process. Attentional sensitivity to differences in grasp appropriateness diminishes between nine and twelve months of age, while semantic processing of the overall action but not the means of grasping emerges around by the end of the first postnatal year. These results suggest that as the ability to process actions as semantic entities emerges, the action's congruence is determined by its goal and not affected by the means of performing the action.

3.1 Introduction

The emergence of tool use in infancy and early toddlerhood signals a convergence of motor and cognitive skills. Many tools require precise manipulations such as the use of a pincer grip, control of wrist rotation, and application of appropriate force with the arm, all of which are still emergent at the end of the first year (Thelen et al., 1993). Appropriate use of a tool requires that multiple mental representations are accessed – it must be associated with a specific target object or category of target objects; there must be a representation of what the tool does to that target object (i.e. its function); and there must also be a representation of how to properly apprehend and manipulate the tool to achieve that function (van Elk et al., 2010). Generally these representations, in the context of actions performed with the tools, are considered to be semantic (Chainay & Humphreys, 2002; Grafton et al., 1997). Infants by the end of the first post-natal year process common actions semantically (Reid et al., 2009). They associate tools with targets (Hunnius & Bekkering, 2010) and hold representations of the effects of tools on targets (Hernik & Csibra, 2015; Träuble & Pauen, 2011). The aim of the series of experiments described in this work is to expand on previous research on semantic processing of actions in infancy and determine whether infants between nine and twelve months of age have acquired the third kind of tool-related semantic representation listed above – a representation of how to hold a tool.

Motor components of action are fundamental to how actions are represented neurally. The mirror system, which represents observed actions in the same manner as planned or executed ones, is a phenomenon that has been extensively documented in humans using functional neuroimaging (Van Overwalle & Baetens, 2009) and electroencephalography (Muthukumaraswamy, Johnson & McNair, 2004; Perry & Bentin, 2009) among other methodologies (Strafella & Paus, 2000). Adult data also show that motor resonance – activation of the motor system in the absence of overt movement – occurs in response to stimuli associated with actions, for example while viewing images of tools (Proverbio, 2012) or naming actions associated with tools (Grafton et al., 1997). Recent studies with infants have recorded neural correlates of motor activity as infants observe goal-directed actions (Marshall, Young & Meltzoff, 2011; Nyström et al., 2011; Southgate et al., 2009), showing that the mirror system is functional in infancy. The processing of actions does not, however, rely solely on motor activation in adults nor infants (e.g. semantic action processing in adults, Proverbio & Riva, 2009; infants encoding tool function despite inability to manipulate tools appropriately, Elsner & Pauen, 2009). In understanding how infants learn to act upon the world around them and how they can begin to use tools to engage in more complex and abstract actions, it is important to understand how the motor representation system and the cognitive action processing system develop and whether interdependencies exist between these systems.

The pathway by which motor activation in response to observed action occurs may be a direct response to the percept of the action or stimulus associated with action, as detailed in an action representation model by Chainay and Humphreys (2002). In the same model the authors indicate that action representation is also semantic. This is supported by alleviation of apraxic patients' difficulties in identifying or miming tool functions via direct interaction with those objects. That is, access to semantic representations of tools can be supported by information from the perceptual route to action. Neuroimaging data supports this model of a convergent conceptual (or semantic) and perceptuo-motor model of action (Watson & Chatterjee, 2011; Yoon et al., 2012). When discussing action as a semantic entity, what is meant is that perception of an action results in expectations about how that action will proceed. These expectations are fundamentally linked to the signification of the action stimulus. For example, although an association may be formed between an action (such as driving) and a stimulus that co-occurs with driving (the smell of car freshener), it is not necessarily semantic unless there is a contingency between the action and the stimulus, or unless the meaning of one hinges upon the other. A reaching action has no significance or meaning without a target of the reach; putting a spoon in the mouth is not eating unless there is food on the spoon. It is important to understand the emergence of semantic processing action in infancy because this kind of conceptual ordering has been shown in other domains to result in more rapid access to information than associative processing (e.g. Thompson-Schill, Kurtz & Gabrieli, 1998). Developing semantic concepts of familiar actions may allow infants to perceive the goals of others and to learn about action functions more efficiently.

In language, words follow one another sequentially and there is a hierarchical generation of meaning – each word generates expectancies about the word that may follow it. This characterisation of meaning or semantics as sequential or hierarchical has been used before in relation to tool use as well as language (Stout & Chaminade, 2009). The comparative literature documents commonalities between the human Broca's area and tool-use modules in non-human primate cortex (Roby-Brami et al., 2012). Semantic processing of language can be measured using a specific event-related component of the human electroencephalogram (EEG). The N400 component is evident in adult event-related potentials (ERPs) over parietal regions for language stimuli and over fronto-central regions for pictorial stimuli (Amoruso et al., 2013; Ganis, Kutas & Sereno, 1996), from about 300 or 400 milliseconds post-stimulus. The N400 peak in the ERP is generally of greater magnitude for semantically incongruous stimuli. An early example from the work of Kutas and Hillyard (1980) shows a larger N400 peak when the sentence "he took a sip from the" concludes with the incongruous "transmitter" compared to the congruent but unlikely "waterfall".

The N400 is also found in response to action stimuli. Sitnikova and colleagues (2008) found a frontal negativity in adult ERPs in the N400 time window that was larger for actions in which an inappropriate tool was used to achieve the action goal (cutting bread with an iron instead of a knife), than for actions in which the tool used was appropriate to the context. These results relate to two of the above listed three means by which a semantic representation of a tool-use action is generated. There is an association between tools and a target, as the bread target elicits expectancies about tools associated with it. The presence of an iron, which is not one of these tools, is not meaningful in relation to the bread and thus is semantically incongruous. There is also the association between the tool and its function – the function of the iron is not to cut bread and when placed in a context in which that function is anticipated, it in incongruous. Measurement of the N400 is an important tool in determining whether semantic processing is occurring and consequently in establishing the means by different kinds of concepts are accessed.

There is evidence that infants engage in the three aspects of tool representation listed above (target, function, apprehension). They associate tools or objects involved in actions with targets. For example, from 6 months of age they anticipate that common tools will be brought to the correct target by an actor – such as a cup or spoon being brought to the mouth (Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010). They also associate functions with tools, looking longer at outcomes that do not match the tool they were performed with (Hernik & Csibra, 2015), and are sensitive to the continuity of actions based on their functional or goal-directed structure (Baldwin et al., 2001; Reid et al., 2007). The work of Perone, Madole and Oakes (2011) with 10-month-olds gives evidence for both of these kinds of representation. Following habituation to a particular action performed on a particular object, infants dishabituate when the habituated action is performed on a novel object, or when a novel action is performed on the habituated object, indicating that infants make bi-directional associations between objects and action. This is comparable to tool-function associations (Hernik & Csibra, 2015) Additional experiments from the same work (Perone, Madole & Oakes, 2011) showed that following habituation to two actions performed on the same object, each with a different outcome, infants dishabituated when one familiar action elicited the effect or outcome associated with the other action. This shows that infants associate outcomes or goals with actions, comparably to the results of Hunnius and Bekkering (2010), and Kochukhova and Gredebäck (2010).

In these cases, the representations held by the infants may be more than an associative target expectancy generated by perception of a tool or other object (or an associative tool expectancy resulting from target presence). There is neurophysiological evidence that infants represent familiar actions semantically. An N400 is present in the neural responses of infants as they observe incongruous actions – actions in which a food item is placed not in the mouth, as would match the expectancy generated by seeing a person holding it, but instead is placed by the forehead or ear (Reid et al., 2009). Research with toddlers has indicated that the action N400 is present into early childhood (Pace, Carver & Friend, 2013) and the morphology of the ERP found in this case bridges the differences (i.e. in latency and topography) between the 9-month-old and adult N400 responses to action stimuli.

These developmental N400 studies detail how infants process semantically the goal-directed structure of action, based upon representations of the target (and perhaps even the function) of familiar actions (Reid et al., 2009) and of the function of the action (disrupted in Pace, Carver & Friend, 2013). The semantic representation of how tools should be apprehended or manipulated has not been investigated neurophysiologically. There is substantial evidence to indicate that infants in the first post-natal year discriminate the grasps used on different objects. When shown a hand reaching for an occluded object, 6- and 9-month-olds look longer when the action conclusion shows the hand holding the (now visible) object with a wider or narrower distance between thumb and fingers than shown during the reach, relative to actions in which the shape of the hand at conclusion matches the shape of the hand during the reach (Daum et al., 2009). Six-month-olds who have experience of performing thumb-to-finger grips are facilitated in this matching of hand aperture to target object (Daum, Prinz & Aschersleben, 2011), and 10-month-olds who can use a pincer grip in functional contexts respond to both the novelty and the functionality of a grasp in observed actions, whereas their peers who do not use pincer grips functionally respond only to grip novelty (Loucks & Sommerville, 2012). Among 4-month-olds the P400 ERP component, associated with the social significance of stimuli (Gredebäck, Melinder & Daum, 2010; Hoehl & Striano, 2012; Melinder et al., 2015; Rigato, Farroni & Johnson, 2010), is elicited differently in conditions showing a hand in grasping posture directed towards or away from the location where an object was previously shown, emerging earlier in those infants who display appropriate use of power grasps themselves (Bakker et al., 2014). Thus we see perceptual, cognitive and neural evidence for the sensitivity of infants to the different means of apprehending objects, in addition to evidence for the effects of motor experience on this sensitivity.

Tool use therefore represents an interesting pivot point from which to explore diverse systems in development. In the case of the present study, the aim is to investigate semantic processing of grasps on familiar objects and relate this processing to the infants' motor development. The reasons why semantic processing is investigated are, as detailed above, the fact that infants process other aspects of action semantically (Reid et al., 2009), and the fact that infants respond differently to actions requiring different grips (Daum et al., 2009; Loucks & Sommerville, 2012). This latter series of findings indicates that infants perceive differences in the relationship between hands and objects. To characterize the systems underlying processing of hand-object relationships, neural encoding was measured in response to grasps that were congruent or incongruent with the form of a familiar tool. It was hypothesized that ERPs associated with both attentional (Nc) and semantic (N400) processes would emerge in infancy and differentiate between these grasps. It was also anticipated that infants' motor development would be related to the magnitude of these components. Characterization of the ERPs elicited in infant EEG in response to the relationship between tools and their means of apprehension would allow for an understanding of how infants learn to manipulate and utilize tools in increasingly complex ways into late infancy (Barrett, Davis & Needham, 2007; Elsner & Pauen, 2007). Connecting these to behavioral motor measures would illustrate the relationship between semantic processing and motor systems during development.

EXPERIMENT 1: ADULTS

Before investigating the development of infant neural responses to others' choice of grasp, it was crucial to establish how this kind of processing occurs in the adult brain. There is neural evidence for differential processing of actions depending on the relationship of the grasp employed to the tool it is enacted upon. Differences in neural oscillations associated with motor activation are found when adults grasp familiar objects in a non-functional manner, such as grasping a water bottle in a spray-bottle hand posture (van Elk et al., 2010). Unrelated semantic tasks interfere with adults' ability to grasp a tool in the correct orientation, whereas visuo-spatial tasks do not, suggesting that the execution of grasps relies on semantic representations thereof (Creem & Proffitt, 2001). Recent research by De Sanctis and colleagues (2013) refers to an "m-N400" component elicited during reach-to-grasp actions. The spatial and temporal features of the m-N400 suggest a commonality with the observed action N400, suggesting again that the semantic representational system is recruited when determining how to grasp an object. What action N400 studies have not investigated to date is the congruence or appropriateness of a grasp in relation to the features of an object, in which the grasp does not confound the function (i.e. by preventing its normal use, van Elk et al., 2010).

The grasps used in research by van Elk and colleagues (2010) were meaningful in their relationship to the function of the associated tool. In the present study, we wished to present grasps on objects that did not prevent use of the object regardless of their congruence with the object. In this way, differences between conditions would indicate processing purely of whether the grasp was appropriate for the object on the basis of object features. Furthermore, the actions shown to participants displayed the reach and grasp on the object only, and not (typical or atypical) use of the object, again preventing confounds relating to semantic processing of other aspects of the action.

3.2 Methods

3.2.1 Participants

Participants were recruited from the University's student population via an internal participant advertising system and emails to graduate students. Other participants (n = 5) made contact with the research group because they wanted recordings of their own EEG for an arts project, and were invited to participate in the research. No remuneration was offered but those undergraduate students recruited from the advertising system received credits towards their research skills modules. Ethical approval for this experiment and the other experiments reported in this chapter were granted by the Lancaster University Research Ethics Committee.

Twenty-four participants were tested, and twenty-one (6 males) were incorporated into the final sample. Two participants were excluded as a result of technical issues – one for corrupted data and the other because the session had to be terminated before sufficient data was collected. The third was excluded because of overall poor data quality. The age range of the included participants was 18 to 26 years (*M* = 20.7 years, *SD* = 2.65 years).

3.2.2 Stimuli

A cup was chosen as the tool to be acted upon. Blue and yellow infant lidded cups were used, one of each colour with handles and one without. Handled and non-handled cups were chosen as each present an explicit manner in which the tool should be held – with the whole hand around the round edge for the non-handled cup and with a more precise and narrow grip on the handle for the handled cups. Two-handled cups were chosen as they limit the possibility of grasping with the whole hand around the non-handled side of a standard cup.

The action of reaching for and grasping the cup was performed on each of the cups (yellow/blue, handled/non-handled) by each of three female actors. The actions were captured in three static images as in Reid and colleagues' (2009) N400 study, so that the event-related response to the final grasping posture could be computed cleanly and without interference from surrounding events, such as incidental movements by the actor. As shown in Figure 3.1, the first image in each sequence of three depicted the actor sitting at a table with one of the cups in front of her. The second showed her reaching for the cup. The reach was identical in all stimuli. All actors used their right hand, which approached the cup from the side. The reaching posture concealed the thumb and showed all four fingers in parallel with one another and touching the adjacent finger. This was to prevent any cues such as hand aperture (e.g. Daum, Prinz & Aschersleben, 2009) that might generate expectations about the kind of grasp that would be used. In using identical reaching postures

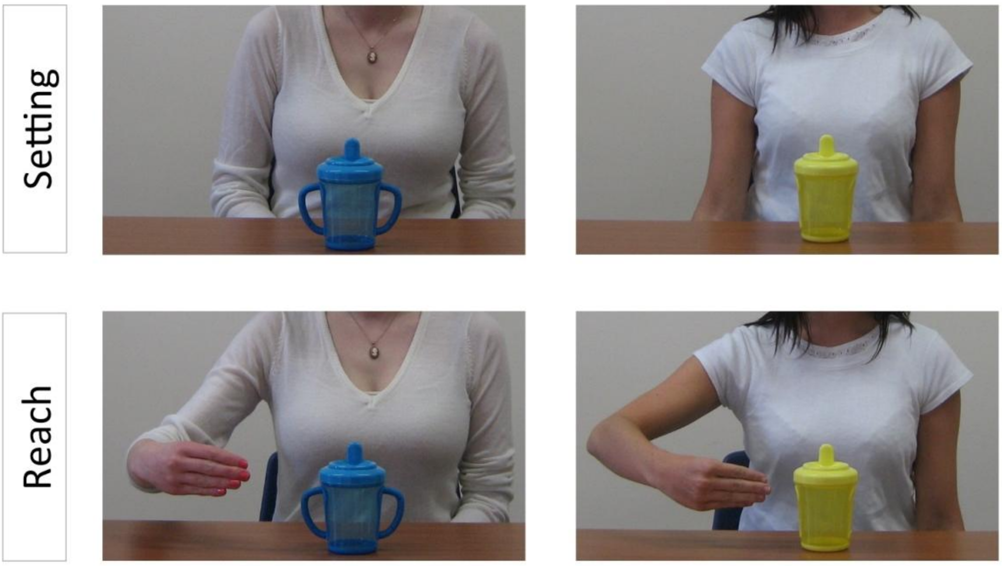

Figure 3.1: *Examples of the first (Setting) and second (Reach) images in each sequence, illustrating equivalence of reaches to handled and non-handled cups.*

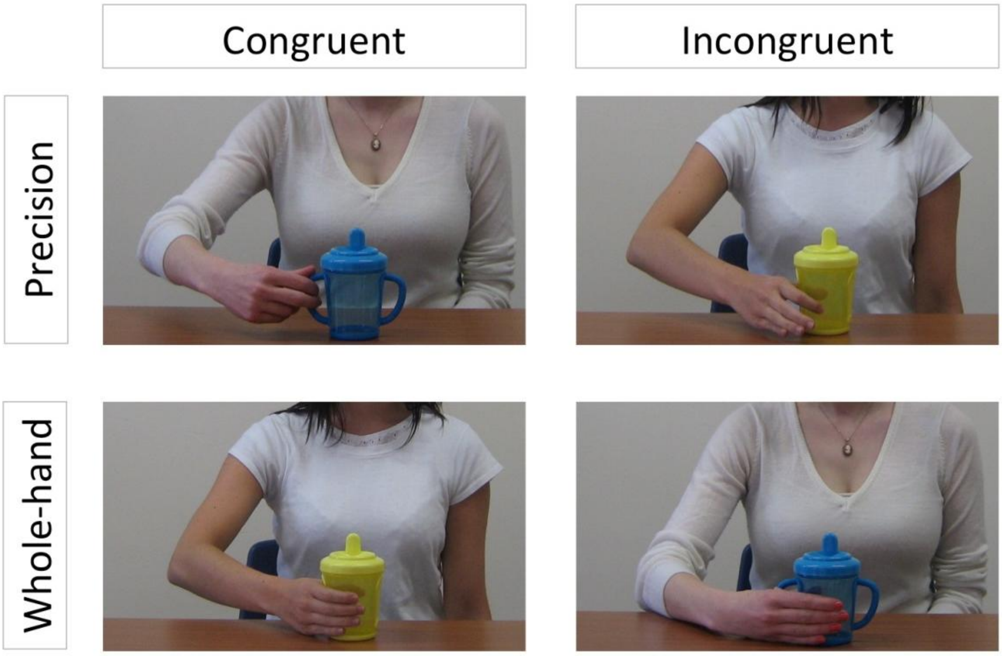

Figure 3.2: *Examples of the critical grasp stimulus across all conditions of congruence and grasp type.*

across stimuli, the expectancies generated would be modified across conditions by the structure of the target cup only.

In the final image in each sequence, the actor grasped the cup with either their whole hand or with thumb-finger opposition. In some cases the grasp was congruent with the cup features, in others incongruent (Figure 3.2). In the case of the incongruent grasp on the non-handled cup, the actor placed the thumb and forefinger only on opposite sides of the cup’s round edge. For the incongruent grasp on the handled cup, the actor placed their hand over the handle, with the pads of their fingers and thumb around the round edge of the cup. Images were edited in such a way that the cup’s position on screen was consistent within each sequence.

3.2.3 Procedure

Participants’ neural responses to the stimuli were collected using an EGI 128-sensor geodesic Hydrocel sensor net (Electrical Geodesics Inc., Oregon). Data was recorded via an EGI NA300 amplifier at 250Hz using EGI Netstation software, and re-referenced online to Cz. Stimuli were presented and the experiment was controlled using Matlab (TheMathworks, Inc., Massachusetts) with Psychtoolbox (Kleiner, Brainard & Pelli, 2007).

Participants viewed the stimuli on a 20-inch CRT monitor with a refresh rate of 60 Hz at a visual angle of 23°, in a dark room. Within each sequence of three images, the first two images were displayed for 600ms and the final one for 1 second. Each image in the sequence followed the next with no interstitial other than the screen refresh rate. Screen space not occupied by the images was grey, and between sequences a white fixation cross appeared in the middle of the screen on a background in the same shade of grey.

Participants were informed that they were part of a study to determine how different kinds of grasps are processed in adults, in order to determine how to investigate the same phenomenon in infants. They were given standard instruction to remain still and try to refrain from blinking while stimuli were being displayed. Participants passively viewed approximately 200 of the reach-and-grasp sequences and were offered breaks after each successive 50 trials, in addition to being permitted to request a break at any other time.

The displayed sequences were determined by a pseudo-randomisation procedure. They were displayed on the basis of random number generation within Matlab with the caveat that sequences with the same congruence or the same kind of cup (handled or non-handled) could not be shown more than twice in a row, and likewise the same actor could not be shown more than twice in a row unless the colour of the cup she was interacting with changed across sequences. This means of displaying the stimuli was used to prevent prediction of stimuli on the basis of presentation patterns, and to maintain interest within the infant sample intended to be tested at a later date.

3.2.4 Analysis

Adult data was analysed within Netstation using the software's waveform tools. It was bandpass filtered between 0.1 and 30Hz and segmented into 1200ms epochs extending from 200ms before the appearance of the third image in each sequence to 1 second after. The Netstation artefact detection process was applied to the data, such that segments with eye movements or blinks were rejected. Channels that varied by more than 400μV within a segment were marked as bad, and segments with more than 15% bad channels were rejected. Channels that were marked as bad in more than 40% of segments were marked as bad throughout. The Netstation bad channel interpolation algorithm was then applied to the data. Baseline correction was applied to each segment based on the 200ms pre-stimulus period (in which the second of the images was onscreen) and data were then re-referenced to the average reference. Finally, an average ERP was computed in each condition for each participant. Given the pseudo-randomisation procedure applied for stimulus presentation, stimuli from each of the four conditions were not presented to the adults in fully equal numbers but the numbers were comparable – following data collection there remained on average for each participant 51.3 (*SD* = 3.4) congruent precision grip trials and 50.3 (3.8) incongruent; 48.2 (3.1) congruent whole-hand grip trials and 48 (2.9) incongruent.

Mean amplitude values were calculated for each participant over fronto-central channels in the 350 to 550ms post-stimulus period. The region investigated is in accordance with previous pictorial (Ganis, Kutas & Sereno, 1996) and action (Amoruso et al., 2013) N400 literature. The time window investigated was chosen on the basis of the morphology of the grand average and in accordance with prior work (Ganis, Kutas & Sereno, 1996). The selected region and the mean ERP over this region are seen in Figure 3.3.

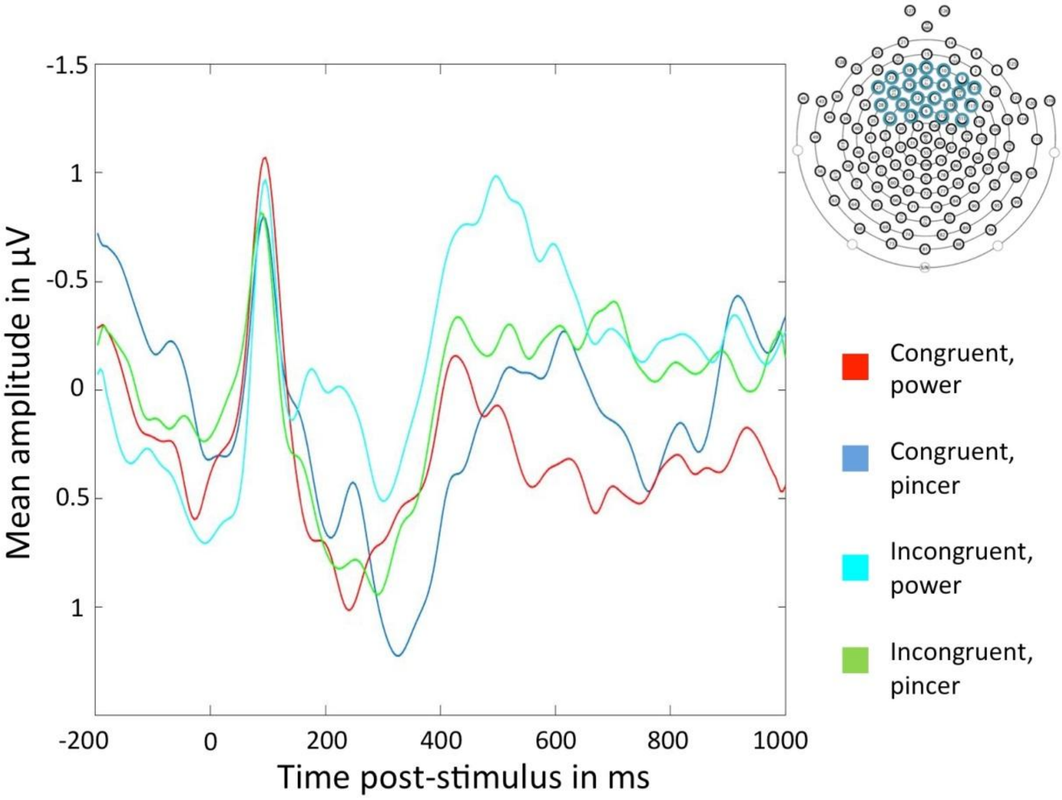

Figure 3.3: *Mean amplitude over fronto-central electrodes (depicted top right in blue) in adults in response to the critical grasp stimulus. Results indicate a larger N400 response to the incongruent than the congruent grasps, as evidenced in the 350-550ms epoch.*

3.3 Results

A 2-by-2 repeated measures ANOVA was conducted on the data. There was a main effect of grasp congruence (i.e. if the type of grasp used matched the form of the cup); F(1,20) = 9.369, $p < 0.05$, $\eta^2 = 0.08$. The mean amplitude of the response to the incongruent grasp was more negative than the mean amplitude of the response to the congruent grasp. There was no effect of grasp type (precision vs. whole hand); F(1,20) = 0.033, $p = 0.857$, $\eta^2 = 0.001$)

nor was there an interaction between the two factors; $F(1,20) = 1.127$, $p = 0.3$, $\eta^2 = 0.02$.

3.4 Discussion

Results show that adults do process the interaction between hand and cup semantically, as evidenced by the presence of a fronto-central N400 in the data and given that this component has long been associated with semantic processing of stimuli including action (Amoruso et al., 2013; Kutas & Federmeier, 2011). This response is modulated by the congruence of the performed grasp relative to the structure of the grasped cup. This provides evidence that when tools or objects are viewed in an action context, the elicited representation incorporates the anticipated means of apprehension. That is, the shape of a cup signifies a means of holding it. The lack of interaction between grasp congruence and grasp type indicates that neither kind of grasp is more expected generally. This is important because there is some asymmetry in the frequency and flexibility of use of the grasps – the more precise grasp on the round-edged cup may be used more frequently than the whole-hand grasp over the handle of the handled cup. If such a cup were to be grasped with the whole hand, it would likely be held around the round edge rather than over the handle. Regardless, results indicate that the N400 effect was elicited more strongly by the incongruent grasps than the congruent grasps and as such the stimuli are appropriate for use to investigate the same effect in a developmental population.

Investigation of the early development of semantic processing of grasp was justified on the basis of these adult results. A nine-month-old age group was selected for a number of reasons. First, this is the youngest age at which the N400 has been previously found (Reid et al., 2009). Second, in this period infants are generally utilizing pincer grips but their means of grasping objects has not yet made the transition to pincer grip dominance – these infants use significantly more power grips than those entering the second post-natal year (Butterworth, Verweij, & Hopkins, 1997). Consequently, individual differences in grasping ability could contribute to a rounded picture of how semantic processing of grasping actions emerges in infancy and how such processing is affected by motor experience.

EXPERIMENT 2: 9-MONTH-OLDS

3.5 Methods

3.5.1 Participants

Participants were recruited from the research centre's participant pool. Thirty infants in total participated in the experiment with their caregivers. Of these, 15 infants in total were excluded, for technical failures (n = 2), experimenter error (n = 2), highly negatively valenced responses to the sensor net (n = 2), insufficient trials attended to during experiment (n = 1) and insufficient valid trials without artefacts (n = 8). The age range of the included infants was 8 months, 13 days to 9 months, 15 days (*M* = 8 months 28 days, *SD* = 11 days). Eight female and seven male infants were included. All families received £10 remuneration and a baby book following their visit.

3.5.2 Stimuli & procedure

The same equipment, stimuli and experimental procedure were used for the infant data with some exceptions.

Eye-tracking data was collected during the experiment with a Tobii TX300 eye-tracker (Tobii AB, Stockholm, Sweden). This data is not reported upon here. Prior to viewing of the action sequences, infants (sitting on the laps of their caregivers) were shown a cartoon of some birds, accompanied by music, on the experiment's CRT monitor. The purpose of this video was twofold – to distract the infants with a pleasant stimulus during application of the sensor net and to ensure the infant's eyes were being detected by the eye-tracker prior to calibration. Lighting to assist with eye-tracking was provided by an LED lamp on the floor. Following application of the net, a standard 5-point Tobii infant calibration procedure was performed. It was repeated only once if the first attempt at calibration was unsuccessful. Subsequently, the experiment began and EEG data was recorded while the reach-and-grasp sequences were displayed. In addition to recording of eye-movements with the eye-tracker, infant behaviour was recorded with a camera mounted adjacent to the monitor on which the stimuli were displayed. The video recordings were tagged with information about the on-screen events occurring simultaneously.

Some additional changes were made to the experimental procedure. Using a random number generation procedure within Matlab, the two images shown prior to the final image in each sequence could be displayed for 800ms, 900ms, 1s, 1.1s or 1.2s. The final image was still 1s in length. The lengthening of the display of the first two images was to ensure any slow wave effects would be terminated by the time the critical image appeared. Differing lengths of presentation were used to ensure that remaining slow wave effects would not affect the ERPs to the critical images in a consistent manner.

Sequences were displayed in series of ten with a pause on a fixation cross after the tenth sequence. The experimenter, guided by the caregiver’s judgment, decided whether to continue at this point or give the infant a short break. The fixation cross was moved so that it would be displayed over the area where the cup was shown. Consequently, infants would be cued to that area and would not have to shift their gaze. Caregivers were instructed that they could try to redirect infants’ attention to the screen with occasional general utterances such as “what’s she doing?” or “look!” but not to refer to specific aspects of the stimuli like cup colour or the nature of the action.

3.5.2a Motor ability task

A behavioural task was added following the EEG procedure. After EEG recording was complete, the sensor net was removed from the child’s head and caregivers and children were given the option to have a break and play for a few minutes. Subsequently, they were accompanied by the experimenter to another room in which recording of the infant’s behaviour in response to a series of grasping tasks was recorded with three overhead video cameras placed at different angles relative to the child. The experimenter sat at a small table opposite to the caregiver, who had the child on his or her lap. The experimenter presented the child sequentially with three items/sets of items taken from the Bayley Scales of Infant Development (BSID) – a small sugar pellet, an orange rod, and a pencil and paper. Objects were presented under the same instructions found in the BSID-II (Bayley, 1993) under motor scale items 41, 49, 56, 57 and 58 (Table 3.1). These particular items were used as they were classified in the BSID-II as the subset of tasks applying to 9-month-olds in which manual interaction was measured.

The use of the BSID-II items was not intended to recreate a comprehensive BSID score. They were used to create a more nuanced picture of the infant's grasping ability than a binary score based on performance or parental report of a pincer grip. The infant's performance on each of the five measures was scored 1 or 0 based on performance of the task during the testing session only. All infants interacted with all objects; there were no refusals.

Table 3.1: *Bayley (BSID-II) motor development scale tasks used with 9-month-olds.*

Item No.	***Item description***
41	Uses whole hand to grasp pellet
49	Uses partial thumb opposition to grasp pellet
56	Uses pads of fingertips to grasp pellet
57	Uses partial thumb opposition to grasp rod
58	Grasps pencil at farthest end

3.5.3 Analysis

Prior to processing and analysis of the EEG data, the videos of the infants' recording sessions were coded for whether or not the infant was looking at the screen for the second and third images in each sequence, for gross movements by the infant during these images, and for other behaviour (e.g. touching the sensor net) that might affect data quality. Segments with unambiguous invalidity were identified for immediate rejection. Segments that were ambiguous (e.g. if the infant might have been swinging their leg out of view of the camera, or if it were not clear that the infant was holding something in their mouth or actively sucking it) were noted. Excluding those infants removed at various stages of the processing procedure, infants sat for a mean of 64.3 trials (*SD* = 12.5) and attended to a mean of 28.5 trials (*SD* = 8.3) without excessive movement.

Data were exported from Netstation and imported into the EEGlab toolbox for Matlab (Delorme & Makeig, 2004). It was bandpass filtered, with a 30Hz lowpass and a 0.3Hz highpass 5500th order finite impulse response filter was applied. Data were segmented into trials spanning the 200ms before the appearance of the third stimulus in each sequence and the 1s after, including correction for the standard lag between Matlab and the EGI NA300 amplifier. Baseline correction was applied using the 200ms pre-stimulus period, during which the reaching stimulus was present onscreen. The invalid segments as identified during review of the session video were rejected immediately. All other segments were manually inspected for artefacts such as blinks or mouth movements, with guidance from notes made during the inspection of the video, and rejected accordingly. A mean of 24 trials (*SD* = 10.7) per infant remained after this step.

All segments were manually inspected again to identify bad channels in each segment. Using EEGlab, additional automated parameters for bad channel detection were applied, such that any channels that breached an upper or lower limit of 250μV were marked as bad in that segment. For each segment individually, interpolation was performed on channels marked as bad by the experimenter or by the EEGlab parameters. Channels marked as bad on 80%+ of segments were interpolated in all segments, and trials in which 15%+ of channels were marked as bad were rejected completely. Following this step, on average 23.6 trials (SD = 10.8) remained per infant

Finally, data for all electrodes in each trial were rereferenced to all electrodes with the exception of the peripheral ones. This procedure has been applied in other work (Bakker et al., 2014) and is used because of imprecise fit of the geodesic sensor nets around the face, jaw, ears and neck of the infant and the consequent tendency to collect noisy data from these regions. Segments were categorised on the basis of condition (congruent or incongruent grasp shown) and average ERPs were computed. Infants with fewer than 6 trials per condition were rejected at this stage. The remaining infants had a mean of 11.5 trials (*SD* = 5.6) in the congruent condition and 12.1 trials (5.9) in the incongruent condition.

3.6 Results

Two components of interest were investigated on the basis of the hypotheses (Nc and N400). An additional component of interest was identified from visual inspection of the grand averaged data – the P400. Investigation of the P400 can be further justified on the basis of previous research centred on infant processing of grasp and gesture (Bakker et al., 2014; Gredebäck, Melinder & Daum, 2010).

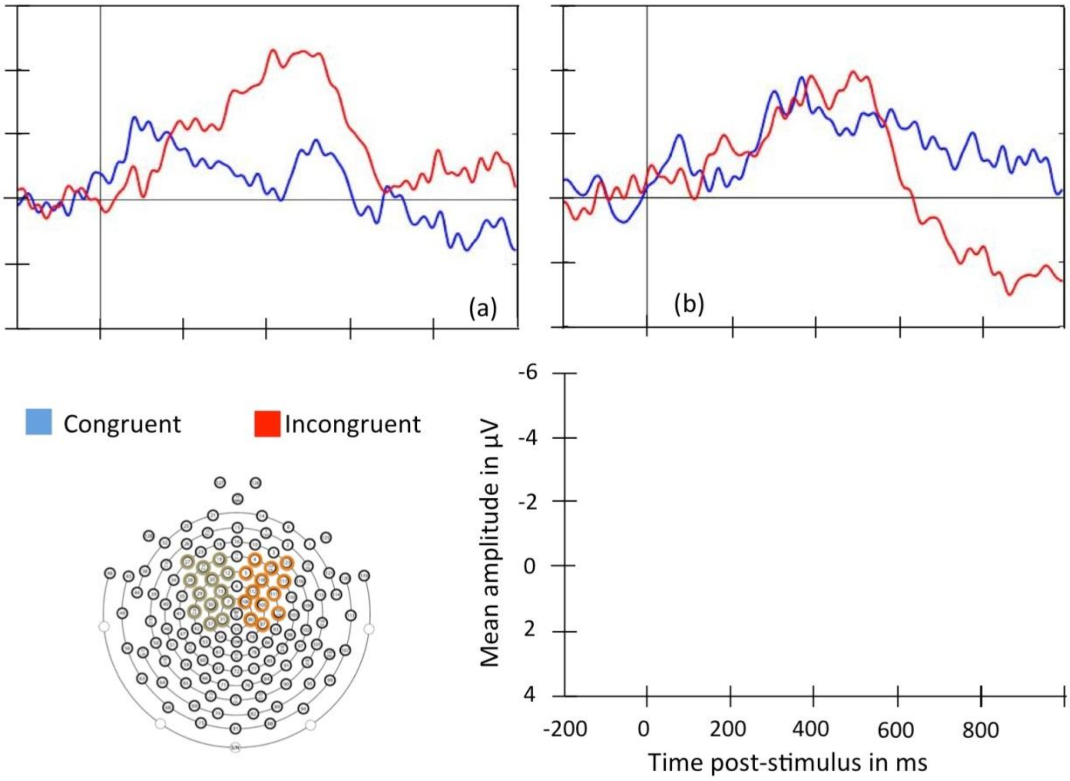

Figure 3.4: *Mean amplitude over fronto-central electrodes in 9-month-olds in response to the critical grasp stimulus. Left fronto-central electrodes are shown in (a), corresponding to brown electrodes in the lower left map.*

Depicted in orange are right fronto-central electrodes, the response from which is seen in (b). An effect is seen in the 300-600ms time window.

An Nc component was visually identified in the left fronto-central region. Given that previous Nc research reports manifestation of the component over left fronto-central (Quinn, Westerlund & Nelson, 2006), right fronto-central (Hoehl, Wiese & Striano, 2008; Quinn et al., 2010) and bilateral fronto-central regions (Marinović, Hoehl & Pauen, 2014; Reid et al., 2009), mean amplitude values for the 300 to 600ms post-stimulus period were calculated for each condition over both left fronto-central and right fronto-central electrodes (electrodes used shown in Figure 3.4). A 2-by-2 ANOVA was subsequently performed. Results indicate no effect of region (F(1,14) = 0.239, p = 0.63, $\eta^2 = 0.004$) but a main effect of congruence (F(1,14) = 4.848, $p < 0.05$, $\eta^2 = 0.13$) in which the Nc is larger (more negative) in response to the incongruent stimuli (*M* = -3.9μV, *SE* = 1.4 μV) than the congruent stimuli (*M* = -1.1μV, *SE* = 1.03 μV). No interaction between the factors was found (F(1,14) = 3.107, p = 0.1, η^2 = 0.05). The grand average ERP is seen in Figure 3.4.

An analysis of the N400 was performed using mean amplitudes between 600 and 800ms post-stimulus over the bilateral parietal region. Although N400 effects to pictorial and action stimuli are generally seen over fronto-central regions in adults (see Experiment 1, also Amoruso et al., 2013; Ganis, Kutas & Sereno, 1996), previous infant action research has found it in parietal regions (Reid et al., 2009). The selection of time window was also guided by the work of Reid and colleagues (2009) and visual inspection of the data. No such effect was found in the present study (Figure 3.5), t(14) = 0.293, p = 0.77, d = 0.12.

Visual inspection of the grand averaged data indicated the presence of a P400 effect (Figure 3.6). Exploratory analysis of this effect is reasonable given the literature in which infants exhibit different P400 responses to pointing and grasping hands in different object-relative orientations (Bakker et al., 2014; Gredebäck, Melinder & Daum, 2010; Melinder et al., 2015). Difference in mean amplitude between conditions was calculated over the same bilateral posterior electrodes as used in Bakker and colleagues (2014). Analysis revealed an effect of condition on this component, t(14) = 2.617, $p < 0.025$, d = 0.8, with a larger amplitude effect for incongruent grasps (*M* = 7.1µV, *SE* = 2.54 µV) than congruent grasps (*M* = 0.78µV, *SE* = 1.35 µV).

The mean score (out of 5) given to infants on the measure of grasping ability was 3.07 (*SD* = 1.71). These scores were correlated with the difference in magnitude of each of the investigated components, that is, the mean amplitude of the component of interest elicited by the incongruent stimulus subtracted from that for the congruent stimulus. In the case of the Nc component, the mean amplitudes in each region were averaged for each condition, given the lack of an effect of region. None of the difference waves correlated with the infants' Bayley scores – P400, r = -0.129, p = 0.32; N400, r = 0.281, p = 0.155; Nc, r = -0.039, p = 0.45. All component magnitude differences are calculated as mean amplitude for congruent stimulus minus mean amplitude for incongruent stimulus.

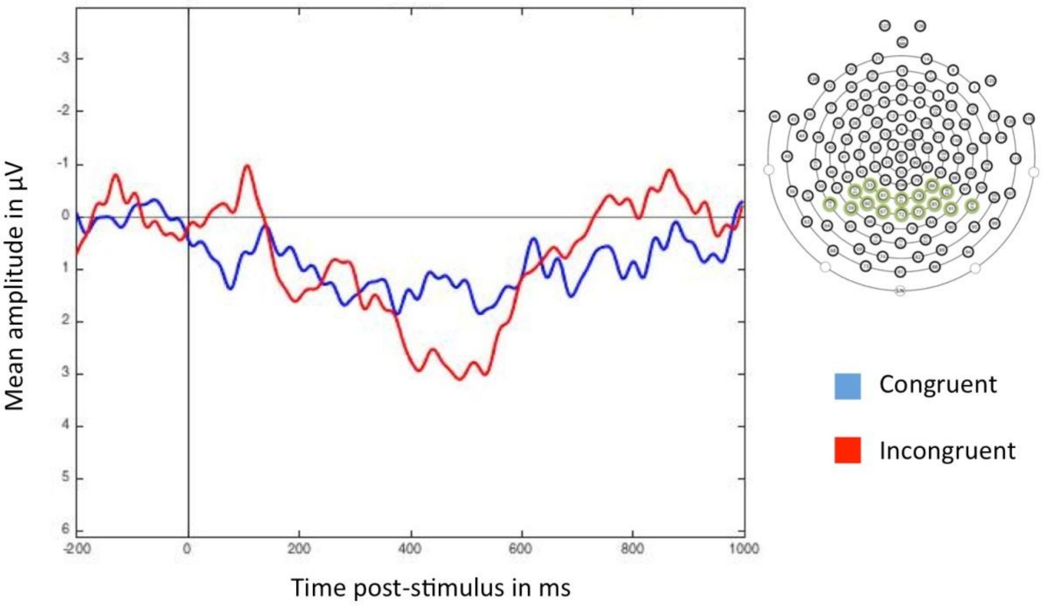

Figure 3.5: *Mean amplitude over parietal electrodes in 9-month-olds in response to the critical grasp stimulus. No effects are seen in the 600 to 800ms time window.*

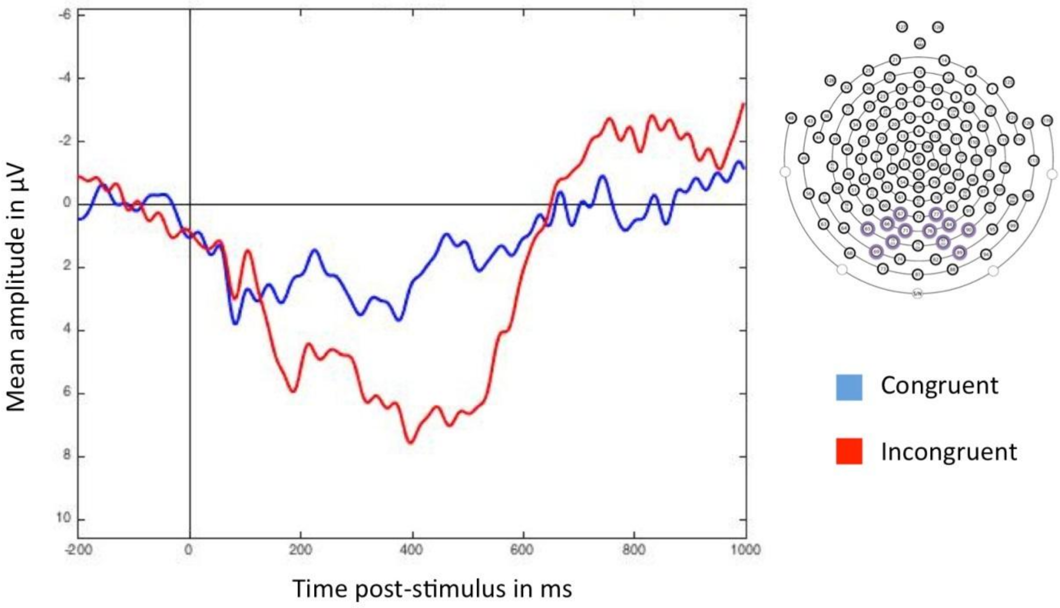

Figure 3.6: *Mean amplitude over posterior electrodes in 9-month-olds in response to the critical grasp stimulus P400 effect is seen in the 300-600ms time window.*

3.7 Discussion

Results indicate that although object-directed grasps are differentially processed at this age, as shown by the Nc and P400 effects, semantic processing of hand-object interaction has not yet emerged. Of interest in relation to the literature on grasp perception at this age, no relationship was found between the difference in magnitude of the components for each infant and the infant’s grasping behaviour. However, other studies indicating relationships between ability to form a particular grasp and the P400 (Bakker et al., 2014) or perception of difference in hand aperture-target object interactions (Daum, Prinz & Aschersleben, 2011) have indicated such relationships in younger infants. Studies with older infants have employed functional tasks in which the infant must decide to use a pincer grip to achieve a practiced goal (10-month-olds, Loucks & Sommerville, 2012), and investigated infants’ perception of grasp functionality as opposed to the structural relationship between hands and objects. It may be that at 9 months, infants have additional experience observational experience of others’ actions and can use this to structure their understanding of grasp in lieu of practical pincer grip experience.

Although no direct comparisons can be made due to differences in the stimuli employed, differences in results obtained here and in Reid and colleagues (2009) suggest that the semantic processing of action does not develop as a holistic process incorporating all aspects of action congruence, but that semantic processing of the congruence of a target in relation to the tool or object implicated in an action emerges before processing of grasp congruence. Alternatively, results may have been affected by the employment of stimuli depicting actors grasping tools instead of eating food, as in the work of Reid and colleagues (2009). The motivational salience of food items may mean that infants form representations of eating actions more rapidly than representations of tool-mediated actions, and thus exhibit semantic ERP components in response to the former actions earlier.

The experiment was repeated with an older age group in order to develop a picture of how infants perceive and process grasps towards the second postnatal year. It was hypothesised that the older age group would exhibit semantic processing of the grasping actions as a result of the changes in neural connection (Huttenlocher & Dabholkar, 1998) and motor ability (Thelen et al., 1993) that arise with increased chronological age.

EXPERIMENT 3: 11.5-MONTH-OLDS

3.8 Methods

3.8.1 Participants

Participants were recruited from the research centre’s participant pool. Twenty-six infants in total participated in the experiment with their caregivers. Of these, 11 infants in total were excluded, for technical problems (n = 2), highly negatively valenced responses to the sensor net (n = 2), insufficient trials attended to during experiment (n = 2) and insufficient valid trials without artefacts (n = 5). The age range of the included infants was 11 months, 8 days to 12 months, 7 days (*M* = 11 months, 21 days, *SD* = 8 days). Twelve female and three male infants were included. Female participants were not targeted specifically; the demography is a random outcome of the available participant pool at the time of the experiment. All families received £10 remuneration and a baby book following their visit.

3.8.2 Stimuli, procedure & analysis

The same experiment conducted with the 9-month-olds was replicated almost exactly with the 11.5-month-olds. The primary exception was that the eye-tracker was not used. Application of the net was performed while infants interacted with a toy for distraction. Despite this difference, the infants included in the final sample sat for comparable numbers of trials before becoming fussy – 56.3 trials on average (*SD* = 20.8 trials). Data were recorded at a higher frequency (1000Hz) and the default EEGlab filter order was applied at the same high and low bandpass levels as applied to the 9-month-olds data. Following visual rejection, a mean of 30.6 trials remained per infant (*SD* = 11.3); 22.75 (7.5) after visual artefact rejection; 22 (6.8) following combined manual and automated bad channel detection and interpolation. There were 11.1 (3.5) and 10.9 (4.2) trials on average for the congruent and incongruent conditions respectively, again with a minimum cut-off of 6 trials.

Table 3.2: *Bayley (BSID-II) motor development scale tasks used with 11.5-month-olds.*

Item No.	***Item description***
49	Uses partial thumb opposition to grasp pellet
56	Uses pads of fingertips to grasp pellet
57	Uses partial thumb opposition to grasp rod
58	Grasps pencil at farthest end
59	Grasps pencil at middle

Additionally, the Bayley tasks on which the infants were scored were adapted to tasks appropriate to this older age group. The tasks used were again the grasping tasks that fit the age group according to the BSID-II – 49, 56, 57, 58 and 59 on the motor scale. These tasks are listed in Table 3.2.

3.9 Results

Mean amplitudes in regions and time windows corresponding to the Nc and the N400 were analysed. Inspection of the grand averaged data did not indicate the presence of a P400 in this age group.

The Nc was computed in the same time window over the same region as in the 9-month-olds' analysis. The Nc component is infant-specific and has been shown in previous studies to disappear from the infant ERP by the second post-natal year (Grossmann, Striano & Friederici, 2007). Consequently an additional factor of time window was added to the data to compare mean amplitude in the Nc window to mean amplitude at baseline. This could then illustrate whether an Nc component was in fact present in the data. The 2-by-2 ANOVA with factors of condition, time window and region (left or right fronto-central) revealed no main or interaction effects for the Nc (see Table 3.3).

Table 3.3: *Results of 2-by-2 repeated measures ANOVA investigating 11.5-month-olds' Nc.*

Factor	***F***	***df***	***p***	η^2_p
Time	1.583	1,14	0.229	0.102
Region	1.269	1,14	0.279	0.083
Congruence	2.309	1,14	0.151	0.142
Time x Region	1.283	1,14	0.276	0.084
Time x Congruence	2.273	1,14	0.154	0.14
Region x Congruence	1.348	1,14	0.265	0.088
Time x Region x Congruence	1.352	1,14	0.264	0.088

Visual inspection of the grand averaged response over the parietal (N400) region identified in the 9-month-olds' data indicated no discernible difference between conditions. Visual inspection also suggested a slightly earlier time window at 11.5 months than was used with the 9-month-olds, 500 to 700ms. This change is justified given that ERPs tend to have shorter latencies as development proceeds (e.g. de Haan, Johnson & Halit, 2003). To establish that the N400 component was in fact present despite any similarities in how it was elicited between conditions, the mean amplitude over parietal electrodes (Figure 3.7) in each condition during this time window was compared to the same during the 200ms baseline period.

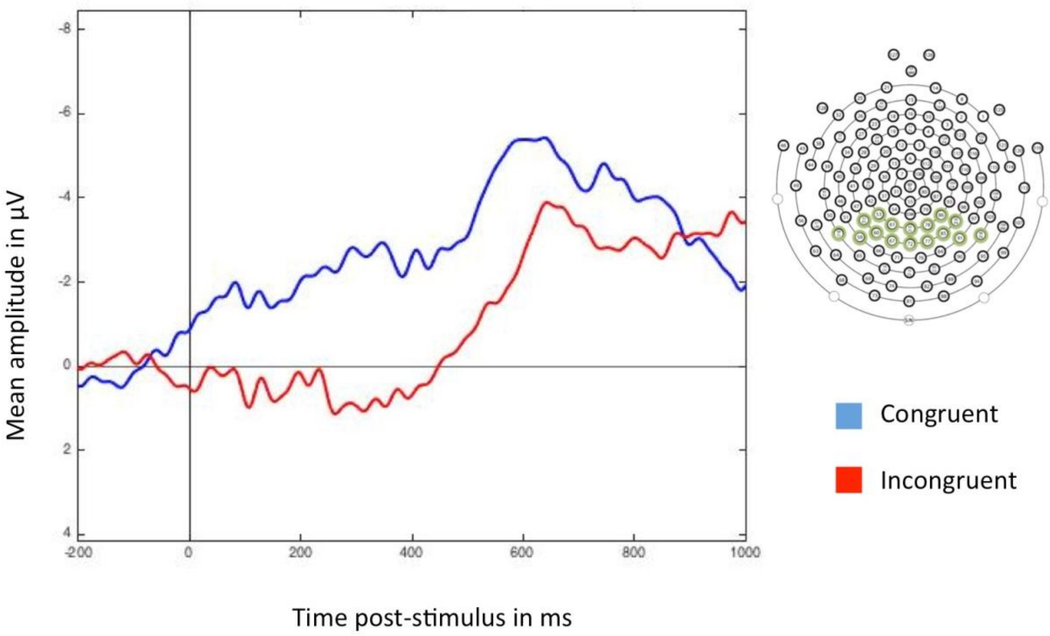

Figure 3.7: *Mean amplitude over posterior electrodes in 11.5-month-olds in response to the critical grasp stimulus. An N400 component is seen in the 500-700ms time window for both conditions.*

A 2-by-2 ANOVA showed a main effect of time period, F(1,14) = 4.718, $p < 0.05$, $\eta^2 = 0.2$, with activity in the 500 to 700ms time-window significantly more negative (*M* = -5.77µV, *SE* = 3µV) than at baseline (*M* = -0.004µV, *SE* = 0.004µV). There was no effect of condition (F(1,14) = 2.789, $p = 0.117$, $\eta^2 = 0.02$) nor any interaction between the factors (F(1,14) = 2.768, $p = 0.118$, $\eta^2 = 0.02$). Although a divergence of conditions is seen in Figure 3.7 from early on in the ERP epoch, the same divergence is evident in the waveforms depicted in other developmental N400 studies (e.g. Friedrich & Friederici, 2008; Pace, Carver & Friend, 2013). Given that no effect of condition was found in the 2-by-2 ANOVA performed on the data in the appropriate time window, this divergence did not affect the data.

The mean behavioural grasping score of the infants was 3.47 (out of 5), with a standard deviation of 1.19 points. There was no correlation between this score and the size of the difference between conditions of the Nc, r = 0.366 $p = 0.09$. There was also no correlation between the difference in magnitude of each of the conditions in the N400 time period, r = -0.096, $p = 0.73$, nor between the difference in the mean magnitude of the N400 component overall and the mean amplitude during baseline, r = -0.257, $p = 0.36$.

3.10 Discussion

Results indicate a wide number of changes in grasp processing in the few months separating the samples. Different components are elicited by the same stimuli, with some (Nc, P400) no longer being present and others (N400) emerging. While a component comparable to the N400 was found in the 11.5-month-olds' data, it did not distinguish between conditions. Interpreting this component as a candidate for the N400, these results suggest that as infants make the transition to semantic processing of actions from potentially associative or familiarity-based processes, they are no longer attending to differences in the means of apprehending objects. Specifically, when infants process reach-and-grasp actions semantically at 11.5 months, they are not incorporating the means of grasping into their semantic representations and not attending to these differences at an earlier stage of processing, such as attention (as indexed by the Nc), either.

3.11 General Discussion

Results from all three experiments illustrate how infants' processing of hand-object relationships changes at the end of the first post-natal year, and how this change makes the means of representing observed action more adult-like in terms of the neural processes recruited. There is also a disjunction in how differences in hand-object relationships are attended to during development. Specifically, at 9 months infants do not exhibit the N400 in response to grasps on cups but at 11.5 months a N400 candidate emerges. This could indicate that semantic processes are being recruited in processing of reach-and-grasp actions at 11.5 months. However, unlike the adult N400, this 11.5-month-old N400 does not differentiate whether the grasp matches the form of the cup or not. Conversely, the ERP components evident at 9 months (Nc, P400) are elicited differently in each condition. This suggests that as infants engage in different means of action processing, sensitivity to differences in those actions changes.

Given that the N400 measured in the experiment with 11.5-month-olds did not differ between conditions, it cannot be said that these infants were processing the semantic relationship between the hand and the cup as the adults did and responding differently when the grasp was not meaningful in the context of the cup's shape. The presence of this ERP might instead indicate that infants respond to actions semantically, that is, as meaningful stimuli with specific structures and mutual expectancies generated by the different components of those actions. On the basis of a previous study in which 9-month-olds exhibited differences in N400 morphology to actions in which actors placed a food item by the semantically correct target (mouth) or an incongruent target (forehead, ear or crown; Reid et al., 2009), it is possible that the specific manifestation of this component arises because infants were processing the semantics of the goal-directed action presented. In the current study, upon seeing a hand reaching for a cup, an expectation could have been elicited about the conclusion of the action (grasping) and the action may have been processed semantically regardless of how the grasp was enacted. It is also possible that at eleven-and-a-half months, infants are more flexible in their processing of sequential stimuli in general as they begin to integrate possibilities into new, semantic means of processing action. With an established conceptualisation of action as goal-directed, means of performance may be allowed to differ before being cemented as semantically congruous or incongruous by adulthood. This possibility mirrors work by Bremner and colleagues (2007) in which two-year-olds are better at generating novel sequences after training than three-year-olds, potentially because their general lower linguistic skills allow greater cognitive flexibility. Constraint on what can be considered a “congruent” grasp may develop later, with enhanced development of the semantic action processing system or more experience with using handled tools.

There are some differences between the candidate N400 ERP elicited here and that measured in Reid and colleagues’ (2009) work, which could be attributed to a difference in task constraints or a difference in age. One of these is the morphology of the N400. In the previous work, no N400 was evident in the response to the congruent actions; it manifested only when the action conclusion was incongruous with the implicated object. In the current work, an N400 is seen in both conditions. Under an interpretation that the 11.5-month-olds’ N400 was elicited as a result of the goal-directed sequence of the action, which was universally congruent with the action of grasping even if the means of grasping was incongruous with cup structure, we see a developmental change in the N400. It is now elicited when the goal of an action fits expectations. What this suggests is that developmental change in how actions are semantically processed. At 9 months, the semantic processing system is only recruited for actions that violate expectations. This kind of selectivity may be important for flagging unusual actions and allocating further processing resources via a developing action understanding mechanism, to allow the infant to compute why such actions are odd. At 11.5-months, actions in which a target object is grasped are processed semantically regardless of the congruence of that grasp. All actions are processed in this manner, likely due to increased maturity of the semantic processing architecture.

Another change between 9 and 11.5 months is the disappearance of the Nc effect. This component of the infant ERP is not always elicited as infants approach the second post-natal year (e.g. Grossmann, Striano & Friederici, 2007; but see alternatively Carver & Vaccaro, 2007) so it is reasonable that it would be present in the younger sample only. However, at 9 months, this component differentiates between the two conditions, with a larger Nc for the incongruent than the congruent stimuli, indicating that the infants allocated more attention to these stimuli. This could be plausibly attributed to the infants seeing the congruent grasps in their daily lives with greater frequency than the incongruent ones, rather than processing of whether the grasp is appropriate for the cup's form or not. The presence of an N400 does not contra-indicate the Nc (Friedrich & Friederici, 2011; Reid et al., 2009), so the lack of Nc at the older age, in conjunction with an N400 that does not differentiate between conditions, may be due to diminished sensitivity to sub-components of actions and a more generalised attribution of meaning to action.

The Nc component is diminished in this study's older infant sample. Previous infant N400 research has suggested that the morphology of the N400 differs between infancy and adulthood (that is, it does not manifest fronto-centrally in infancy) because a large Nc is present in that region (Reid et al., 2009). In the current work, the N400 is apparent over the parietal region despite an absent Nc component. This indicates another developmental difference in infant and adult N400 ERPs. Amoruso and colleagues (2013) suggest that despite similar differences in topography, adult N400s to actions and to language share a common generator. The difference in topography in this study's samples may be the result of developmental factors related to measurement of the EEG at the scalp, such as wide-ranging changes in synaptic density that continue into toddlerhood (Huttenlocher & Dabholkar, 1997), and differences in scalp and skull density (Reynolds & Richards, 2009). It may also be due to developmental differences in how semantic processing of action occurs at the neuronal population level that are beyond the scope of this work to further elucidate.

The P400 is another component that is not seen in the 11.5-month-olds' data but manifests at 9 months and differs between conditions. Previous research has shown that the P400 responds to differences in social stimuli. This component is differentially elicited by shifts of eye gaze toward and away from the infant (Elsabbagh et al., 2012), and by different emotional facial expressions (Hoehl & Striano, 2008). Other research has shown a larger P400 in response to congruous stimuli, in the sense that the direction of a pointing or reaching hand matched the previous appearance of an object (Bakker et al., 2014, 6-month-olds; Gredebäck, Melinder & Daum, 2010, 8-month-olds). At thirteen months, the P400 is larger in response to incongruently oriented hands. In the present study, a larger P400 was found for grasps that did not match the structure of the apprehended cup. No strong conclusions can be drawn given that the manifestation of the P400 was incidental, that is, the study was not designed to elicit it. Furthermore, the P400 has no established adult homologue. Initially, the P400 was believed to be a face-sensitive component analogous, as part of the N290-P400 complex, to the adult N170 (de Haan, Johnson & Halit, 2003). Investigation of the N170 in relation to perception of hands is sparse. An early N170 study by Bentin and colleagues (1996) found that the component was responsive to faces and not to hands or objects. However, Allison, Puce and McCarthy suggest that the generator of the N170 lies in the superior temporal sulcus, which has been shown (via positron emission tomography) to encode body and hand stimuli. Gredebäck, Melinder and Daum (2010) find that an N200 in adults distinguished between hands pointing toward or away from objects. A negative component in such close temporal proximity to the N170 may indeed be the same component. The conflict with the results of Bentin and colleagues (1996) may be due to the specific “communicativeness” of the hands in the Gredebäck, Melinder and Daum (2010) work. That is, because the hands in the latter study were associated with the appearance of targets in specific spatial locations, they may have been processed differently from the hands presented without context in the former study. Nonetheless, if we assume that 9-month-olds, like 8-month-olds (Gredebäck, Melinder & Daum, 2010), exhibit larger P400 components to socially salient stimuli, the incongruent grasps may have elicited this response as the infants perceived the unfamiliar grasp as having communicative relevance.

With the precise processes indexed by the P400 and its potential adult homologues outside of face perception, categorisation and recognition not strongly determined, interpretation of its function in the present study cannot be strongly deterministic. Likewise, without analyzing adult data for a P400 homologue such as the N170 or N200, the conclusions that can be drawn about the development of grasp encoding are limited. For example, if a P400 homologue were found in the adult data in addition to the N400, it would rule out the possibility that the infant P400 is a precursor to the N400. Conversely, if it were not found, it might suggest further differences in how infants and adult encode action and would strengthen the case that the development of grasp encoding is U-shaped, with modes of processing grasp developing, being suppressed, and re-emerging before adulthood.

The absence of correlation effects between the infants' grasping scores and the relative size difference in the elicited components suggests that motor experience and concomitant motor representations are not integral to associative and semantic representations of grasps. Previous studies drawing connections between processing of grasp size and orientation and grasping ability (Bakker et al., 2014; Daum, Prinz & Aschersleben, 2012) involved younger participants. Those with comparably aged infants employed a functional task to assess ability to use precision grips, rather than a task in which the infant had to directly apprehend an object in front of them (Loucks & Sommerville, 2012). At 9 months, the relationship between a cup and the grasp executed upon it may be processed on the basis of observational experience. At 11 months, infants do not differentiate between the grasp-object relationships at the semantic level and this lack of distinction is not explained by individual differences in grasping ability.

One explanation of the results is that the kinds of processes reflected in the neural components evident in the infant samples – likely including attention to grasping, sensitivity to the social or communicative elements of the same, and semantic processing of the action – are separable from motor experience and potentially from motor processes more generally. If the study were designed to incorporate an index of motor or ideomotor activation such as mu desynchronization (e.g. Southgate et al., 2010) a relationship to grasping ability may have emerged. Alternatively, it is possible that the lack of relationship between the behavioural and neural measures could have been driven by the inappropriateness of the specific grasping measures employed. The grasping scores from the adapted Bayley measures were homogenous within each sample, indicating that most infants from 9 months onward can pick up an object with thumb-finger opposition. A functional task along the lines of that used by Loucks and Sommerville (2012) may have captured individual action execution differences explicative of neural processing differences. Their task required that infants shaped their hand appropriately in advance of grasp execution, indicating prior knowledge of the appropriate action end-state. Such knowledge may be the foundation of representations of appropriate manual interactions with objects of different shapes.

3.12 Conclusions

The infant data suggest that the path from early processing of the relationship between cups and hands to adult processing of the same is not linear. Nine-month-olds are sensitive to the difference between grasps that match the form of the (familiar) object being acted upon, and those that do not match it. This sensitivity is manifested at the attentional (Nc) level and also in the P400 component which is associated with processing of social or communicative stimuli (e.g. Gredebäck, Melinder & Daum, 2010). At 11.5 months, these stimuli elicit a candidate N400 component, but the distinction between the two, even at an earlier attentional level, is no longer present. In adulthood, the N400 distinguishes between grasps that are congruent with the form of the object being apprehended and those that are not.

Other research has shown that infants do not form (potentially semantic) associations between actions, objects and outcomes linearly (Perone, Madole & Oakes, 2011; Perone & Oakes, 2006) – all aspects of an action are not equal in infant representations. The results obtained here indicate that as infants' processing of actions becomes more adult-like in their employment of what, based on correspondences with previous research (Kutas & Federmeier, 2011; Pace, Carver & Friend, 2013; Reid et al., 2009), appears to be a developing semantic representational system, aspects of the action unrelated to the overall target of the action or the relationship between the object employed and the goal are not processed. Initial semantic representations of actions rely on the goal-directedness of the action in order to establish the action as meaningful, as in Reid and colleagues' work (2009), and this is likely what was encoded by the older infant sample in this study, if the identified component is an N400. Other aspects of the action, which convey something meaningful about the action but do not prevent the goal of the action or violate the typical use associated with the implicated object, are not incorporated into these representations at this period in infancy.

Before development of a semantic representational system, infants process diverse aspects of a tool-mediated action, including whether the shape of the grasp matches the form of the tool. Whether because of greater visual experience with specific grasps on familiar objects, or because of some other form of matching (e.g. associating wide apertures with large targets), 9-month-old infants allocate more attention to the grasps that are incongruent with the implicated object. They also process them in the same manner as they would for many kinds of socially salient action, such as pointing fingers and direct gaze. With the initiation of a semantic processing system certain aspects – those that give overall significance to the action – are prioritized for processing. Other elements of the action, such as the tool-hand interaction, are not semantically processed at this period in development. Semantic processing of grasp congruence may emerge when the system is more mature (e.g. biologically), or when representations of typical actions, such as grasping a cup or other common tool, are sufficiently entrenched to allow other elements of the action to capture semantic processing resources.

Prelude to Chapter 4

If motor component of actions do not play a role in semantic action processing in the first post-natal year, is there a relationship in the other direction? Do semantic aspects of action affect motor processing?

The preceding series of experiments showed that adults incorporate the relationship between object and hand into semantic representations of action and respond with a larger N400 component when the shape of the grasp used does not fit the shape of the target object. They also showed that there is a fundamental, quantitative change in how the same stimuli are processed in the first post-natal year. At nine months of age, infants allocate additional processing resources to stimuli depicting incongruent grasps on objects but these differences disappear by around eleven-and-a-half months of age. Instead, at this later stage, we see evidence for semantic processing of all stimuli, suggesting that although semantic processing of action has emerged it does not incorporate this information about the precise means of performing a grasping action. Taking into account the lack of correlation between grasping skill and neural processing of these stimuli, motor resonance does not seem to affect conceptual processing of reach-to-grasp actions at this age.

Comparative single-cell recording (Umiltà et al., 2001) and functional neuroimaging (Chao & Martin, 2000) research indicate that semantic and motor processes are linked in action perception. There is also the involvement of the primate homologue of Broca’s area in mirror system function (Gallese et al., 1996; Rizzolatti et al., 1996) to consider, in conjunction with parietal and superior temporal sulcus (STS) input to premotor areas (Kilner, Friston & Frith, 2007; Rizzolatti & Craighero, 2004). In humans, Broca’s area has been associated with semantic processing (Dapretto & Bookheimer, 1999; Rodd, Davis & Johnsrude, 2005), the inferior parietal lobule with integration of visual and motor inputs (Mattingley et al., 1998), and the STS with processing and integrating the meaning of perceptual input, particularly with regards to its communicative elements (Redcay, 2008; Redcay, Kleiner & Saxe, 2012).

Thus the regions involved in the mirror system according to the predictive model of Kilner, Friston and Frith (2007) are collectively involved in creating associations between visual and motor input and evaluating the significance of those associations. Thus, they offer evidence for the joint involvement of semantic and motor processes in the mirror neuron system.

Another study found that meaningful actions engaged a fronto-temporal action processing system more strongly than meaningless actions (Decety et al., 1997). This finding and the above studies all indicate that action mirroring could be a two-step process, as proposed by Gallese and Goldman (1998), in which processing of the meaning of observed actions feeds into motor activation. In extended terms, action mirroring is a series of feedback and feedforward loops in which superior temporal sulcus, parietal regions and premotor regions are all involved, incorporating in their activity Bayesian inference based on prior information about actions and current progress of the action (Kilner, Friston & Frith, 2007).

Gallese and Lakoff (2005) also suggest that conceptual elements of action are accessed via the sensorimotor system alone, independent of other cortical regions. However, results within Chapter 3 partially contradict this. At 9 months, the differential allocation of attention to congruent and incongruent grasps on objects suggests some kind of associative action processing that exists with no relationship to grasping skill. This is because grasping skill likely indexes the ability to access a motor representation of observed grasps (Daum, Prinz & Aschersleben, 2011; Loucks & Sommerville, 2012). When semantic processing of reach-to-grasp actions emerges (as a goal-directed as opposed to means-focused process), again this relationship between execution and perceptual or conceptual processing is absent. It may be that conceptual elements of action *can* be accessed via the sensorimotor system alone once conceptual representations are entrenched, but conceptual and sensorimotor representations of action may initially develop in isolation from one another. More recent, associative accounts of mirror system function (Cook et al., 2014) support this conceptualisation of motor representation of action in development, as repeated associations between observed actions and performed actions result in responses to observed action that are elicited via ideomotor resonance after sufficient repetitions of the association. Recent work by de Klerk and colleagues (2015) also suggests that the mirror system in development operates via visuomotor matchings. It may be that in the previous study, the 9-month-old infants were simply too young and inexperienced with precise object manipulation for associative processes to have been linked to grasp execution. In the 11.5-month-olds group, the developmental trajectory had changed, with grasp not incorporated into semantic or associative processing of action and consequently there could be no direct visuomotor-mapping relationship between these processes and production of precision grasping.

Another way to investigate the relationship between motor and semantic processes in development is to take actions that are identical in their motor elements, but differ in their meaning. In the previous chapter, semantic processing of grasp was measured. In the next chapter, changes in mirror system function in response to identical grasps that differed in congruence were measured. In this study, the shape of the actor's hand as it grasped a spoon was the same in all conditions. If the grasp were a radial grasp (functional end of tool near thumb/index finger) a normal action would ensue. If it were an ulnar grasp (functional end near little finger) the ensuing action would not be one typically associated with (or congruent with) the tool, although the end goal would be accomplished in all cases.

Desynchronization of EEG activity in the 6-9Hz bands, over central or fronto-central electrodes, is thought to represent activation of the motor system. This kind of activity is found in infants from about 9 months as they observe others' goal-directed actions (Nyström et al., 2011; Southgate et al., 2010), and is thought to be homologous to the firing of premotor neurons in macaques as they observe goal-directed action (Gallese et al., 1996; Rizzolatti et al., 1996). If this activity is elicited purely by sensorimotor matching, no difference in response to the execution of the grasps would be expected. If this activity arises from mirror system function in the sense of a two-stage (Gallese & Goldman, 1998), Bayesian (Kilner, Friston & Frith, 2007) or conceptual sensorimotor (Gallese & Lakoff, 2005) system, it would be expected that motor activation would be affected by semantic differences in the grasp-object relationship, provided that the age group studied had formed reliable associations between the orientation of a grasp on a tool and success in using that tool.

Taken in context with the previous studies in this thesis, there is cause for some precaution in designing such a study. Chapter 2 indicates that 16-month-olds do not encode object orientation when associating specific tool-ends with actors' goals. However, the tool used in Chapter 2 was a dual function tool and consequently presented elevated complexities in encoding (Barrett, Davis & Needham, 2007; Paulus, Hunnius & Bekkering, 2012) relative to a simple tool with a familiar function, such as a spoon used for eating. Results from Chapter 3 illustrate that during development, differences between grasps congruent and incongruent with a familiar object's shape are detected. Work on infant use of spoons (McCarty, Clifton & Collard, 1999; McCarty, Clifton & Collard, 2001) illustrates that appropriate grasps on spoons for efficient eating can be executed as young as 9 months and become more consistently executed early in the second post-natal year.

By measuring 9- to 11-month-olds' neural activity associated with mirror system function in response to motorically similar but semantically distinct spoon-use actions, and by relating those responses to the infants' own motor-planning skills during spoon use, it may be possible to determine how the semantic or conceptual elements of actions, beyond goal-directedness, are represented in the motor system. This was the purpose of the following study.

Chapter 4

Infant mirror responses to motorically similar and semantically distinct actions.

Abstract

Mirror system function is a two-stage process, incorporating attribution of meaning to observed actions in addition to motor resonance in response to those actions. The aim of the present study was to elucidate how pre-existing conceptual representations of action modulate mirror system function in the developing brain. In order to do so, EEG data were recorded from 32 infants (14 retained) between nine-and-a-half and eleven months of age as they watched videos of actors grasping and eating from spoons using identical grasps that differed in orientation relative to the spoon and consequently in congruence with eating. Event-related desynchronization in the 5 to 9 Hz band of EEG activity over central electrodes was measured and compared for congruent and incongruent grasping and eating actions. Participants' motor planning was measured during a self-feeding task performed by the infants. Results affirm that motor activation during action observation is a predictive process. No overall effect of action congruence on motor activation was found but correlation of motor activation with self-feeding behaviour indicates that better ability to plan actions is related to the size of the difference in response to incongruent and congruent actions. These results have implications for visuomotor association and predictive coding accounts of mirror system function.

4.1 Introduction

Research into mirror system function suggests that premotor neural activation is a fundamental component of how we perceive others' actions (Fadiga et al., 1995; Gallese, Rizzolatti & Keysers, 2004). Single cell recordings in non-human primates indicate a correspondence between firing patterns for the same actions performed and observed (Gallese et al., 1996). Mirror system principles have been applied to research on diverse topics from imitation (Brass & Heyes, 2005) to empathy (Carr et al., 2003) to psychiatric illnesses (Arbib & Mundhenk, 2005). Investigation of mirror system function is particularly interesting in the context of developmental action perception. In characterising the operation of the mirror system in infancy it becomes possible to determine whether other means of processing action – social, associative, teleological, and semantic – are dependent on the development of initial ideomotor correspondences or emerge as independent systems. In the work described here, the relationship between motor and semantic action processing systems at the end of the first post-natal year was investigated.

One means by which mirror system function can be characterised is via the mu (sensorimotor alpha) and beta rhythms of electroencephalographic (EEG) activity. Parallels are drawn between activity in these frequency bands and activation of brain regions associated with mirror system function in studies using magnetoencephalography (MEG; Caetano, Jousmäki & Hari, 2007) and functional magnetic resonance imaging (fMRI; Perry & Bentin, 2009). Using mu desynchronization as a correlate for mirror system function has also been justified by studies showing its modulation by the same factors that modulate mirror neuron activity in primate studies (Muthukumaraswamy, Johnson & McNair, 2004). Mirror activity is generally recorded over fronto-central and central electrodes and occurs in adults at 8 to 12 Hz (mu) and 12 to 24 Hz (beta; e.g. van Elk et al., 2010). In infants, beta is less well-characterised (but see van Elk et al., 2008) whereas mu desynchronization has been widely studied (Marshall, Young & Meltzoff, 2011; Nyström et al., 2011; Southgate & Begus, 2013; Southgate et al., 2010). Alpha activity in general (including mu) manifests in infants at a lower frequency than in adults, around 6 to 9 Hz (Stroganova et al., 1999). Mirror system function and more general motor resonance processes are indexed by a decrease in power in the alpha band of EEG recorded over central scalp regions. This power decrease or suppression is the result of desynchronization of population activity. Consequently, motor activation, mu desynchronization or suppression and decrease in mu power are terms used with high but not full interchangeability in the literature. In the present work, *motor activation* and *mirror activation* will be used to describe the general phenomenon under investigation and *mu desynchronization* to describe the specific phenomenon measured.

The question of how semantic processing systems interact with the mirror system is fundamental. Since the initial primate research, mirror neurons have been specifically stated to respond to goal-directed actions (Gallese et al., 1996; Rizzolatti et al, 1996). Goals provide semantic context or meaning for actions. The presence of a goal or target makes an action predictable. While mirror activation can be thought of as an ideomotor, automatic or involuntary response (e.g. Brass, Prinz & Bekkering, 2001), if pre-existing representations of the implicated actions did not exist, there would be no justification for why motorically similar but conceptually or semantically dissimilar actions could result in differential mu desynchronization, as happens in many infant studies (Nyström et al., 2011; Southgate et al., 2010; Stapel et al., 2010). Returning to the earliest works on mirror system function, Gallese and Goldman (1998) indicated that although superior temporal sulcus (STS) and premotor (inferior frontal gyrus/IFG, macaque F5) neurons are involved in semantic and motor processing of observed action respectively, both systems "could represent distinct stages of the same analysis" (p. 499, Box 2). That is, mirror system activation follows initial visual or auditory (e.g. Caetano, Jousmäki & Hari, 2007) detection of meaning in a perceived action. A later conception of mirror system function moved from a model in which representations are fed forward from STS to prefrontal regions via parietal regions, to a Bayesian model in which prior expectations or typically co-activated pathways allow each mirror system module to provide predictive representations to its preceding module (Kilner, Friston & Frith, 2007). This model provides further justification for why semantic and motor processing of actions are strongly linked, as ideomotor responses to actions can be elicited in anticipation of a specific goal based on previously-held representations of actions similar to the observed action, rather than being dependent on having a complete representation of the current action. This goes some way to explaining why mirror neurons respond to actions before their completion (Gallese et al., 1996) and when the completion is occluded from view (Umiltà et al., 2001).

This relationship between motor aspects and semantic elements of actions is borne out in the infant mu desynchronization research. The mirror system is differentially activated by actions with an occluded but plausible goal and those with no discernible goal, even when the actions are motorically identical (Southgate et al., 2010). It is also differentially activated by actions casually initiated by the actor and those occurring coincidentally (Nyström et al., 2011), and by actions that match the context in which they are performed and those that do not (Stapel et al., 2010). Thus, the conceptual or semantic aspects of these familiar actions modulate the infants' ideomotor responses. There is extensive evidence that infants hold representations of many different elements of actions, including action structure (Baldwin et al., 2001; Reid et al., 2007), actors' goals (Woodward, 1998) and artefact function (Perone, Madole & Oakes, 2011). Drawing direct parallels with the above-cited mu desynchronization findings, they represent occluded targets of reaching (Daum et al., 2009, relating to Southgate et al., 2010), associate common artefacts with specific targets (Hunnius & Bekkering, 2010, relating to Stapel et al., 2010), and respond differently to causal and associated action effects (Träuble & Pauen, 2011, relating to Nyström et al., 2011). Consequently, it is reasonable to infer that even in infants, there is an element of prediction in mirror system function, with semantic representations from STS and parietal regions feeding forward to IFG and other premotor regions, and receiving feedback as action processing continues.

The work of Stapel and colleagues (2010) integrates well into the predictive coding model of Kilner, Friston & Frith (2007). Whereas no mu desynchronization was found in response to the non-goal-directed actions shown by Southgate and colleagues (2010) and Nyström and colleagues (2011), Stapel and colleagues (2010) found that greater mu desynchronization is elicited by observed actions that violate the goal usually associated with an implicated object. They showed 12-month-olds videos of actors bringing cups to the mouth or to the ear. Their explanation of the results was that whereas the lifting of the cup elicited motor activation in both cases, the bringing of the cup to the ear elicited greater motor activation as the representation needed to be updated for the novel action. The resultant stronger motor activation can be accounted for as premotor activation in response to the action feeds back to semantic processing regions, leading to updated representations and predictions. In the case of the standard use of the cup, feed-forward activation without extensive feedback modulation or iterative Bayesian predictions is sufficient to represent the action.

Developmental populations do create some challenges for a predictive, STS-parietal-premotor model of mirror system function. There is no evidence of the N400 event-related potential (ERP) at 7 months of age (Reid et al., 2009), indicating that infants at this age do not process actions semantically, or at least have a qualitatively different means of doing so than older infants, children and adults. However, there is evidence from near-infrared spectroscopy (NIRS; Shimada & Hiraki, 2006) and independent component analysis (ICA) ERPs (but not mu desynchronization; Nyström, 2008) that the infant motor system responds differentially to observed actions and observed motion at six to seven months of age. There remains a theoretical question of whether what was measured in these studies was mirror system function or general motor resonance. The distinction between these two processes can be drawn via Uithol and colleagues' (2011) characterization of interpersonal and intrapersonal motor resonance – in the former case, the resonance is between the motor states of executor and observer, in the latter, it is between the observer's perceptual representation of an action and their motor representation thereof. While mirror system function involves both inter- and intrapersonal resonance, motor resonance may be purely intrapersonal and can be elicited by stimuli other than goal-directed actions. For example, Proverbio (2012) found that the mu rhythm is desynchronized (in adults) more strongly to images of tools than images of non-tool artefacts. Neural activation in response to tool pictures as measured by fMRI (Chao & Martin, 2000) and positron emission tomography (PET; Grafton et al., 1997) occurs in regions associated with execution and observation of actions. Consequently, neural measures of mirror system function without source localization or conceptual or semantic manipulation may be confounded with measures of motor resonance. As the work of Shimada and Hiraki (2006) and Nyström (2008) compared congruent actions with non-action moving and static stimuli, it is possible that the motor activation measured in infants before the emergence of semantic action processing relates to general resonant processes rather than the mirror system specifically. Later work with older infants (e.g. Nyström et al., 2011; Stapel et al., 2010) compared conceptually different actions to find differences in mu desynchronization that may be more strongly related to the developing mirror system. It is also important to note that associative rather than semantic representations of action may modulate mirror system function during development (Gerson, Bekkering & Hunnius, 2014).

Despite or perhaps because of the challenge of the different chronological emergence of motor activation in response to observed actions and of semantic action processing, characterizing the relationship of these action processing systems to one another in early development is important. In asking such a question it also becomes possible to see how motor experience affects mirror system function. The first two years of life show a marked transformation from the neonate who cannot lift her head, to the crawling and upright-sitting infant, to the toddler who can walk unassisted and manipulate small objects with ease. All of these changes are accompanied by concomitant perceptual or cognitive developments (Anderson et al., 2013; Corbetta, Thelen & Johnson, 2000; Soska, Adolph & Johnson, 2010). Looking at neural mirroring in development allows the investigation of the question of whether observing others' actions leads to resonance in the representation of the goal or of the minutiae of the action itself. For example, while adults might learn novel motor sequences via observation and show similarities in motor activity during observation and execution of such sequences (Cross et al., 2009), participants in studies of these phenomena generally have the physical motor capacity to perform each step in the sequence even if they have not done so previously. Infants, however, may have motor restrictions on their performance of certain actions. Van Elk and colleagues (2008) compared mu and beta desynchronization is 14- and 16-month-old crawlers and walkers. They found greater beta suppression for videos of infants crawling relative to walking, and found that the difference in the size of mu and beta effects for crawling relative to walking was correlated with the infants own crawling experience. That is, infants with more months of crawling experience showed greater relative mu and beta suppression to crawling videos than their peers with less crawling experience. Thus we see that the achievement of a motor milestone such as walking does not fundamentally and immediately alter neural responses during observation of the same action, but that greater experience of an action, such as crawling, does lead to stronger motor representations.

The contribution of experience as sustained process and not a one-off event can be seen in the work of de Klerk and colleagues (2015). Seven- to 9-month-old infants were given walking experience on a treadmill with contingent or non-contingent observation of their own or another infant's legs stepping. All infants, including those receiving no training, showed greater mu desynchronization to observation of others' stepping at post- than at pre-test. While there were no overall group differences, among the infants in the contingent condition, there was a correlation between the amount of training received and mu desynchronization at post-test relative to pre-test. Thus, a greater degree of experience, whether motor (van Elk et al., 2008) or visuomotor (de Klerk et al., 2015), leads to stronger mirror representations of actions. This fits with predictive coding accounts of mirror system function (Kilner et al., 2007) and associative accounts of mirror system development (Cook et al., 2014). However, given that infants with no walking experience also exhibited differences in mu desynchronization between pre- and post-test, there emerges a question of how mere visual experience can elicit mirror system activation in a purely associative manner. It is possible that this is due to goal simulation. Alpha desynchronization occurs in 9-month-olds in response to the movement of a toy (an action they can perform), regardless of whether it is moved by a hand or a claw, or self-propelled (Southgate & Begus, 2013). The results of this study suggest that early mirror system function may be driven by teleological or other conceptual representations of action (e.g. Csibra, 2003). This might result in responses driven by elicitation of action representations of achieving the assumed goal of the observed action, rather than following its specific gestural or motor elements. This developmental work (Southgate & Begus, 2013) and the motor experience work (de Klerk et al., 2015; van Elk et al., 2008) suggest that the mirror system incorporates resonance in terms of both the goal of an observed action and the means of performing that action.

The research detailed above indicates that (1) ideomotor responses are found in infants in response to actions from 6 months of age (Shimada & Hiraki, 2006), (2) by the end of the first post-natal year, these responses are modulated by conceptual aspects of actions and thus relate to mirror system function (Nyström et al., 2011; Southgate et al., 2010), (3) motor activation is predictive and enhanced during simulation of novel actions (Stapel et al., 2010), and (4) visuomotor experience of the specific motor components observed action are not necessary for the action to elicit mu desynchronization (de Klerk et al., 2015). From the state of current knowledge about the mirror system in infancy, some key questions remain. One of these is the extent to which conceptual or semantic action information modulates mirror system activation, in the absence of differentiating motor information. Another is the extent to which mirror system activation is predictive for actions that differ in this manner. Finally, if mirror system activation is predictive of the conclusions of actions that are conceptually congruent or incongruent, it may not be that overall visuomotor experience with a particular movement is necessary for the elicitation of mirror responses. Rather, it may be that the infant’s ability to execute a movement in line with an overarching goal, that is, the ability to plan an action on a combined motor-semantic level, affects their mirror system’s response to others’ actions.

To address these questions, infants were shown videos of actors eating from spoons and given opportunity to execute self-feeding actions with a spoon afterwards. A 9- to 10.5-month-old age group was tested, as at this age the ability to self-feed with spoons and to grasp handled tools appropriately is emergent but variable (McCarty, Clifton & Collard, 1999; McCarty, Clifton & Collard, 2001). In order to investigate both the predictive nature of mirror system function in infancy, and its responsiveness to semantic modulation without concurrent motor differences in the execution of the action (e.g. the change in object trajectory in Stapel and colleagues, 2010), actors executed an identical grasp on a spoon perpendicular to their reach. Depending on the left-right orientation of the spoon to their grasp, the self-feeding action could be executed congruently with standard spoon use, or incongruently, at an angle not usually associated with spoon use. After observation of these videos, the infants were given a self-feeding task similar to that presented by McCarty, Clifton and Collard (1999). Their motor planning ability was rated based on whether they grasped the spoon by the handle, whether they needed to transfer the spoon between hands, and whether they succeeded in eating from the spoon without first making an error such as putting the handle in the mouth.

It was hypothesised that the size of the difference in mu desynchronization at the time of the actor's grasp on the spoon would be correlated with the infant's action planning ability. That is, those infants who could pick up a spoon correctly for eating would perceive the difference in the relationship between the hand and the spoon. This would manifest as greater motor activation in response to the incongruent grasp because the ensuing eating action would require an update of existing motor programs, as in Stapel and colleagues' (2010) work. Such a result would indicate that mirror system function is predictive in infancy, that semantic or conceptual aspects of action modulate it, and that it is affected by action planning ability. It was further hypothesised that there would be no group differences at the time of eating but that there would be an overall difference in mu desynchronization between conditions at this time – specifically that the incongruent action would elicit greater desynchronization, again because of the need to update existing action representations. Results in line with these hypotheses would illustrate that mirror system activation in response to self-feeding with tools incorporates semantic representations and has predictive elements prior to the end of the first postnatal year. These results would also elucidate the effects of action planning experience, in contrast to motor or visuomotor experience, on action processing in infancy.

4.2 Methods

4.2.1 Participants

Participants were 32 infants recruited from the database of interested families held by the Baby Research Centre at Radboud University, Nijmegen, where this study was conducted. Ethical approval for the research was granted in accordance with regulations for research with infants and children at Radboud University Nijmegen. At the time of the study, infant participants ranged between 9 months, 18 days and 10 months, 22 days in age. Eight infants were excluded for overall poor data quality. One infant was excluded due to experimenter error (no video recording of experiment). One infant was excluded for attending to insufficient trials without simultaneous movement (< 9 trials). With a liberal inclusion criterion of three trials per condition (e.g. Gerson, Bekkering and Hunnius, 2014), six further infants were excluded for not having sufficient artefact free trials. In the case of these six infants, sufficient good quality trials were available in the experimental conditions but not in the baseline condition.

4.2.2 Stimuli

Stimuli were a series of videos depicting actors picking up and eating from spoons. Actors were seated at a table with a spoon resting on a plate in front of them. Three actors were used, and for each actor a total of eight scenarios were filmed. The handle of the spoon was placed on the left or right side of the bowl; the actor used their left or right hand; and for visual variety to encourage a longer period of attentiveness from the infant, the spoon contained either vanilla yoghurt or chocolate mousse at the beginning of the video.

The actions were timed with a metronome to maintain consistency across actors and scenarios. Videos were each approximately 6 seconds long. At the beginning of each video, the actor was shown for one second (one metronome beat) sitting at the table with their hands concealed from view below it. During the second metronome beat, they reached for the spoon and on the third grasped it at the middle with a whole hand grasp. On the fourth beat they picked it up and brought it to the mouth, opening the mouth and inserting the spoon on the fifth beat and holding the spoon in the (closed) mouth on the sixth. Videos originally contained the removal and replacement of the spoon on the plate and the placing of the hands back below the table-top but these steps were removed during editing. Final videos were not exactly six seconds long because of naturalistic variations in the actors' timing of their movements. The average video length was 6.004 seconds, with a standard deviation of 22ms. Given that the trials were defined by specific time-points within the videos linked not to the metronome but to the actor's own actions, and given that each time point was equal in length and contained the same part of the action across trials, these minor variations could not have affected results.

The critical manipulation came from the relationship between the hand used by the actor and the orientation of the spoon. In half of all scenarios, the spoon was grasped in a radial grip. That is, the thumb and forefinger were nearest the bowl of the spoon, as in a normal means of using a spoon. The spoon was then brought to the mouth and inserted from the same side of the body as the hand used, resulting in a straightforward eating action. In other cases, the spoon was grasped in an ulnar grip, with the little finger nearest the functional end. In this case the spoon was brought across the midline of the body and the bowl inserted at the opposite side of the mouth from the arm used, resulting in an unusual endpoint that would be difficult to achieve from a motor standpoint (and actors did express the challenge of eating thus). Crucially, the shape and motion of the hand was identical during the reach for, grasp on and lifting of the spoon. Nothing about the action, until the movement of the arm to either side of the midline, was predictive of how it would proceed except for the relationship of the radial and ulnar sides of the actor's hand to the functional end of the spoon.

Videos were edited to remove sound and to restrict the view such that the actors were seen from the nose down. This was to prevent the actors' faces from being a distraction to the infants during the critical manual action, and to prevent any changes in stimulus processing that might result from facial ostensive cues from the actor or a lack thereof.. Example frames from the videos can be seen in Figure 4.1. Figure 4.2 depicts the motor similarities in the grasps in each video at the grasping time points, as well as the differences in the eating time points.

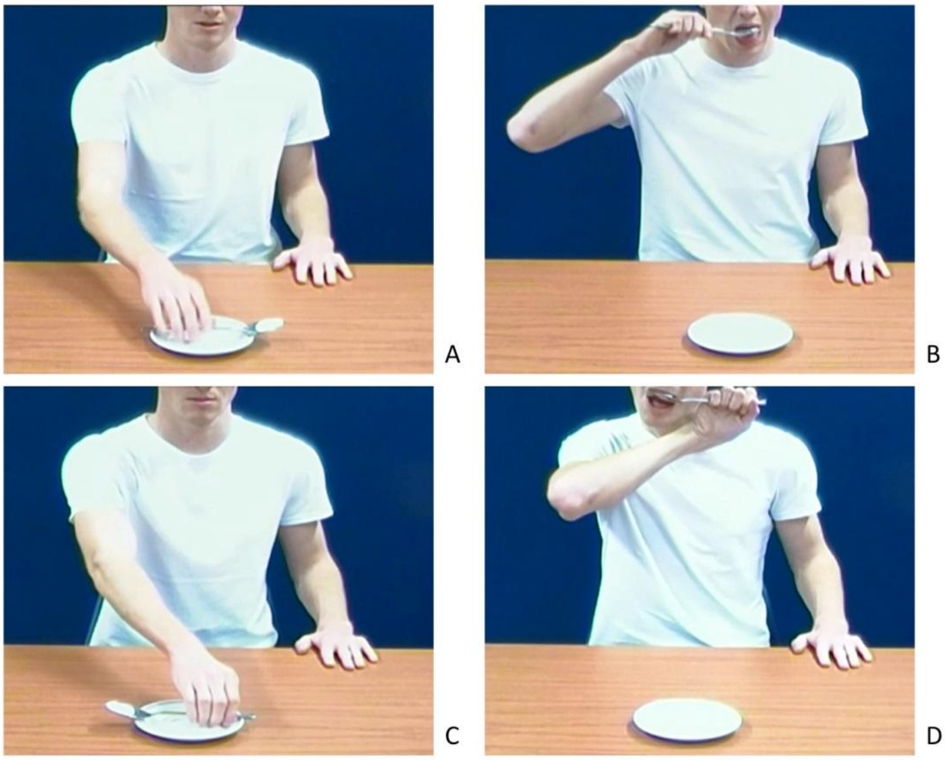

Figure 4.1: *A series of frames from the stimulus videos. A and B are frames from the same video. An actor grasps the spoon in a manner in which the radial hand orientation is congruent with standard use of the spoon (A). He then brings it to the mouth in a standard manner (B). Frames C and D come from a video depicting an incongruous, ulnar grasp orientation for spoon use (C), resulting in an unusual eating action (D).*

For the baseline trials, static abstract images were used. These were similar to those employed in previous infant action observation studies (Marshall, Young & Meltzoff, 2011; Saby, Marshall & Meltzoff, 2012). The mu desynchronization exhibited by infants in response to such images has been identified as one of a number of appropriate baseline measures for such studies (Cuevas et al., 2014). Images were displayed for an equal amount of time to the videos (6 seconds).

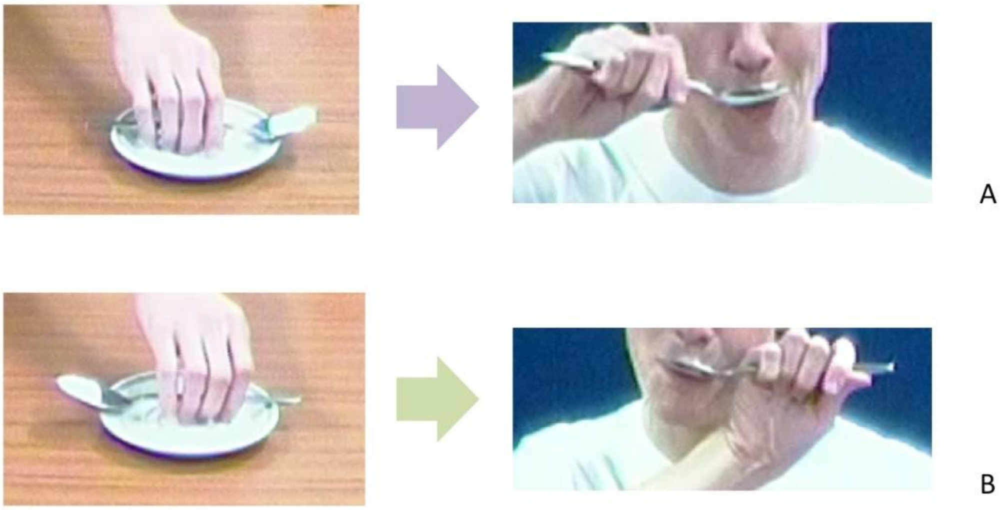

Figure 4.2: *Images showing close-ups from frames of the stimulus videos. In row A, the congruent stimuli are shown, with row B showing the incongruent stimuli. Note that the posture of the hand is similar in both cases except for its relationship to the functional end of the spoon. The final, eating posture differs in both hand posture and hand-spoon relationship.*

4.2.3 Procedure

4.2.3a EEG recording

The study contained two parts. In the first part, infants watched the video stimuli during EEG recording. In the second part, infants were presented with a range of spoons in a paradigm adapted from McCarty, Clifton and Collard (2001). Before the study began, infants were given some time to play and interact with the experimenters while the study was explained to the caregivers and consent to participate was given. Parents were given standard instruction for developmental EEG research – not to allow the child to move around excessively and to try to re-orient the child to the screen if necessary but not to engage in communication with the infant about the nature of the videos.

EEG data was obtained using a 32-electrode ActiCap EEG system (Brain Products, Munich) arranged according to the 10-20 system. The signal was rereferenced to the vertex during recording, amplified using a BrainAmp amplifier (Brain Products, Munich) and digitised at 500 Hz. Following application of the EEG cap and electrodes to the infant's head, electrodes were checked for impedance ranges and in the case of electrodes with poor impedance (above 60 kΩ) attempts to improve it were made (i.e. by improving adherence of the electrode to the scalp or adding additional electrolyte gel to the associated well). The infants and their caregiver were then brought from the experiment control room into the adjacent stimulus presentation room. The infant was seated on the lap of their caregiver in front of a computer monitor at a distance of approximately 50cm. The electrodes were connected to the amplifier at this time.

The infant's EEG was recorded using BrainVision Recorder (Brain Products, Munich). The ongoing EEG was monitored using this program from the control room. An overhead camera in the stimulus presentation room recorded the infant's behaviour, allowing for later rejection of trials in which the infant was moving or looking away from the stimuli. The video feed was also monitored from the control room, such that experimenters could be engaged by the caregiver for assistance or respond to issues during recording such as the infant pulling at the electrode cables. The experimenters were generally not present in the stimulus presentation room during the video portion of the experiment but entered for a small number of participants to reorient the infant's attention or address technical issues as on one occasion when the infant removed an electrode from the cap.

Infants were shown up to 84 stimuli, with equal numbers of the congruent and incongruent stimuli represented within those stimuli. Presentation order was determined using pseudorandomization software (Mix, van Casteren & Davis, 2006) with no constraints on randomisation procedure. Stimuli were presented using Presentation® software (Version 0.69, www.neurobs.com). Infant-directed instrumental music was played via speakers during stimulus presentation to aid infant attentiveness. On average, 56 (*SD* = 18.5) stimuli were presented before the infant became fussy and would no longer reliably attend to the screen. Following coding of valid trials, there were on average 31 (*SD* = 14.6) trials available for the grasping action and 28 (*SD* = 14.4) available for the eating action. Following rejection of trials containing artefacts, a mean of 13.4 (*SD* = 5.4) trials remained per condition for the grasping action and 11.4 (*SD* = 5.3) for the eating action. Given that the same baselines were used for each action, a mean of 6.3 baseline trials (*SD* = 2) remained in both cases.

4.2.3b Behavioural task

Following the conclusion of presentation of the video stimuli, infants were engaged in a motor planning task. A small table, a chair for the experimenter and an additional video camera were brought into the stimulus presentation room. The chair on which the caregiver and infant sat was turned perpendicular to the display set-up, and the table and experimenter's chair placed opposite them. The additional camera was set up with a slightly elevated side view of the experimenter, table and infant.

The task was based on the work of McCarty, Clifton and Collard (2001; 1999). Infants were presented with a series of up to twelve spoons with the handles oriented toward their left or right hand. The spoons were presented on the experimenter's hands such that the tip of the handle and of the bowl rested on either outstretched palm, with the bulk of the handle free to be grasped from above or below (Figure 4.3(A)). Although in the original work (McCarty, Clifton & Collard, 1999) a wooden holder was used to present most of the handled objects to infants, in this study the experimenter's hands were used as McCarty, Clifton and Collard (2001) noted that 9- and 14-month-olds were reluctant to grasp from the holder. They also stated that the potential restriction on underhand grips from experimenter-mediated presentation was not empirically important, as fewer than 4% of the grips produced by their sample of children up to 24 months were underhand.

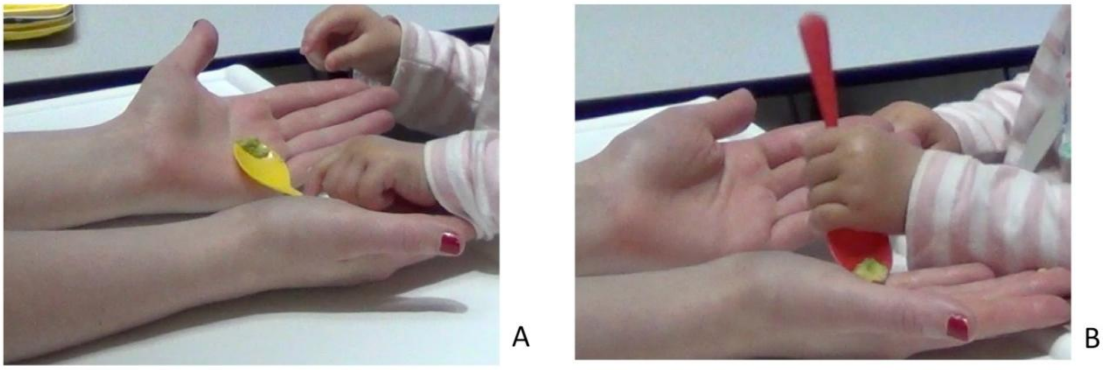

Figure 4.3: *Frames from experiment videos depicting experimenter's presentation of the spoon stimuli in accordance with McCarty, Clifton and Collard (2001). Frame A shows the infant preparing to execute a radial grip. Frame B shows the infant using an ulnar grip.*

Food was placed on the end of the spoon to encourage the infants to eat. At the time of booking the visit, caregivers were instructed to bring food that the infant liked which could be eaten from a spoon. Whereas applesauce was the most commonly used foodstuff in the work of McCarty, Clifton and Collard (2001), bananas and other mashed fruit, yoghurt and baby food were used in the present study. In the event that a caregiver forgot to bring food, fruit flavoured baby foods were available. Presented spoons were made of blue, yellow, red and green plastic, approximately 10cm in length. Food was scooped onto each spoon from the side that would face the infant (i.e. the right side of the bowl if the handle was to be presented toward the infant's left hand). Infants were presented with a maximum of twelve trials, with the orientation and colour of the spoon on each trial pseudorandomised using a software algorithm (Mix, van Casteren & Davis, 2006). The procedure was constrained so that within every four trials, each spoon colour was used once and each orientation was employed twice. This gave the experimenter opportunity to prepare four spoons in advance of beginning the task. It also ensured infants who did not engage in many trials would be presented with the handle near their preferred hand as often as the bowl was, helping to allay issues of infants underperforming because of stimulus presentation constraints. Although handedness is generally not observed so early in life, hand preferences in apprehension of handled tools have been observed (Connolly & Dalgleish, 1989; McCarty, Clifton & Collard, 1999).

Trials were ended if the infant did not interact with the spoon in any way within 20 seconds of presentation. Touching the spoon but not picking it up was considered an interaction. For all infants, the experimenter engaged the infants in mutual gaze and joint attention to the spoon and used simple words and phrases to engage the infant in the task, such as the Dutch for “for you” and “yummy”. The experiment was concluded if the infant did not interact with the spoon in any way for two consecutive trials. For those infants included in the EEG analysis, video recordings of the spoon use task were coded for which hand was used; which part of the spoon was grasped and in the case of grasps on the handle, in which orientation; how many touches occurred before the spoon was picked up; whether the spoon was transferred between hands after being picked up; and whether the infant put the spoon in their mouth (and if they put the handle in their mouth instead of the bowl). The included infants engaged with the spoon on an average of 10 trials from a possible 12, with a standard deviation of 2.8 trials.

4.2.4 EEG processing and analysis

Overhead video recordings were inspected using ELAN frame-by-frame video analysis software (Max Planck Institute for Psycholinguistics, Sloetjes & Wittenburg, 2008) to identify valid trials. The video recordings included an inset display of what was presented on the stimulus presentation monitor at the time of recording. Responses to the grasping time point and the eating time point were considered separately. This was because each could be considered as a conceptually different goal-directed action. It was also because infants did not reliably attend to the full video but did attend to parts of videos, and because in the baseline trials, infants would not watch the screen for the four to five seconds required for an appropriately long baseline measure for comparison. Consequently, valid trials for the grasping analysis were those in which the infant watched the video for one second before and one second after the actor’s first touch of the spoon. Valid trials for the eating analysis were those in which infants watched the video for one second before and one second after the actor's bottom lip touched the spoon. Valid trials for the abstract image baseline stimuli were those in which the infant's first look at the image lasted for two consecutive seconds. Additionally, trials were only valid if the infant did not engage in movement while watching the video.

During presentation of each video, the EEG data file was tagged with a marker indicating when the actor's hand first made contact with the spoon in each video and when an abstract image had been onscreen for one second. The time difference in each video between the first touch of the actor's hand on the spoon and the first contact of the actor's bottom lip with the spoon was known from inspection in ELAN software. Consequently, the number of EEG samples between the grasping event tag and the presentation of this eating event was known for each presented video. Each infant had two event files, one that contained the sample information for the grasping action and one that contained the sample information for the eating action. In the case of grasping, each file contained the sample numbers for each valid trial that corresponded to 850ms or 425 samples before and after the actor made first contact on the spoon with their hand. For the eating time points, these numbers were 850ms or 425 samples before and after the initial touch of the bottom lip on the spoon. The reason why each trial was defined as 850ms either side of the defining event was because this length ensured no overlap in the EEG recorded during each grasping trial and each eating trial.

Baseline trials were defined as follows. If the infant's first look at the baseline stimulus lasted continuously for at least two seconds, the trial was considered valid. The "midpoint" of the trial, comparable to the first touch of the hand on the spoon for the grasping trials and the touch of the bottom lip to the spoon for the eating trials, was defined as the time at which the infant had been looking at the stimulus for one second. These timings were all determined through use of frame-by-frame analysis in ELAN software. Periods extending 850ms before and 850ms after this one-second point were used as the baseline for the corresponding periods before and after the actor enacted the grasp on the spoon or put the spoon in their mouth..

EEG data were processed in Matlab (version 2014a, TheMathworks, Inc.) using the FieldTrip toolbox (Donders Institute for Brain, Cognition and

Behaviour, www.ru.nl/neuroimaging/fieldtrip). Each infant's EEG recording was bandpass filtered with highpass and lowpass thresholds of 1 and 50Hz respectively. A detrending procedure was applied. Each infant's EEG recording was then segmented in line with the event files. This data was inspected visually for artefacts and bad trials and bad channels were removed. Data for each infant were then rereferenced to the whole head minus the bad channels. A fast Fourier transformation was performed on the data with a 500ms sliding Hanning taper and spectral smoothing of 3 Hz. This provided mean power values for each frequency between 1 and 50Hz represented in the EEG data at each electrode for each trial. These methods are in accordance with standard procedures for event-related desynchronization studies (Gerson, Bekkering & Hunnius, 2014; Meyer et al., in press) This process was performed once for the grasping events and once for the eating events.

The average of these values for each infant at each of the electrodes C3, Cz and C4 for each of the frequency bands 6, 7, 8 and 9 Hz, before and after the defining grasp or eating event, in each of the three conditions (congruent, incongruent, baseline) was obtained, again once for the grasping events and once for the eating events. For each set of events, the ratio of each of these values for the congruent and incongruent conditions relative to the matched baseline value was found. A base 10 log transformation was then performed on the data, in line with standard practice for event-related desynchronization research (Cuevas et al., 2014). This means that negative values indicate less power and hence more desynchronization of mu activity relative to baseline. Positive values indicate more synchronisation relative to baseline. At this stage, one infant was excluded from all analyses for mu desynchronization values more than 3 standard deviations above the mean at the post-eating time point. Fourteen infants remained for inclusion in the analysis.

4.3 Results

4.3.1 Grasping time point

A 2-by-2 analysis of variance was conducted on the data relating to the actor's grasp on the spoon, with factors of condition and of time (before or after execution of the grasp by the actor). There was no effect of condition, F(1,13) = 0.102, p = 0.754, η^2_p = 0.008, nor was there an interaction between condition and time, F(1,13) = 0.301 p = 0.592, η^2_p = 0.023. There was an effect of time, F(1,13) = 4.878, $p < 0.05$, η^2_p = 0.273, with greater desynchronization prior to execution of the grasp than after (M = -0.06 dB, SE = 0.03 dB before, M = 0.04 dB, SE = 0.05 dB after; Figure 4.4).

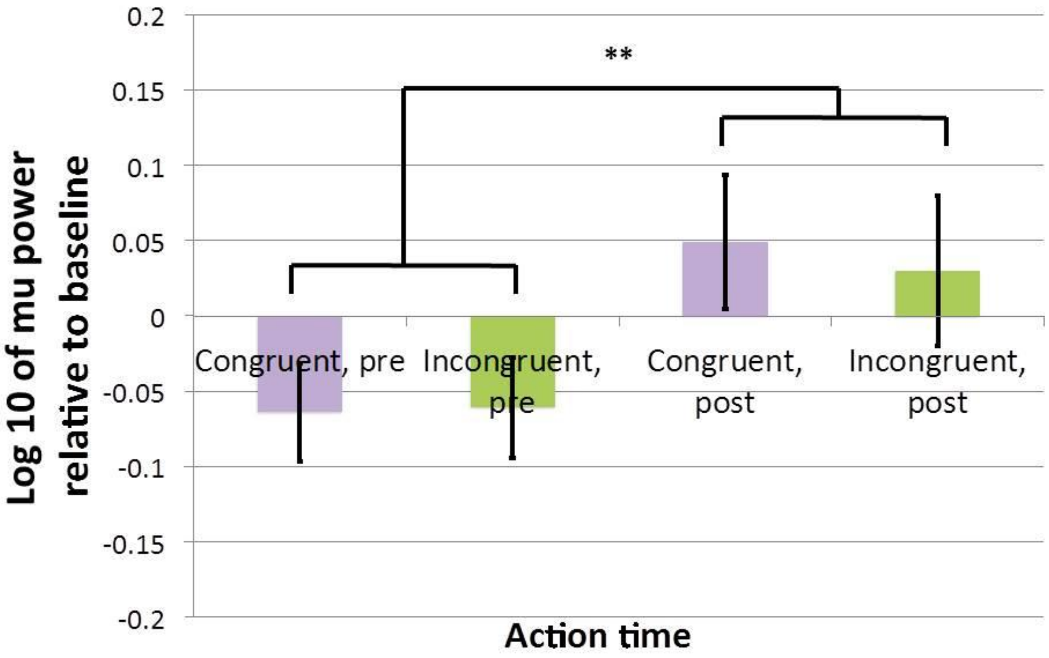

Figure 4.4: *Log10 of mu power during grasping period of stimulus videos relative to power during observation of baseline stimuli.*

Error bars represent standard error.

*** indicates $p < 0.05$*

4.3.2 Eating time point

The same analysis was conducted on the data corresponding to the placing of the spoon in the mouth by the actor, with the factor of time in this case referring to values before and after the execution of this action. There were no significant main effects of condition, F(1,13) = 0.045, p = 0.835, η^2_p = 0.003, or of time, F(1,13) = 3.703, p = 0.076, η^2_p = 0.222. There was no significant interaction between these factors, F(1,13) = 4.489, p = 0.054, η^2_p = 0.257. Although in the case of the interaction there was a trend towards significance, from inspection of Figure 4.5 it is clear that such an interaction would stem from a difference in one of the conditions between time points, and not a difference between both conditions at one of the time points.

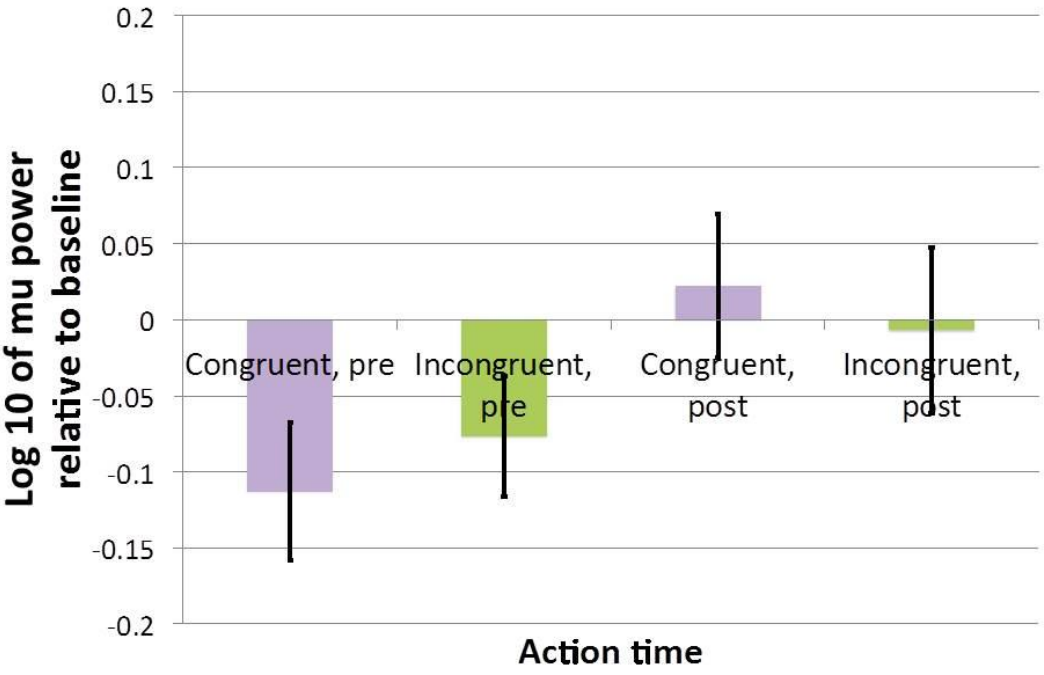

Figure 4.5: *Log10 of mu power during eating period of stimulus videos relative to power during observation of baseline stimuli.*

Error bars represent standard error.

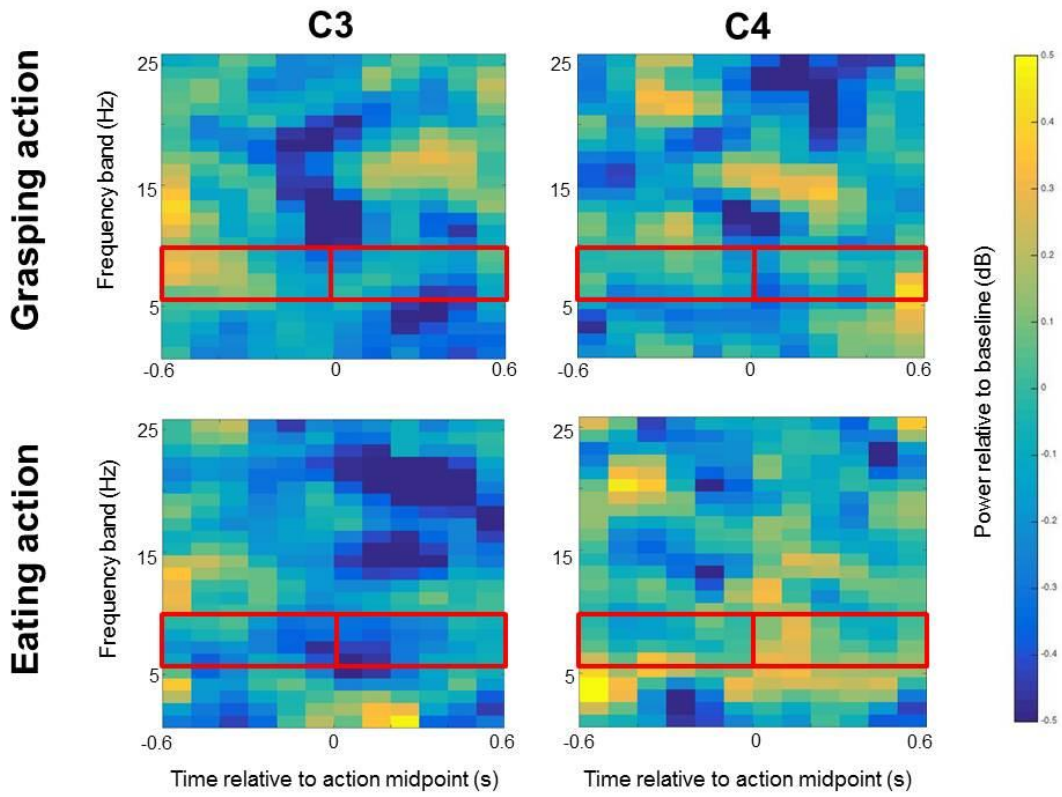

Figure 4.6: *Log10 of mu power during eating and grasping periods of stimulus videos relative to power during observation of baseline stimuli. Mean activity over electrodes C3 and C4 is represented. The analysed frequency bands, 6 Hz to 9 Hz, are represented within the red boxes. These boxes are split to show the "pre" and "post" action periods. Action congruence is not represented given lack of effects.*

4.3.3 Alternative analysis: Grasping and eating as parts of a single, continuous action

In an alternative analysis in which all four time points (pre-grasping, post-grasping, pre-eating, post-eating) were compared, similar results are borne out. A main effect of time is found with Greenhouse-Geisser correction applied, F(1.36, 17.68) = 4.141, $p < 0.05$, $\eta^2_p = 0.242$. Given the anticipation of predictive activation, greater desynchronization before the execution of each action was expected and no correction was applied to pairwise comparisons between before and after grasping and before and after eating. In this case a significant difference was found between pre- and post-grasping, $p < 0.05$, but not between pre- and post-eating, *p* = 0.076 (M = -0.095 dB, SE = 0.04 dB before, M = 0.01 dB, SE = 0.05 dB after), although the latter effect is marginal. Comparison between post-grasping (M = 0.04 dB, SE = 0.05 dB) and pre-eating (M = -0.095 dB, SE = 0.04 dB) is significant without correction, *p* = 0.028, but must be considered with caution given the lack of a priori hypothesis about differences between these time points. Corrected as one of three comparisons, the threshold of *p* < 0.017 is not met. Frequency maps for each action over selected central electrodes can be seen in Figure 4.6.

4.3.4 Correlations

A planning score was assigned to each infant on the basis of coding of his or her behaviour. The coded behaviours included the following:

- Mean number of spoon touches before picking up the spoon on trials in which the spoon was picked up.
    - Mean 1.56 touches, standard deviation 0.77 touches.
- Mean number of transfers between hands per trial in which the spoon was picked up.
    - Mean 0.61 transfers, standard deviation 0.56 transfers.
- Proportion of presented trials in which the spoon was picked up in the correct orientation and the same orientation was maintained throughout the trial.
    - Mean 35.8% of trials, standard deviation 21.3%.
- Proportion of all possible trials in which the spoon was not picked up.
    - Mean 18.37% of trials, standard deviation 28.38%.
- Proportion of presented trials with no eating from the spoon.
    - Mean 61.12% of trials, standard deviation 32.29%.
- Proportion of presented trials in which there was no eating from the spoon OR the handle was placed in the mouth first.
    - Mean 66.82% of trials, standard deviation 27.4%.

Table 4.1 indicates that many of the factors are related to one another but are not universally correlated. The proportion of presented trials with no eating, and the proportion with erroneous attempts to eat or no eating, correlate with one another (as might be expected). This pair of factors each correlate with the number of trials on which the spoon was not picked up, which again makes sense as without pick-up there can be no eating. This pair of factors also correlate with the mean number of touches executed on the spoon before pick-up per pick-up trial. Finally, a marginal trend is seen in the relationship between trials with no pick-up and the mean number of transfers on pick-up trials, with more transfers associated with fewer no pick-up trials.

These metrics were correlated with each infant's motor activation score at each of the time points for each of the actions. To get the motor activation score, the log of the ratio of the mu power relative to baseline for the incongruent condition was subtracted from the congruent condition. A more positive score therefore means more motor activation in the incongruent condition (relative to baseline) than in the congruent condition (also relative to baseline).

Given the hypothesis that greater motor activation during incongruent relative to congruent actions would be found for infants with more established motor representations or better motor planning skills, one-tailed bivariate correlations were performed. In the case of transfers between hands, a two-tailed correlation was performed given that transfers of objects can be considered "sophisticated manual actions" (p. 129, Soska, Adolph & Johnson, 2010) or an indicator of poor action planning (McCarty, Clifton & Collard, 2001; 1999). Data satisfied parametric assumptions and consequently Pearson's correlations were performed on all metrics and all periods of the observed action. Results are shown in Table 4.2.

Results indicate various relationships between motor activation in response to eating from spoons and the infant's own motor planning ability. Specifically, it is shown that infants who pick up a spoon with fewer touches (greater ease, a more rapidly formed plan) are those who show a larger difference between the response to congruous and incongruous grasps on the spoon as the actor brings the spoon to the mouth (Figure 4.7).

Table 4.1: *Correlations between all motor planning factors.*

Factor	*Mean no. touches*	*Mean no. transfers*	*Trials with correct orientation from pick-up to conclusion*	*Trials with no spoon pick-up*	*Trials with no eating*	*Trials with no eating or eating error*
Mean no. touches	1	-0.248	0.0003	0.298	0.633**	0.616**
Mean no. transfers	-0.248	1	-0.346	-0.497*	-0.272	-0.183
Trials with correct orientation from pick-up to conclusion	0.0003	-0.346	1	-0.35	-0.354	-0.4
Trials with no spoon pick-up	0.298	-0.497*	0.35	1	0.558**	0.506**
Trials with no eating	0.633**	-0.272	-0.354	0.558**	1	0.869**
Trials with no eating or eating error	0.616**	-0.183	0.4	0.506**	0.869**	1

** indicates significance at $p < 0.05$ level for one-tailed Pearson correlations.

* indicates $p < 0.1$ for one-tailed Pearson correlations, non-significant but noted for marginal trends.

Table 4.2: *Correlations between each factor and size of difference in mu between responses to congruent and incongruent actions.*

Factor/**period**	**Grasp, pre**	**Grasp, post**	**Eat, pre**	**Eat, post**
Mean no. touches	r = 0.157	r = -0.066	r = -0.815**	r = -0.347
Mean no. transfers	r = -0.065	r = 0.575$^{\#\#}$	r = 0.117	r = -0.195
Trials with correct orientation from pick-up to conclusion	r = -0.139	r = -0.284	r = -0.222	r = 0.513**
Trials with no spoon pick-up	r = -0.055	r = -0.238	r = -0.231	r = -0.526**
Trials with no eating	r = 0.241	r = 0.274	r = -0.338	r = -0.501**
Trials with no eating or eating error	r = 0.449*	r = 0.355	r = -0.319	r = -0.319

** indicates significance at $p < 0.05$ level for one-tailed Pearson correlations.

$^{\#\#}$ indicates significance at $p < 0.05$ level for two-tailed Pearson correlations (i.e. $p < 0.025$).

* indicates $p < 0.1$ for one-tailed Pearson correlations, non-significant but noted for marginal trends.

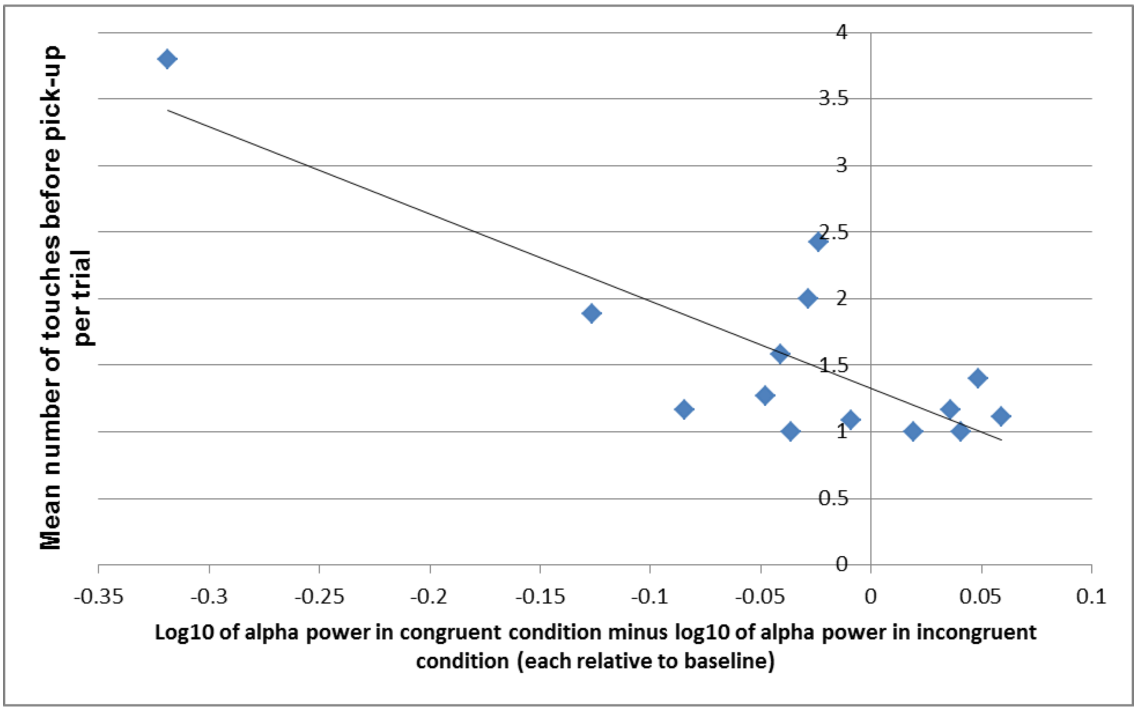

Figure 4.7: *Inverse correlation between the number of touches on the spoon before picking it up per trial, and the difference in mu desynchronization between congruent and incongruent conditions before the spoon is placed in the mouth.*

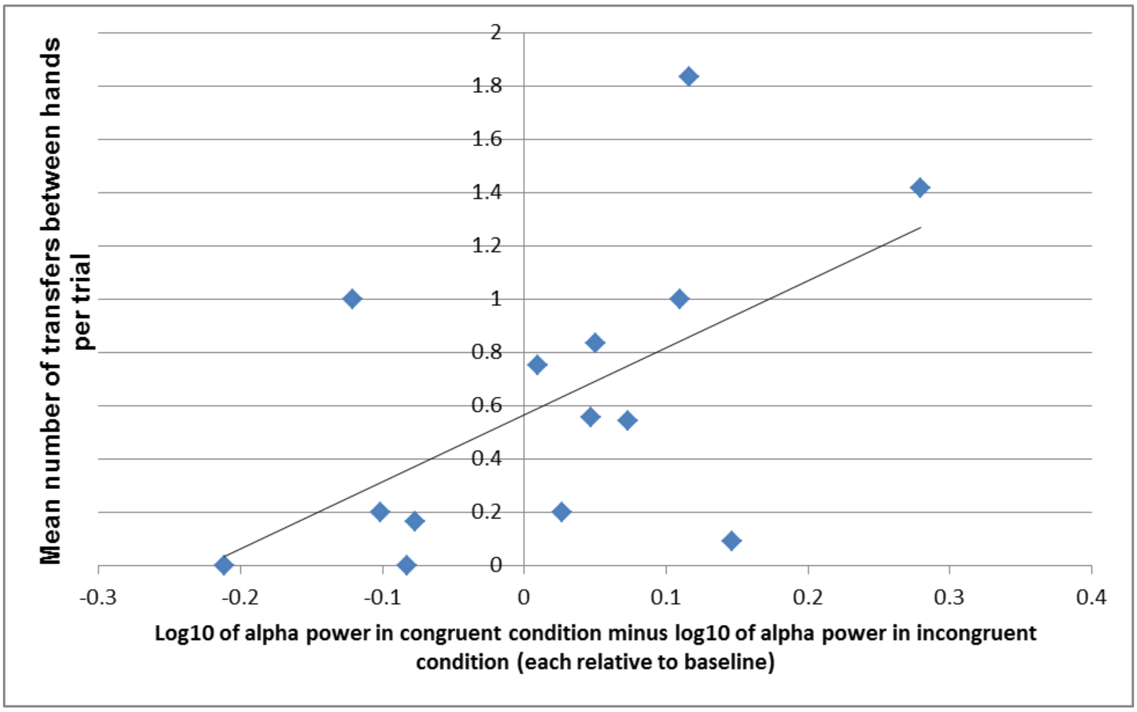

Figure 4.8: *Correlation between the number of transfers between hands per trial and the difference in mu desynchronization between congruent and incongruent conditions after observed grasp execution.*

Those infants who execute a greater number of transfers of the spoon between hands (e.g. to get it into the preferred hand or into the correct orientation for eating) show a larger difference in the response to the observed grasps on the spoon after the grasp has been executed (Figure 4.8). Infants who engaged with more trials and picked the spoon up on those trials show a larger difference in the response to the observed actions after the spoon has been placed in the actor's mouth (Figure 4.9), as do infants who succeed in eating from the spoon (Figure 4.10). Finally, infants who picked up the spoon in the correct orientation (a radial grip) and held it in that orientation throughout the trial also showed a larger response to the incongruent than congruent action after the spoon has been placed in the mouth (Figure 4.11).

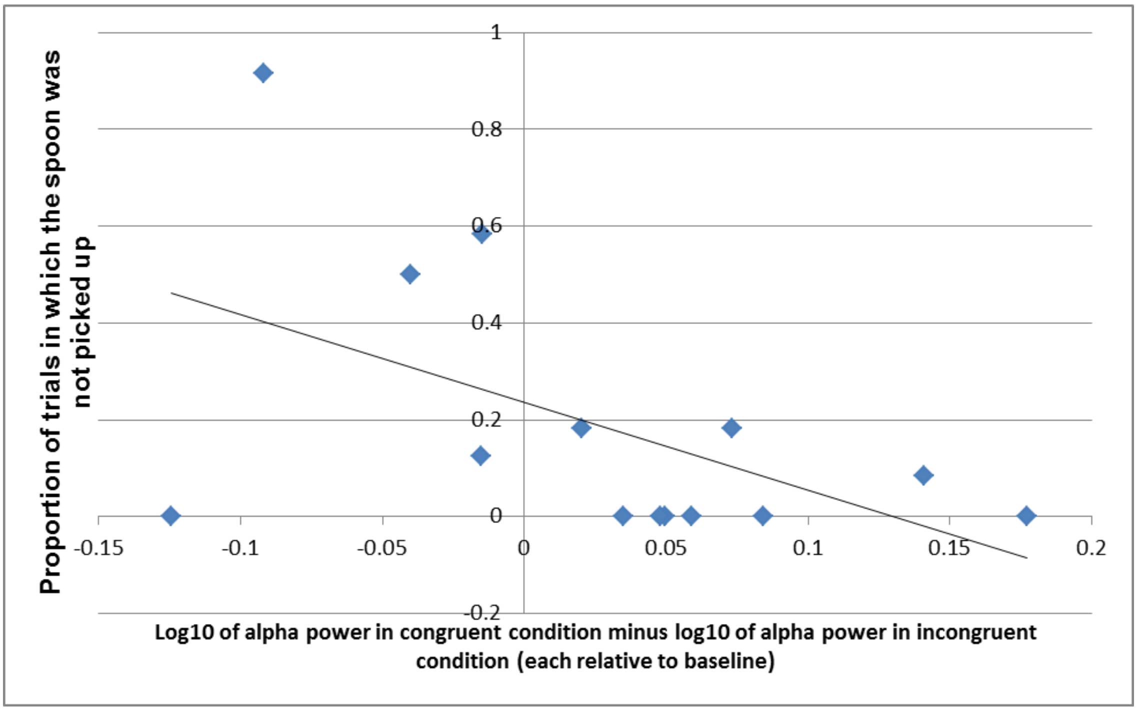

Figure 4.9: *Inverse correlation between the proportion of total trials in which the spoon was not engaged with, and the difference in mu desynchronization between congruent and incongruent conditions after the spoon is placed in the mouth during the observed action.*

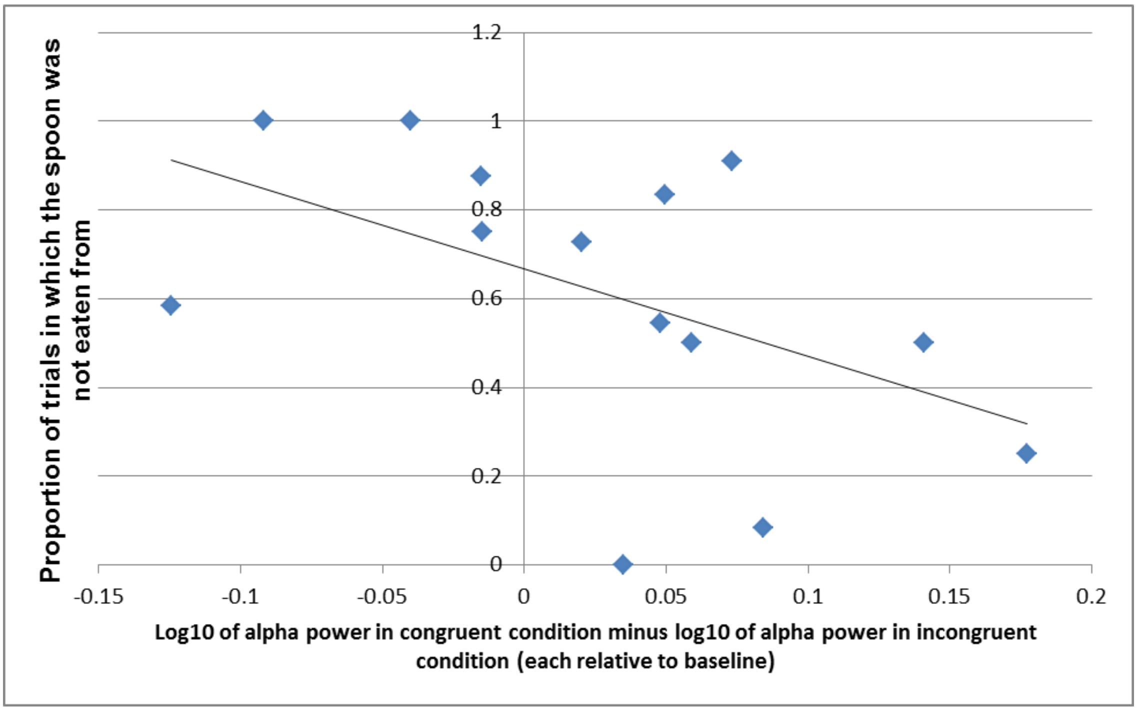

Figure 4.10: *Inverse correlation between the proportion of total trials with no eating, and the difference in mu desynchronization between congruent and incongruent conditions after the spoon is seen placed in the mouth.*

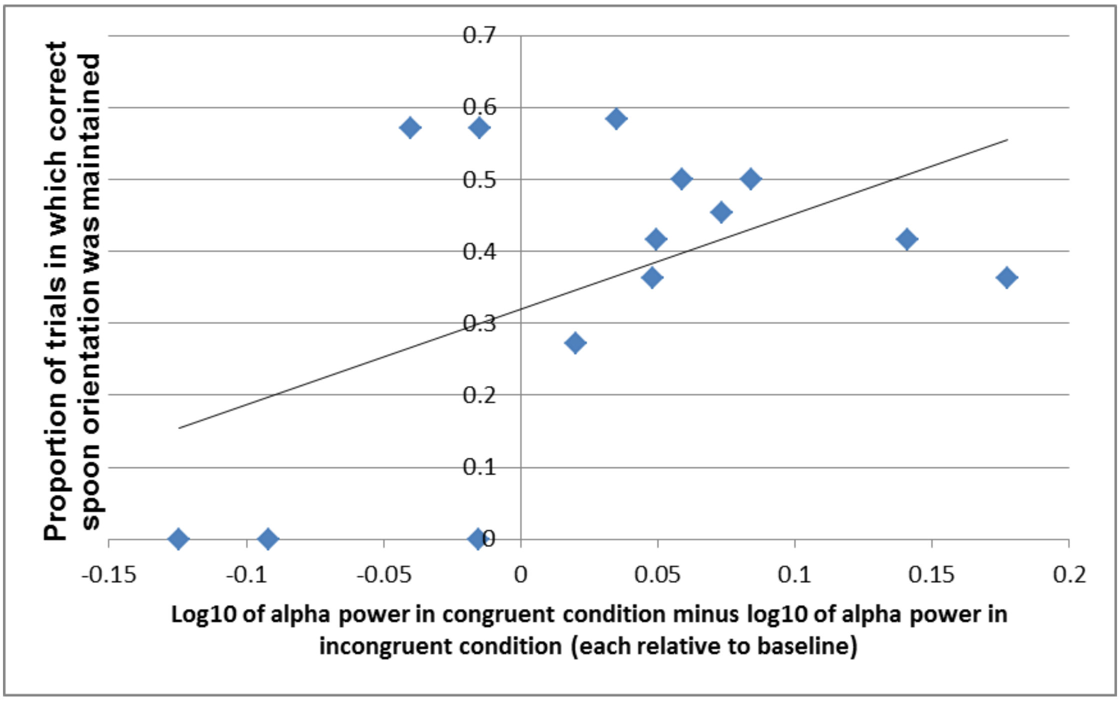

Figure 4.11: *Correlation between the proportion of presented trials in which the spoon was picked up and maintained in the correct orientation, and the difference in mu desynchronization between congruent and incongruent conditions after the spoon is placed in the mouth in the observed action.*

4.4 Discussion

The results of this study indicate that mirror system activation around ten months of age does not differentiate between motorically similar but semantically distinct actions, as shown by the results of the analysis of infant responses to the grasping actions. There were also no differences in activation in response to the congruent and incongruent eating actions despite the strong motor differences in execution of the action, that is, the need to bring the arm across the body into an unusual posture to execute the incongruous eating action. Results did show that mu power increases after execution of a grasp, reaffirming the predictive nature of mu desynchronization and the step-wise means by which infants perceive action.

Some patterns emerged in the relationship between the size of the difference in motor activation between conditions and the infants' abilities to plan tool-mediated self-feeding actions. After observing the execution of the grasp on the spoon, infants who were better at planning self-feeding actions and engaged in more self-feeding showed a greater degree of motor activation for the incongruent than the congruent action than those who were not as good as planning actions and did not engage as frequently. However, given the small number of infants in the sample, this result must be discussed with caution. There were no effects prior to the execution of the grasp, indicating that infants at this age cannot process the congruence of an ensuing self-feeding action on the basis of grasp orientation alone, even if their motor systems are responding to the reach.

Interpretation of the mu desynchronization results as emergent exclusively from motor activation must be approached with caution. Although previous research has relied upon analysis of central and fronto-central electrodes only (Stapel et al., 2010) to draw similar inferences, without a comparison point from other scalp regions it is difficult to draw conclusions specific to sensorimotor brain regions. Recent conceptions of mirror system function refer to general associative cortex as a potential source (Cook et al., 2014), suggesting that non-motor regions are a valid source of such activation. Other EEG research suggests that there is desynchronisation in frontal and parietal as well as central regions during observation of an action, whereas central desynchronisation only is seen in response to performance (Marshall, Young & Meltzoff, 2011). Thus what can be said about the results is that the activation seen is central desynchronization in response to a grasping action prior to its execution, which synchronises past baseline levels following that execution. This activation cannot be said to be either exclusively or non-exclusively central on the basis of the analysis performed. Nonetheless, a pattern is seen in the degree of activation relative to the "congruence" of the action, dependent on the motor planning and self-feeding performance of the child. This suggests a relationship between motor processes and processing of the stimuli in question. Whether this relationship is dependent on mirror system function (e.g. Southgate et al., 2010), on visuo-motor mapping (e.g. de Klerk et al., 2015) or on a more general interaction between developmental progress in different domains (e.g. Soska, Adolph & Johnson, 2010) cannot be inferred from the present analysis.

4.4.1 Overall processing of grasping and eating

One clear result from the data is that infants showed greater mu desynchronization in response to the grasping action prior to the execution of the grasp than after. This result affirms an aspect of the mirror system that has previously been suggested to exist in infancy. That is, mirror system activation is predictive or preparatory, not in the sense that it involves a preparation to perform the same action as observed (Gallese et al., 1996), but in the sense that it is stronger before the execution of the intended grasp. Previous infancy work by Southgate and colleagues (2010) has illustrated this. Nine-month-old infants exhibited mu desynchronization in response to reaching actions even when the action conclusion was occluded, indicating that infants could predictively infer the goal-directed nature of the action.

Strongly related to the present results, Southgate and colleagues (2009) found that during observation of reach-to-grasp actions, 9-month-olds exhibit an initial desynchronization of mu power upon appearance of the reaching hand. Following a brief rebound, there was sustained motor activation as the hand held and removed a grasped object. By splitting the measured time period in the present study into before and after the execution of the grasp, it was shown that for 10-month-olds, encoding of a reach-to-grasp action within the mirror system is predictive and mu power increases after the grasp has been executed even in the context of a continuing action. The marginal difference in mu desynchronization between the post-grasp and pre-eating periods may be akin to the rebound found by Southgate et al. (2009), suggesting, in line with previous research, that actions are perceived as delineated sequences of multiple stages (Baldwin et al., 2001; Pace et al., 2013; Reid et al., 2007). Thus the actor's behaviour, from spoon pick-up to eating, is not perceived as a holistic or fluid action but a series of goal-directed steps.

It is possible to consider these results in a visuomotor or associative account of mirror system function in development (e.g. Cook et al., 2014; de Klerk et al., 2015). Infants at 10 months may have extensive experience with grasping objects, and may have representations of the targets associated with those objects (e.g. Kochukhova and Gredebäck, 2010). However, they potentially have little experience engaging in subsequent, precise, target-directed use of the objects and the associated motor programs may not yet be present. Connolly and Dalgleish (1989) wrote that demand to self-feed with spoons generally emerges only in the second year of life, and McCarty, Clifton and Collard (1999) found that 9- and 14-month-olds tended to grasp a spoon without planning the subsequent steps of the action. The motor planning scores of the infants in this study were highly variable, indicating similar difficulties in tool planning and use for the present sample. Thus, 10-month-olds may show motor desynchronization only in response to the part of the action with which they have formed strong visuomotor or ideomotor associations, which is more likely to be grasping than self-feeding.

4.4.2 Action planning

The relationships between infant action planning and motor activation between conditions were multifaceted. To restate, a larger difference in mu desynchronization (relative to baseline) for incongruent than congruent actions, indicating attribution of greater processing resources to the unusual or less predictable action, correlated with most of the motor planning factors measured but at different stages of the observed action. The size of this difference at the time immediately after the actor had grasped the spoon correlated with the mean number of times infants transferred the spoon between hands in each trial. As the spoon was being brought to the mouth, activation difference correlated inversely with the mean number of touches the infant executed on the spoon before grasping it. Finally, after execution of the eating action, it correlated inversely with both the proportion of trials in which the infant did not pick up the spoon and the proportion of trials in which the infant did not eat from the spoon.

Integrating the presence of a rebound after grasping and the perception of actions as a series of sub-steps with the finding that infants who engaged in more transfers of the spoon between hands showed a larger difference in between-conditions motor activation after grasp execution adds nuance to the visuomotor account described above. As stated previously, infants process actions as sequences with sub-steps and natural junctures (Baldwin et al., 2001; Reid et al., 2007). This does not mean that infants perceive these junctures as action conclusions. Much research shows that infants in the latter half of the first post-natal year generally look to actors’ mouths after a spoon or cup has been grasped (Hunnius & Bekkering, 2010; Kochukhova & Gredebäck, 2010; Stapel et al., 2010), indicating that they anticipate further action. One might expect that the ability to perform an action fluidly, without needing to adjust the grasp on a tool, would be associated with mirror representations that might incorporate the reach-to-grasp on the spoon as part of a single, eating-directed action rather than its own action. Consequently, it might be expected that motor activation would be sustained after the grasp, particularly in the incongruent condition (in accordance with Stapel et al., 2010), by those infants who perform actions fluidly.

The actual results suggest that the opposite is correct. There was no significant inverse correlation between number of transfers and proportion of trials in which the spoon was grasped correctly to begin with. That is, infants who transferred the spoon more often did not necessarily do so because they picked it up incorrectly in the first place. Thus more transfers may illustrate, as Soska, Adolph and Johnson (2010) suggest, greater motor ability. The behaviour of the infants may have incorporated exploration of and curiosity about the object as well as goal-directed action. For these transferring infants, the size of the rebound was smaller for the incongruent grasp than the congruent. Thus transferring was associated with a difference in step-wise processing of standard and unusual actions. Either unusual grasp execution was not perceived as a juncture in the same way as congruent grasp execution, or this is evidence of the kind of enhanced processing of novel but reproducible action relative to standard action seen in Stapel et al. (2010). The results might be explained within a visuomotor account of developing mirror system function. Infants who are more adept at manipulating handled objects or who have more experience of re-evaluating and adjusting tool-mediated actions may have stronger visuomotor associative encoding of the natural junctures in action. This encoding might drive differential processing of actions that conform to or violate standards at the time of the juncture (e.g. Baldwin et al., 2001).

This result can also be accounted for in accordance with the predictive coding account of mirror system function (Kilner, Friston & Frith, 2007). For the group overall, the mu rebound after grasp execution may have been driven by a strongly entrenched representation of grasp, meaning that a Bayesian prediction was generated before grasp execution. The correlation between difference in motor activation between conditions and transfer of the spoon suggests that infants who were more motorically adept may have detected a mismatch between their representation of spoon use and the observed execution in the incongruent condition and generated more iterations of the action prediction within the Bayesian mirror system network. Given that there was no overall effect of condition this suggestion is speculative.

The other correlations between motor activation and motor planning can be accounted for more directly. Infants who touched the spoon more often before picking it up (suggesting indecisiveness or slowness in generating an action plan) showed a smaller difference in motor activation between conditions in the pre-eating stage than infants who were better at planning. This suggests that as the congruent or incongruent conclusion of the action becomes evident via cues other than grasp, better planners tend to show greater motor activation in response to the incongruent than the congruent action, in line with the work of Stapel et al. (2010). At the conclusion of the action, when the difference in action congruence is evident, infants who picked up the spoon and who ate from it more often showed more motor activation in response to the incongruent action relative to the congruent action, as did infants who picked up and maintained the spoon in the correct orientation to begin with. The emergence of these correlations at the pre- and post-eating stages only suggest that motor cues other than grasp, such as cross-body movement and the proximity of the spoon to the (mouth) target were employed by the better action planners to distinguish between the congruent and incongruent actions. These results point to an association between representation of observed actions and action planning that is likely to be general to all tool-mediated actions rather than a specific visuomotor association with self-feeding. This is because fewer than 15% of the infant participants (4 of 32) had self-fed with spoons before participating in the study. Thus the more adept action planners may have been integrating visual experience of seeing others use spoons with their own motor experience of holding objects in different postures and identifying unusual actions, with reference to both motor and conceptual processing systems.

Others’ results indicate that mirror system development is tied to visuomotor experience (de Klerk et al., 2015). Although no overall effects of condition were found in the present work, this series of correlations suggests that as experience with tool-mediated action emerges, differences in how actions are performed on the basis of how tools are used begin to be encoded. It may be that the level of experience required is more substantial than that exhibited by the sample of infants in this study. An older age group with greater self-feeding experience may yield clarifying results, as work by Yoo and colleagues (in press) found developmental differences between nine and twelve months in whole-scalp mu desynchronization in response to tool-mediated actions.

4.4.3 Theoretical accounts

The lack of overall differences in response to the semantically congruous and incongruous actions can be explained along a number of dimensions. One potential explanation is that the mirror system is not responsive to tool-mediated action, as early work on the mirror system with non-human primates (Rizzolatti et al., 1996) found no mirror response to such actions. However, in this case the tool was novel to the monkeys. Spoons are familiar tools and by 6 months infants anticipate spoons being brought to the mouth (Kochukhova and Gredebäck, 2010). Furthermore, mu desynchronization in response to tool use has been found in infants of comparable age to those studied here (Southgate & Begus, 2013; Stapel et al., 2010; Yoo et al., in press). In the Stapel et al. study, it was also made evident that the function of a tool is incorporated into the motor representation of the action and that incongruous tool use elicits greater motor activation as the new action requires an update of previously held representations. In Chapter 3 of the present thesis, it was shown that although infants at 9 months perceive differences in the relationship between hands and objects on the basis of the object's shape, by 12 months of age they exhibit no neural evidence of differential attentional encoding of such grasps. It may be that the infants in the present study fell within the period of development in which hand-object relationships are not attended to. It may also be that the minutiae of the hand-object relationship in this study were difficult to encode, because there was no difference in hand shape between the stimuli as there was in the previous work in this thesis.

What is more puzzling is that there was no difference in mu desynchronization during the eating portion of the action, in which arm movement employed was quite different for the congruent and incongruent grasps and the motor profile associated with the incongruent tool-use action was unusual (as in Stapel et al., 2010). This may be an indication that infant encoding of action is largely goal-directed or teleological and that the infants in this study were attending to the accomplishment of the goal of eating, as conveyed by the spoon, and not the manner of achieving that goal. Southgate, Johnson and Csibra (2008) found that 6- to 8-month-old infants look longer at inefficient actions than biomechanically impossible actions, so it may be that the presence of a goal allowed infants to represent the action in a motoric manner despite difficulties in simulating the precise means of performing the action. Behavioural studies show that 12-month-olds can learn the functions of novel tools by observation but fail to employ those tools effectively (Elsner and Pauen, 2007), again suggesting that the lack of differential response to normal and unusual employment of a spoon may have occurred because infants' mirror responses are generated on the basis of the inferred goal rather than the performed action. This possibility again supports the predictive coding model of mirror system function (Kilner, Friston & Frith, 2007) with the most reliable aspect of the action – the goal – modulating the infants' response to the action whereas less reliable aspects – the means of holding the tool – have no effect.

This assumption can be supported by the correlations between motor planning factors and difference in motor activation between the incongruent and congruent actions. Infants who pick up the spoons more often, who do so with fewer initial touches and in the correct orientation, who are comfortable transferring the spoon between hands, and who succeed in eating from the spoon more often, show a larger difference in activation to incongruent relative to incongruent actions, predominantly after the grasp has been executed and the conclusion of the action has become evident from postural rather than purely manual factors. These better planners may have a stronger representation of the visuomotor or ideomotor aspects of a successful action end-point for eating from a spoon. No infant could reliably perform the action perfectly, that is, no infant could pick up a spoon in the correct orientation for eating from it and maintain it in that orientation throughout the trial (the individual highest percentage of trials with a grasp in the correct orientation maintained to trial conclusion was 58.33%). This may provide an explanation for why a relationship between planning skill and motor activation differences between conditions did not arise reliably throughout the entire observed action. The infants may not have had strong prior information about the correct way to hold a spoon, particularly for the initial grasp on the spoon, because they were not frequent or proficient users of spoons. Gerson, Bekkering and Hunnius (2014) showed that infants at 10 months exhibit greater motor desynchronization to sounds associated with actions they have performed than those associated with actions they have merely observed. Thus, motor experience and related prior information about actions are important for the generation of mirror system representations of such actions. It may have been that in the case of the present study, the kind of motor representation and experience required for differentiation of grasps was beyond the reliable experience level of the age group studied.

4.5 Conclusions

Results of the present study indicate that the operation of the mirror system at 10 months of age is goal-directed and does not incorporate information about the means by which the action is performed. In contrast to the predictions enumerated in the introduction, it appears that once a predictable goal is encoded by the infant on the basis of the action, the means of performing that goal are rendered secondary to the accomplishment of the goal itself, as in the work of Southgate, Johnson and Csibra (2008). We cannot draw precise conclusions about whether motorically similar actions elicit differential mirror system activation on the basis of their semantic components. This is because the spoon-feeding action shown to participants did not modulate mirror system activation even at the point at which there were motor differences between conditions (that is, when the spoon was brought to the mouth). However, the presence of correlations between motor planning skill and a larger difference in motor response between incongruent and congruent actions as the action conclusion became predictable (or was executed) tentatively suggests that with greater motor experience or stronger internal representations of action, differences in mirror system responses to congruous and incongruous grasps may emerge. In order to establish the development of the relationship between the motor and semantic components of the mirror system, a simpler action would need to be presented or a slightly older age group would need to be studied. McCarty, Clifton and Collard's (2001; 1999) work has shown changes in planning of self-feeding actions between nine, fourteen and nineteen months of age, changes that are promising for future study of the mirror system along these lines.

Results of the present study do show that during reach-to-grasp actions, infants exhibit motor activation predictive of the performed action. This activation rebounds towards baseline values after the grasp has been executed, even when the overall action is incomplete. This suggests that, in line with infant behaviour in which spoons are grasped and subsequently adjusted for eating, infants perceive actions as a series of steps that are processed separately. This assumption is supported by the renewed desynchronization of mu activity as the spoon is brought toward the mouth, indicating that eating is the goal of the action. In sum, more evidence has been added to the argument for predictive mirror system function in infancy (Southgate et al., 2010; 2009) and results indicate that with further study the relationship between motor and semantic processes in developmental mirror system function can be characterised with the same or a similar paradigm through examining infant capacities at different stages of development.

Chapter 5: General Discussion

5.1 Introduction to the Discussion: Revisiting the theoretical background

5.1.1 Why study the development of semantic processing to understand mirror system function?

Simulation of others' actions in a manner neurally homologous with one's own preparation or performance of similar actions is an often-recorded aspect of human brain function. The finding of "mirror neuron" or "mirror system" function in primates (Gallese et al., 1996; Rizzolatti et al., 1996), and in humans specifically (Fadiga et al., 1995; Iacoboni et al., 1999), can be thought of as a paradigm shift (Kuhn, 1996/1962) in psychological science. Precise characterisation of the human mirror system is in progress, with questions of its origin as phylogenetically ancient (Bonini & Ferrari, 2011; Gallese et al., 2009) posed against an associative learning account wherein domain-general architecture and processes support emergence of the mirror system (Cook et al., 2014; Heyes, 2010), and a moderating ideomotor account in which perception-action associations and related neural communications develop in an endogenously constrained manner (Brass, Bekkering & Prinz, 2001). Despite these unresolved etiological questions, the discovery of the mirror system has brought conceptualisations of the primate brain as an entity defined by social processes to the fore. For example, mirror system responses are seen as rapid, relational and automatic (e.g. Carr et al., 2003) whereas research prior to the mirror system paradigm shift characterised adult simulation of others' actions as intentional and elicited via bottom-up perception-action mappings (e.g. Decety et al., 1997). The former means of responding to others' actions has been applied to a plethora of topics in psychological research, with emotion perception, autism spectrum disorders, sign language and processing of music among those listed by Cook and colleagues (2014). Although the relationship to these topics is still under investigation, it is inarguable that the early mirror neuron work has caused a change in how perception of others' actions is approached in research.

The question of meaning, of semantics, is integral to the mirror system (Umiltà et al., 2001) and to action processing more generally (Amoruso et al., 2013; Decety et al., 1997). Meaningful actions are actions in which a particular goal is achieved, causally, and that goal is congruent with the specific tools employed and the context of the action. It is because of the expectancies generated by the context of an action and by the tool used (Sitnikova et al., 2008), by the orientation and appropriateness of that tool (Bach et al., 2009), and by the overall possibility of inferring a goal (Proverbio & Riva, 2009) that actions can be perceived as meaningful and that perception-action matching can occur. Thus, in order to understand how the mirror system develops, it is essential to study semantic processing of action as well as the emergence of motor resonance and action mirroring.

5.1.2 Differences in the developmental trajectories of semantics and motor processing – research to date

As often stated in this thesis, semantic integration of goals of familiar actions develops in the first post-natal year, as evidenced by the N400 ERP (Chapter 3, this thesis; Reid et al., 2009). In the same period, infants show increased attention to or enhanced encoding of actions that do not end at natural junction points (that is, after the completion of specific goals or sub-goals) via dishabituation (Baldwin et al., 2001) or increased frontal neural activity (Reid et al., 2007). "Rebounds" or increases in mu power following such junctures (Chapter 4, this thesis; Southgate et al., 2009) also highlight how they are used by infants to structure action. By 24 months of age, these kinds of action boundaries can be used as a general means of determining whether an action makes sense, and thus of processing novel actions semantically (Pace, Carver & Friend, 2013). The semantic processing literature focused on language development shows that novel meanings can be integrated in a rudimentary manner in the second post-natal year (Friedrich & Friederici, 2008) but also shows that low productive language skills at 30 months of age are associated with the absence of a (language) N400 effect at 19 months

(Friedrich & Friederici, 2006). It is not evident in this case whether development of underlying neural architecture allows behavioural acquisition, whether behavioural change drives neural development, or indeed whether the neural and behavioural development are different ontological means of conceptualising the same entity. Nonetheless, this work shows that for an entity such as language or action to be processed semantically, an initial developmental shift, indexed by the presence of the N400 ERP, must occur.

Evidence for motor responses to observed actions is found before the emergence of the N400 ERP (NIRS evidence at 6 months, Shimada & Hiraki, 2006; no N400 ERP at 7 months, Reid et al., 2009). Given that initial semantic evaluation of an action is integral for mirror system function (Gallese et al., 1996; Southgate et al., 2009; Umiltà et al., 2001), it is puzzling that mirror processing of action may occur prior to semantic integration of action goals. Indeed, work on the infant mirror system, albeit with age groups at which semantic processing of action is emergent, indicates strongly that only meaningful actions (as defined in section 5.1.1) elicit motor activation (Nyström et al., 2011; Southgate et al., 2009). Perception of action as meaningful or non-meaningful is evident in infancy. Infants process actions as causal, goal-directed entities that conform to a specific structure (Baldwin et al., 2001; Reid et al., 2007; Träuble & Pauen, 2011). Developmental research on motor activation shows that infants exhibit such activation in response to actions with a visible or inferred target (Southgate et al., 2009) and to actions with an effect causally generated by the actor (Nyström et al., 2011), and not to actions without targets, nor non-causal actions. This shows, conceptually, that it is mirror system function that is being measured and not general motor resonance (Uithol et al., 2011). This theoretical puzzle – how to have neural evidence for mirror system function without accompanying evidence for semantic integration – motivated the work in the preceding thesis. The general objectives of the preceding work were to understand how semantic and motor processing of action develop in infancy, to understand how action production skills play a role in action perception and processing along these trajectories, and to understand how infants learn to interact with tools. The more specific aim of the work was to understand how these means of action processing develop in conjunction with one another and whether one can operate without the other. Hand-object interactions were used as the platform from which to investigate these systems.

The main conclusion to be drawn from the present work is that the development of mirror system function and the expansion of semantic action processing in infancy are interconnected in ways that are not easy to disentangle. The development of each system is not yoked to the other but they still show relationships, albeit weaker ones than are found in behavioural research. In the following sections, the specific findings of the work will be discussed and integrated with one another and with the wider field of research.

5.2 Summary of findings

5.2.1 Existing evidence for integration of social, semantic and motor action processing in infancy

A broad review of the relevant developmental perception, cognition and cognitive neuroscience literature conducted in Chapter 1 showed that conceptual links exist between social, semantic and motor resonance frameworks of infant action processing. Particular note was made of how measures of motor resonance are affected by action semantics, and how indicators of semantic processing incorporate motor aspects of actions. Examples of the former include studies of motor activation in which infant mu desynchronization differs between congruent and incongruent actions, such as when an action has no goal (Southgate et al., 2010) or has a goal that does not match the implicated tool's function (Stapel et al., 2010). Examples of the latter include studies in which infant perception of incongruities in hand-object relationships, whether in relation to grip size (Daum et al., 2011) or grasp type (Loucks & Sommerville, 2012), is associated with motor experience.

The identification of these empirical relationships between semantic and motor processes in developmental action perception was brought into the context of mirror system theories, in which motor and semantic processes are engaged and feed into one another (Cook et al., 2014; Gallese & Goldman, 1998; Kilner, Friston & Frith, 2007; Uithol et al., 2011). These links justified investigation of the core questions of the thesis, which target how the semantic processes and motor processes employed in action perception develop, if employment of one process depends on activation of the other, and if they are manifestations of the same process at different levels of ontology.

5.2.2 Semantic processing of tool use in the absence of differences in motor aspects of hand-object relationship

In Chapter 2, we aimed to examine how semantic processing of novel tool use occurs when there is minimal input from ideomotor or motor simulation processes. Two groups of 16-month-old infants were presented with stimuli showing the use of a novel dual function tool on two different novel objects, producing distinct but similarly salient actions on each one. Previous studies with a dual function tool showed that 20-month-olds could rapidly learn to predict on which of two novel objects the tool would be used, on the basis of how the tool was grasped (Paulus, Hunnius & Bekkering, 2012). The intention of this work was to examine the extent to which the infants' predictions were aided by perception-action matching on the basis of those grasps.

To realise this intention, the dual function tool was created in such a way that it could be held in a whole-hand grasp for each function, with orientation determining its intended use. Two actors were depicted using the tool, each using a different end of the tool on one of the two novel objects. We anticipated that, given infants' strong encoding of goals (Hunnius & Bekkering, 2010; Woodward, 1998) and their tendency to associate specific actors with goals but not transfer those goals to another actor (Buresh & Woodward, 2007), using different actors would facilitate encoding of function. Infants were shown the tool's functions and actors' goals via demonstration videos, and then shown side-by-side critical images in which the actor held the tool in an orientation that matched (goal-congruent) and an orientation that did not match (goal-incongruent) the use appropriate to their goal. Infants' looking times to the critical images were measured.

Results of both experiments showed that infants did not form an association between the orientation of the tool and its function. They did not encode the ulnar or radial relationship between the actor's hand and the tool part that actor used. Rather, they formed an association between the tool part itself and the actor via the actor's demonstrated goal, and during presentation of critical stimuli they looked longer at the tool part they had not encoded in relation to that actor. These results suggest that when the functions of a dual function tool cannot be distinguished on the basis of perceptual-motor mapping, 16-month-olds do not attend to the relationships between hand and tool features that might facilitate prediction of tool use.

5.2.3 Semantic processing of motor differences without manipulation of the action's goal

Chapter 3 describes a series of experiments in which semantic processing of grasp information was measured. Goals of actions are processed semantically from about nine months of age (Reid et al., 2009) but the meaningfulness of an action lies in more than its target (e.g. Bach et al., 2009; Sitnikova et al., 2008). The means in which a tool is held can determine the meaning of an action (Paulus, Hunnius & Bekkering, 2012). In order to investigate how grasp is processed semantically, and to do so independently of goal manipulation, stimuli were created in which actors grasped cups in a manner congruent or incongruent with the overall shape of the cup.

An initial study with adults established that this aspect of action is processed semantically in the adult brain, as a fronto-central negativity in the N400 time period was found to distinguish between congruent and incongruent grasps on the cups. Results from 9-month-olds indicated that are differences in how infants process congruent and incongruent grasps. A larger Nc component for the incongruent grasps suggested increased orienting of attention to these stimuli. This effect cannot be attributed to an overall ability to process how hands and objects fit together but is likely driven by visual experience of seeing others hold cups in specific ways. A larger P400 component for the same stimuli suggested that the difference in attention to each stimulus category was driven by social factors. This is reasonable given that goal inference may be more difficult in the context of the less familiar grasps. No

N400 component was present. An N400 component was evident in the neural responses of 11.5-month-olds, indicating that grasps are processed semantically at this age. However, this component was not modulated by grasp. Consequently, the N400 effect was likely a response to the overall goal-directedness of the stimulus and not to the minutiae of the grasp. In contrast to the work of Reid and colleagues (2009) the component was seen in both conditions, indicating that the neural architecture underlying semantic processing of goal-directed action has matured by this age.

5.2.4 Motor processing of semantic differences in action in the absence of differences in motor aspects of hand-object relationship

In the final experiment described in this thesis, in Chapter 4, infants between nine-and-a-half and eleven months of age were shown videos of actions in which the motor components were identical (up to a particular time point) but the meaning of the actions differed. Specifically, the execution of a radial or ulnar grasp on a spoon was predictive of whether the spoon would be used in a standard manner or whether it would be eaten from in an unusual, motorically unfamiliar posture. It was hypothesised that all infants would show greater motor activation in response to the unfamiliar action at the conclusion of the action, indicating the need to update previously held motor representations of self-feeding in accordance with Stapel and colleagues' work (2010). It was also hypothesised that only those infants who were more capable of planning their own self-feeding actions, as measured in a self-feeding task, would show similar differences at the time of the grasp on the spoon. This would indicate that only those infants with strongly entrenched representations of grasps on handled objects would be able to predict an unusual ensuing action from the ulnar grasp.

Results indicate that infants did not encode the differences between the congruent and incongruent means of holding the spoon at any point from the initial grasp through to the completion of the action. This result may have arisen because the infants simply did not have much prior experience with self-feeding with spoons and consequently could not reliably represent the differences in the displayed action. One emergent result was that mu rhythm desynchronized before execution of the grasp, rebounded after completion of the grasp, and desynchronized again (a marginal effect) as the spoon was brought toward the mouth. This indicates three things. The first is that the significant difference between the pre-execution and post-execution stages of the grasping part of the action, but not between the eating parts of the action, suggests that grasping is represented more strongly by infants at this age, possibly as a result of more extensive motor or visuomotor experience with grasping than with tool use. The second is that the results reaffirm the predictive nature of mirror system function even in infancy (e.g. Southgate et al., 2010). The third is that they reaffirm that infants process goal-directed actions in terms of their sub-steps (Baldwin et al., 2001; Reid et al., 2007) and offer evidence for the neural basis of action parsing.. An additional finding from this work is that action planning and motor skill correlate with differences in activation during observation of congruent and incongruent actions, with greater planning and execution skills associated with a stronger response to the unusual action.. These results suggest that although no overall effects were found in the present study, differences might emerge in an older age group with more experience of action planning and stronger motor representations of tool-mediated action.

5.3 Theoretical implications

5.3.1 Demonstrated links and disjunctions between semantic and motor processing

The research conducted within this thesis indicates that the development of motor processing of action and semantic processing of action are not irrevocably linked. Tool parts can be associated with actors and goals in the absence of distinguishing motor information. Differences in motor aspects of action, such as in the relationships between hands and objects, are processed early in development. In the studies described here, such processing was not shown to be linked to grasp execution ability. Slightly later in development, as semantic processing of goal-directedness of action emerges, these differences in grasp are no longer encoded and again, no relationship to grasping ability was found. Finally, motor activation in response to observed action, strongly established by other work to be present by nine months of age (Nyström et al., 2011; Southgate et al., 2009, 2010), is not affected by semantic elements of grasp at this age. However, differences in responses to incongruent versus congruent stimuli are linked to action planning and motor ability, suggesting that semantic and motor processing of grasp do become linked as motor representations of actions are established via experience.

The disjunction in emergence of mirror processes and semantic processes referenced earlier was not explained by the work in this thesis. In fact, results suggest that specific semantic elements of action do not affect mirror system function before the end of the first post-natal year (Chapter 4), and that motor elements of action are not processed semantically at this stage (Chapter 3). Given the established “two-stage” model of mirror system function (Gallese & Goldman, 1998) and the fact that infants show differential motor responses to meaningful and non-meaningful actions (Nyström et al., 2011; Southgate et al., 2010), it is not correct to suggest that the mirror system operates in infancy without some form of semantic processing. Rather, results suggest that infants do not attend to the motor minutiae of goal-directed actions with familiar, single-function tools in the first post-natal year, or with novel, dual-function tools in the second post-natal year. Rather, it is possible that infants adopt a teleological stance (Csibra, 2003), that is, they attend to the goal of the action to give that action meaning. In the case of the first study (Chapter 2), this was the tool part used by the actor. In the case of the second study (Chapter 3), this was the execution of a grasp on a cup. In the third study (Chapter 4), this was the execution of a grasp on a spoon.

The lack of difference in response before and after placing the spoon in the mouth in this study may be due to weaker representations of precise, tool-mediated, self-feeding actions relative to whole-hand reach-to-grasp actions. Developing motor representations may also explain the results of Chapter 3. Without strong motor representations of the differences in power and precision grips, the ability of 9-month-olds to detect whether an observed hand posture is appropriate for the grasped object (as opposed to whether hand aperture size is appropriate) might be based on associative or attentional processes independent of motor activation. Given the results of Chapter 2, it is possible for infants to represent relationships between an actor's goal and the tool they employ without simulating the minutiae of the manual interaction between hand and object.

A final consideration is that infants rely on cues from others to structure their learning about the world (Reid & Striano, 2007). There are many studies demonstrating manifestations of this means of encoding information in infant brain activity, including studies showing that communication about object appearances via hands is processed differently depending on whether the hand is oriented in the direction of a previously displayed object or not (Bakker et al., 2015; Gredebäck, Melinder & Daum, 2010; Melinder et al., 2015). Given that all studies in this thesis contained human actors and were consequently social in nature, and that evidence of modulation of a "social" ERP component, the P400, was found in Chapter 3, results need to be considered within a social framework as well. In the following sections, the theoretical considerations of the work presented will be applied to models of action processing from infancy research and from mirror system research.

5.3.2 The teleological stance

Attending to and processing the manual minutiae of an action may be difficult, especially considering the need to simulate precise positions of digits in relation to the tool used, and precise gestural components, both of which are aspects of action that develop over an extended trajectory (Butterworth, Verweij & Hopkins, 1997; Corbetta et al., 2000). However, the 9-month-olds in Chapter 3 did show a differentiation between congruent and incongruent grasps, albeit not on a semantic level. Other research shows that detection of grasp differences develops between six and nine months of age, depending on the infant's motor skills (Daum et al., 20011), and that motorically adept infants process grasps in terms of function around ten months of age (Loucks & Sommerville, 2012). In the present work, it was when evidence of the semantic N400 component was found (Chapter 3, 11.5-month-olds) that differential processing of grasp via other components disappeared. This result suggests an overall shift in how infants process grasps occurring once actions are processed in terms of their semantic structure.

It indicates that although infants are sensitive to general differences in and novelty of grasping actions between eight-and-a-half and nine-and-a-half months of age, once they begin to process actions semantically, they no longer attend to elements of the action other than the teleological, that is, the goal. This teleological stance-driven semantic processing may explain the lack of effect of grasp on motor activation in the Chapter 4 experiment, as infants in this age range may be beginning to process action semantically and to attend to the overall goal to the omission of other elements. It also applies to the results of Chapter 2. Infants' encoding of the relationship between tool and object omitted the manual minutiae in the form of information about the orientation of the goal-congruent tool part. Instead, the association was formed between the actor and the tool part they used. This indicates a focus on the end-state of the action seen by the infants (particularly in Chapter 2, Experiment 2, in which the final demonstration video shot showed the tool in contact with the target), and not on the precise means of achieving that end state.

The interpretation of these results in relation to the teleological stance (Csibra et al., 1999) is deliberately sparse. Much of the focus of this thesis, particularly in Chapter 3, has been on encoding of action in the absence of factors that would alter the efficiency of that action. Consequently, the theorising underlying the thesis has incorporated factors other than efficiency and rationality. Six- to 8-month-olds infants might have found the efficient but biomechanically impossible actions shown by Southgate, Johnson and Csibra (2008) less unexpected than inefficient, possible actions, but infants at this age are aware of the constraints of human physiology. A P400-like neural response is seen in 8-month-olds in response to biomechanically impossible body schemas (Reid et al., 2008). Infants inhabit bodies and their perception of actions has been shown repeatedly to rely on bodily factors such as motor activation (e.g. Saby, Marshall & Meltzoff, 2012; Stapel et al., 2010) and representations of what one's body can do (Daum et al., 2011; Loucks & Sommerville, 2012). It is for this reason that when considering the results of the preceding studies in the context of infants having a teleological stance, the interpretations relates to encoding the action with primary focus on the end state, and not on efficiency (Csibra et al. 1999) or rationality (Gergely, Bekkering & Király, 2002). Indeed, given the definition of meaningful actions as actions with goals, it might be suggested that semantic processing of goals shifts encoding of action such that infants exhibit a teleological stance, instead of allocating attention to action stimuli on the basis of novelty. This shift is demonstrated in Experiments 2 and 3 in Chapter 3, as described in the first two paragraphs in this section.

Returning to questions of efficiency and rationality, we might suggest that the 16-month-olds in Chapter 2, the 11.5-month-olds in Chapter 3, and the 10-month-olds in Chapter 4 did not encode the differences in the hand-object interactions because the precise means of holding the tool in each case did not inhibit efficient performance of the action if the infants were ignoring the constraints of human biomechanics as in the work of Southgate, Johnson & Csibra (2008). However, the correlations found in Chapter 4 offer a refutation to this interpretation. These results suggest that infants who are better planners and more motorically adept show differences in how they encode the normal, easily performed congruent eating action, and the motorically more unusual or difficult incongruent eating action. It is not that attention to or encoding of differences in motor minutiae disappears permanently once semantic or goal-oriented encoding of action emerges. The adult results from Chapter 3 illustrate this, as in adult functioning the congruence of grasp is processed semantically. It appears that perception of differences in grasps diminishes once semantic processing of action begins, perhaps because of top-down allocation of attention to attributes of stimuli that define or predict the action’s goal. Then, as infants learn to plan and perform grasping actions with more aptitude, they incorporate the specific manual information into their representations of observed actions. The results of Chapter 2 can be accounted for in this manner as well. Actions involving dual-function tools require that, upon detection of the tool, the actor and the interaction between the two, one action representation much be activated and another inhibited. In the absence of precise manual information distinguishing between both actions, the action is represented in terms of its end-state. Nonetheless, the results of all three chapters indicate that although infants might represent actions in terms of their goals, as their own motor skills develop, attention to the efficiency of actions is supplanted by incorporation of motor representations.

5.3.3 The two-stage and predictive coding models

It is in Chapter 4 that we see how motor ability affects representation of actions on a conceptual or semantic level. Differences in activation were seen before versus after a spoon was grasped, but not before versus after the spoon was placed in the mouth. On the assumption that infants have more experience grasping objects directly than manipulating handled tools to perform actions such as eating, this result suggests that actions with stronger motor representations are better represented in the infant's mirror system. The motor planning results suggest that those infants who are better planners and more motorically adept show a greater divergence in their responses to typical or unusual means of grasping and eating from those spoons than less motorically capable peers. The relationships found were predominantly between motor planning and responses to the different types of action before and during eating, but the significant and marginal correlations found for the grasping actions, both of which are linked to transferring and manipulating the spoon rather than well-planned performance of action, suggest that motor ability helps to distinguish semantic differences in motorically-identical grasps that will results in motoric (and semantic) differences in later action performance.

Good action planning in infants could be attributable to having strong motor representations of tool use, and substantial motor abilities may result in the efficient formation of such representations. Given the patterns seen in Chapter 4, one might suggest that the re-emergence of processing of action minutiae by adulthood (Chapter 3), and their incorporation into semantic representations, could be driven by both visuomotor associations and action experience. Much of the emphasis of the two-stage conception of mirror system function (Gallese & Goldman, 1998) is on semantic representations of actions feeding into motor areas, such that once an entity is defined as a goal-directed action, the mirror system is activated. This model is supported by the extensive number of primate and infant studies cited in this thesis in which correlates of the mirror system are not elicited by actions with no discernible goal (Nyström et al., 2011; Southgate et al., 2010; Umiltà et al., 2001).

Conversely, the work in this thesis supports the more recent predictive coding model of mirror system function (Kilner, Friston & Frith, 2007), in which there is mutual activation in parietal, superior temporal and frontal motor areas, and motor representations can be fed back to modulate activation in the preceding areas. An example of this in prior infant research comes from the work and Stapel and colleagues (2010) in which mu desynchronization is stronger in response to actions with novel goals, indicating that as a mismatch was found between the motor trajectory of the actor’s motion and the motor trajectory usually elicited by a cup activation in the system was enhanced. Initial expectation of a particular motor trajectory would naturally be generated in the semantic systems further posterior but the motor mismatch may have been signalled in frontal motor areas.

As detailed in section 5.3.2, the work in this thesis shows that although infants are initially sensitive to differences in how objects are grasped, as semantic representations of action develop the emphasis shifts to the goal of the action. As infants learn to plan actions, they must represent motor specifics such as the orientation in which a handled tool must be grasped. Motor representations such as these could feed into the semantic representations of action, resulting at some later stage in development in the adult patterns found in Chapter 3, in which motor minutiae alter the semantic representation of tool use. Results in the present thesis showed no semantic processing of grasp at nine months, mirror system activation in response to overall grasp at ten months, and semantic processing of overall grasp at eleven-and-a-half months. Taken in conjunction with motor activation studies performed with nine-month-olds (e.g. Nyström et al., 2011; Southgate et al., 2010), we can suggest that semantic processing of action does not need to be present for mirror system activation to occur, as per the Gallese and Goldman (1998) model. The developmental trajectories of motor and semantic representations of action may be separate, despite the links between both systems. This possibility is supported by the predictive coding model of mirror system function (Kilner, Friston & Frith, 2007). Within the predictive coding mirror system, semantic representation of action does not flow unilaterally into motor activation. Each means of action processing is mutually modulated. Developing motor representations of tool-use actions might assist detection of semantic or conceptual differences in those actions, as shown by the correlation results in Chapter 4. This may occur before such actions are represented semantically or as such representations are in development, given that Chapter 3 shows that semantic representation of overall grasping action (and not of differences in grasp) develops between nine and twelve months of age.

5.3.4 The directed attention model

Nearly two decades of research on infant perception and processing of actions shows that encoding of action as a special class of stimulus emerges early in life, with perception of differences between actions determined by the actor's goal (Woodward, 1998) or means of achieving that goal (Daum et al., 2009). Action perception has a social element – stimuli with the movement characteristics of actions are not processed as such if the actor is not perceived as agentic (Hofer, Hauf & Aschersleben, 2005; Kamewari et al., 2005; Luo & Baillargeon, 2005). Actions are one example of the diverse kinds of social stimulus for which there is evidence of differential neural processing early in life (Grossmann & Johnson, 2007). Actions can have diverse forms. Actions shown to and processed by infants within the scope of this thesis include reaching to grasp many different objects, eating from spoons, and manipulating novel tools to move parts of novel objects in different ways. Even within the relatively limited scope of this work, which focused on grasping, different patterns of arm and hand movements are seen. The facts that infants in this work could parse multi-step actions into their subcomponents (Chapter 4), attribute different (novel) goals to different actors (Chapter 2) and determine differences between grasps or incorporate those grasps into semantic sequences (Chapter 3) suggests that infants have aptitude in taking such sequences of object-directed movement from amidst the changing visual stimulation they experience from moment to moment, and making sense of them as singular (or multi-component) entities.

One proposal for how infants select such stimuli for attention and processing is the directed attention model. This model suggests that following detection of “socially relevant” or biological entities through low-level features such as patterns of movement, and identification of those entities as caregivers or conspecifics, attention is directed to specific features of the environment via social cues from those entities. There is evidence that social cues assist infants’ perception and encoding of novel stimuli. Work with infants between four and nine months of age shows greater attention to and encoding of objects in paradigms in which there is mutual and joint gaze (Hoehl et al., 2014; Parise et al., 2008; Striano, Reid & Hoehl, 2006), and in which adults direct their gaze toward (rather than away from) objects (Michel et al., 2015). All of these results show that social cues help infants to direct their attention appropriately within a stream of extensive sensory-perceptual input, and form representations of key stimuli. A speculative attempt to account for infants’ apparent precocity in processing actions might be that attention is frequently drawn to actions because they are stimuli or sequences of stimuli of which both biological motion and object-directed attention are an integral part.

The results found in the research in this thesis can be accounted for within the directed attention framework. One direct example of sensitivity to adults’ gaze is the behaviour that differed between experiments from Chapter 2. Infants who participated in the experiment in which the actors made direct eye contact with the camera during demonstration of the tool’s functions looked significantly longer at the faces than the tools during the critical image stimuli. Infants who saw only the core part of the demonstration (Experiment 2) did not. In this case, the bid for joint attention inherent in direct gaze did not alter how 16-month-olds encoded the functions of the tool. Instead, it seems to have primed the infants to attend to facial communicative cues from the actors. This result, although incidental, illustrates that although older infants attend to social cues from digital stimuli, direction of attention to social factors within such stimuli could be dependent on the richness of the cue. For example, direct eye gaze within the context of biological motion could be necessary for eye gaze to be attended to within still images later. The overall results of this study can be accounted for in this manner as well. Infants may have segmented the tool into two parts and associated one part with each actor because of processing constraints. Within the directed attention model, social cues from others are used to direct attention to aspects of the environment that should be prioritised for encoding but working memory limits are imposed such that maintaining different social cues from two actors towards the same object may be challenging (Reid & Striano, 2007). Consequently, encoding of multiple object functions in the context of different actor preferences may be challenging, and breaking the object into parts instead of attended to it as a whole, oriented in different ways, might involve relatively reduced working memory load and require fewer processing resources for the infants.

Also relevant to the work in this thesis is the question of how manual gesture is processed as a social cue, potentially in the communicative or orienting manner of eye gaze. The P400 component of the ERP, generally associated with processing of eye gaze (Rigato, Farroni & Johnson, 2010), is elicited by hands pointing toward or away from objects (Gredebäck, Melinder & Daum, 2010; Melinder et al., 2015). This indicates commonalities in how non-verbal communication is processed regardless of the body part implicated. Recent research has shown that hands in grasping postures are processed in this manner like pointing hands (Bakker et al., 2015). The results from the nine-month-old sample in Chapter 3 show an enhanced P400 component for incongruous grasps, occurring in addition to an enhanced Nc component. This conjunction of results suggests that infants allocated additional attention to the unusual means of grasping the cup but also suggests that they encoded the hand as a communicative element of the stimulus. It may be that infants' perception and processing of action is facilitated by the gestural or movement components therein. These components, hand movement and shape in particular, may help to direct attention to the salient, meaningful components of the action (i.e. the implicated objects and the targets of the action). This offers an explanation for why encoding of goals occurs for grasping hands but not claws (Woodward, 1998) except in contexts in which an actor is known to control the claw (Hofer, Hauf & Aschersleben, 2005). Familiarisation with a conspecific in control of the claw alters its social relevance and consequently how the infant uses it as a means of directing their attention.

A final consideration of the links between the directed attention model and the work in this thesis comes from Chapter 4. A result from this study relates to action parsing. Following execution of a grasp on a spoon, the degree of motor desynchronization decreases (mu power increases). This result fits into a literature that shows that in the second half of the first post-natal year, infants' representations of actions are parsed at relevant junction points (Baldwin et al., 2001; Pace et al., 2013; Reid et al., 2007). In toddlerhood, actions are conceptually organised into sub-components parsed at these junction points (Loucks & Meltzoff, 2013). Within the directed attention model, such parsing would arise from infants attending to adults engaged in action. First, the biological motion inherent in the action would be detected. Identification of the person proceeds and is important in contexts such as Chapter 2, where preferences differ between actors (infants distinguish actors' preferences; Henderson & Woodward, 2012). Through mutual gaze and shared attention, the infant would be engaged to attend to the action and infer its goals. The targets or objects and gestures associated with specific action sub-steps would be consistently seen together although the sub-steps may not always be combined in the same way. This would result in encoding of actions centred on sub-steps and junction points rather than representation of extended actions as singular, continuous stimuli.

There are two findings about action parsing from Chapter 4. The first is that it is evident from the mu desynchronization pattern. The second is that this pattern of desynchronization and rebound is statistically significant for the grasping action, and not for the eating condition, although it is marginal for the renewed desynchronization between the conclusion of the grasp and the preparation to eat. The reason why parsing might result in a rebound in mu power following grasp execution recalls the predictive coding model of Kilner, Friston and Frith (2007). If the mirror system is thought of as a Bayesian system, when prior information is complete, uncertainty is minimal, and system activation will be reduced. Once an action juncture has occurred – for example, a spoon has been grasped – there is no further uncertainty about how that part of the action will continue. Although the presence of a spoon on the table may constrain the possible actions of a reaching hand or reduce uncertainty, other possibilities (e.g. error; Meyer et al., in press) remain until the execution of grasp is complete. Bringing the predictive coding model together with the directed attention model, we can characterise the reach as an action with communicative relevance. In the work of Bakker and colleagues (2015) and in Chapter 3, a P400 is elicited in response to hands in grasping posture. This ERP is elicited in response to communicative stimuli (Gredebäck, Melinder & Daum, 2010; Hoehl & Striano, 2012; Melinder et al., 2015; Rigato, Farroni & Johnson, 2010). In Chapter 3, it was larger when a grasp incongruent with object structure was performed relative to a congruent grasp. What this suggests is that when a standard, congruent grasp is performed, the communicative flexibility or uncertainty of the reach is reduced. In the case of the incongruent grasp, the uncertainty remained, driving the infants to direct their attention to the action via this social mechanism. Given that no overall effects of congruence were found in Chapter 4, we can assume that execution of the grasp in general reduced uncertainty, whether we think of that uncertainty as Bayesian or as social and communicative.

The absence of the parsing effect for the eating action has a number of explanations. It may be that the difference in uncertainty between a hand holding a spoon and bringing that spoon to the mouth is smaller than for the reaching hand. This would be related primarily to the infant’s own visuomotor experience, and not to the fact that reaching to grasp an object could elicit many possible conclusions at the end of the sequence (eating, feeding another, moving the spoon), whereas once the hand holding the spoon moves to the mouth predictions are semantically constrained (as shown in Reid et al., 2009). Even adults cannot detect the motor differences in others’ reaches to grasp a spoon for eating versus moving it to another location (Naish et al., 2013). Alternatively, it may be that infants have less experience with self-feeding than with grasping objects. The correlation results of Chapter 4 show that the ability to perform and plan tool-mediated actions alters mu desynchronization patterns, and so extensive experience with reaching but not self-feeding leads to a difference in the conceptual-motor encoding of these actions. Finally, coherent with the directed attention model, shared attention may not be elicited as frequently from the infant during an adult's self-feeding actions than during reach-to-grasp actions. Consequently, encoding of junction points in eating may be less strong than encoding of grasp junction points.

5.3.5 Integration of frameworks

This work suggests that multiple models of action perception and processing in infancy can be integrated. The directed attention model draws on social and conceptual elements of infant function. The predictive coding model is a framework for mirror system function. The teleological stance is a strongly conceptual model. Nonetheless, results from the preceding work indicate that all three can operate in conjunction with one another, just as the literature review in Chapter 1 shows that social, semantic and motor processes are all employed during action perception and processing in infancy.

Results show that infants are initially sensitive to different perceptual elements of grasping actions, such as the means of grasping used (Chapter 3, Experiment 2). Subsequently, actions are encoded in conceptual or semantic terms, with an emphasis not on the means of action performance but on the end-state of the action (Chapter 3, Experiment 3; Chapter 4). In later infancy, infants associate the parts of a dual-function tool with its different uses but not its overall orientation, again indicating that for sufficiently complex tools or actions encoding of the means of action performance does not happen.

Taken in accordance with the models discussed above, we can assume that via the mechanisms of the directed attention model, infants attend to actions. Prior to the development of a semantic processing system, perceptual aspects are encoded. Once the semantic system develops, the teleological stance becomes strong and these perceptual aspects or action minutiae are no longer processed. Instead, the emphasis is purely on how the achievement of the end-state associated with a specific action. Differences in how the object is grasped or brought to the target are not important. Predictive coding in the mirror system distinguishes between those points in the action at which an end-state is achieved and those at which it is not. Returning to the directed attention model, uncertainty in action end-states can be linked to the communicative relevance of the action involved or to how likely such end-states are to have been seen in communicative or shared attention contexts. When predictive motor coding of an action end-state is difficult, such as in the context of a dual-function tool held in the same hand posture (albeit in different orientations) for all goals, direction of attention to each function by separate actors can result in partial action encoding – tool parts are associated with end-states but the precise means of performing the action is not. In order for actions to be encoded in full, social, motor and semantic information must be processed. Directed attention, a teleological stance, and predictive coding all contribute to the formation of a full representation of action.

5.4 Limitations and directions for future research

5.4.1 Specific limitations of the work

The question asked in this thesis was how semantic and motor representations of action develop and how these systems of action processing operate in conjunction with one another in infancy. The conclusion to be drawn is that although each system may develop along its own trajectory, there is evidence that they operate together to process actions in terms of their end-states. Interpretation of results within the frame of the secondary question of the thesis – how infants process conceptually or motorically different means of performing tool-mediated actions – leads to further questions rather than specific conclusions. Indeed, each experimental chapter in this thesis leads to the same question. If representations of the precise means of interacting with a tool are not present in semantic or mirror representations of the presented action now, then when do they become present during development?

A specific limitation of the work is that each of the three main questions – how infants associate dual-function tools with goals on the basis of how they are held, how semantic processing of grasp-object relationships develops, and how the congruence of means of holding tools is integrated in mirror system function – could be answered more completely with additional information on the developmental trajectory. The Chapter 2 paradigm could show if tool orientation is important for processing single-function tool use earlier in development, or if dual-function tool orientation is ever utilised in distinguishing between its functions. Given that the adult neural correlates of grasp processing differ from the 11.5-month-olds' correlates in incorporation of grasp congruence, investigation of further age groups could illustrate when the specifics of the grasp-object relationship are incorporated into semantic representations of grasping actions. Finally, study of additional older age groups within the Chapter 4 paradigm would likely illustrate the developmental trajectory of predictive motor processing of grasp, particularly because of the emergent relationship illustrated by the correlation analyses in that chapter. An adult sample could also indicate whether prediction of the motor minutiae of an action on the basis of grasp occurs in the developed mirror system.

Another limitation in the work in this thesis is the nature of the specific tasks employed to characterise infants' motor development. In Chapter 2, no such task was presented but the conclusion that 16-month-olds failed to associate a specific means of holding the tool with the actor's goal because they could not differentially simulate the different means of holding the tool might be better supported if a sample, given opportunity to imitate the actors, differed in their results from the groups in Experiments 1 and 2. In Chapter 3, a motor experience measure was employed but no correlations were found between grasping ability and the difference wave for each neural component analysed. This may be because the components measured respond to conceptual elements of action only. Given that other research has shown relationships between grasping ability and looking times (Daum et al., 2011; 2009) and the P400 component (Bakker et al., 2014), it may be that the components measured in this study do not incorporate ideomotor processes or at least no longer do so at the ages studied. In order to capture the effects of the infants' held motor representations, that is, their ability to simulate the differences in the thumb-to-finger and whole hand grips shown and potentially encode the relationship of those grips to the structure of the implicated object, other components (such as the motor ERP found by Nyström, 2008) might be targeted for analysis in a similar paradigm.

Alternatively, the specific task used may have been inappropriate. From the correlations in Chapter 4, we see that with better action planning, a combined motor-conceptual procedure, semantic differences in observed actions elicit increasingly divergent responses. Assessment of the infants' abilities to use thumb-finger opposition in Chapter 3 may have been more relevant to the measured components if the task captured the infants' plan or choice to use thumb-finger opposition (as in Loucks & Sommerville, 2012), because even at nine months use of a pincer grip approaches universality. It must also be noted that sample sizes in Chapters 3 and 4 were small. Larger samples in Chapter 3, Experiments 2 and 3 may have illustrated a more subtle relationship between pincer grip use and semantic and perceptual processing of grasping. Although moderate correlations were found in Chapter 4, a larger sample size may have clarified the results of the marginal correlation between the difference in activation between conditions in the pre-grasping period (critical for understanding ability to predict actions from grasps) and the infant's ability to eat from the spoon without error.

A final limitation to consider bridges some specific limitations of the work and a general limitation of the field. This limitation refers to the extant question of when infants make the transition from associative to semantic processing in action. Before discussing the specific issues in this thesis, we must define the difference between the two. They can be conceptualised in opposition to one another although arguably, semantic relationships are a specific kind of association. Associations are specific in terms of the related stimuli, but general in terms of how stimuli can be related. Semantic relationships are general in terms of related stimuli, but specific in terms of how stimuli can be related. An association is a relationship between two or more specific stimuli or stimulus classes – a blue sky and the memory of sitting on a beach, typing on a keyboard and the taste of coffee, a hammer and the act of hammering.

The last of these associations is causal – hammering usually requires a hammer – the others are not, having simply arisen from being paired contiguously but not contingently. That is, a blue sky and a beach can be experienced apart from one another, whereas the act of hammering is contiguous with having a hammer and has a very high (though not exclusive) contingency with that tool. Semantic relationships are created specifically between causally or structurally linked stimuli, but once a causal or structural form is known, it can be modified. For example, if I know that the structure of a hammering action is to use a hammer to hit a nail or other object with force, I might not associate a shoe with hammering and while I might find someone hammering with a shoe to be engaging in an unexpected action, it is not incongruous because the overall causal structure of the action is not violated.

Kutas and Hillyard (1980) write about “strongly” and “moderately” incongruous stimuli. Following the sentence fragment “he took a sip from the”, certain representations associated with sipping are activated – cup, glass, and perhaps less strongly, tap. If the sentence concludes with the noun “transmitter”, this is strongly incongruous. The representation of the act of sipping does not conform to one’s knowledge of what a transmitter is and what can be done with it. However, the noun “waterfall” may be congruous or moderately incongruous. If we do not have other contextual information, “waterfall” is congruous but unexpected; if our prior knowledge includes the fact that the agent is at home, sipping from a waterfall is incongruous with that context.

There are two extant developmental questions arising here. First, when do infants make the transition from purely associative to associative and semantic processing? Second, does an association become semantic through repeated exposure (contiguity) or do infants generate structural knowledge about, for example, actions, and determine if a semantic relationship is valid via contiguity, contingency and context? That is, are infants’ semantic associations initially developed from specific associations, or from general rules? Under the assumption, rife in the literature, that infants differentiate between actions and non-actions on the basis of a number of cues – agency

(Hofer, Hauf & Aschersleben, 2005; Kaduk, Elsner & Reid, 2013; Kamewari et al., 2005), discernible goals (Southgate et al., 2010; Woodward, 1998), contingency of the outcome on performance of a causal action (Nyström et al., 2011; Träuble and Pauen, 2011), and upholding the standard function of objects (Reid et al., 2009; Stapel et al., 2010) – the results of the reported studies can be interpreted as the result of semantic processing on the part of the infants. Infants process similar combinations of movements, objects and end-states differently if there are violations of the general nature of actions in place, even if they are shown these combinations frequently enough to form associations. Examples of paradigms showing this include the wrong movement performed with an object (Reid et al., 2009; Stapel et al., 2010), no discernible goal (Southgate et al., 2010), and a novel action performed with a tool that violates rules of physical causality (Träuble and Pauen, 2011). This last example shows that if the general structure of action is violated, infants do not process the sub-components of that action (e.g. the tool used) in the same way as when the action is causal and does not violate general knowledge or principles of actions. On the basis of Hebbian learning, associations should be formed between frequently co-occurring stimuli, but in this case the semantic violation seemed to prevent the infants from doing so.

Under these assumptions, in chapter 2, infants associate tool-ends with actors not because of a co-appearance of the actor and that tool-end in a salient context (demonstration of the tool-end's use), but because infants understand that an action has an actor with a goal, and that goal must be performed with a specific tool-part. In chapter 3, this assumption leads to interpretation of the Nc effect as indicative that infants hold an association but not a semantic association between tool shapes and grasp postures at nine months, and at 11.5 months such associations might be more flexible or infants simply do not attend to hand-object relationships. Finally, in chapter 4, the assumption is that, revealed by mu power differences at different action sub-steps, infants' conceptions of actions as semantic, structured entities affect mirror system function, but they do not have a semantic, mirror-system-affecting conception of how tools must be interacted with to attain specific goals (i.e. eating).

The interpretation of semantic processing in chapter 2 is particularly susceptible to an associative-only interpretation if we assume that at 16 months, infants do not necessarily encode all action as semantic. Looking patterns could be explained via the counter-interpretation noted above, that is, that infants may have just formed an association between a tool-end and an actor because of the tool-end's salience (held upright during demonstration, used to effect outcome). In chapter 4, we might suggest that sub-steps are separated associatively, as infants might have many possible actions associated with reaching but few associated with completing a grasp on a spoon, and thus the need to continue to simulate the action in order to predict it is diminished at that sub-step. In chapter 3, we see evidence for associative processing via the Nc, but no evidence for N400-differentiated semantic processing of grasp-object conformity. Decades of research tell us that the N400 indexes semantic processing (Kutas & Federmeier, 2011), but in developmental contexts we know very little about its emergence. By focusing research efforts on the developmental N400, other congruence-modulated developmental components (e.g. P400; Bakker et al., 2015) and indeed associative components (e.g. Nc; Quinn, Westerlund & Nelson, 2006), the question of when and how infants make the transition from associative to semantic processing could be better investigated. This would allow inferences and assumptions about how infants process action, whether semantically or associatively, to be founded in evidence from the literature. For example, in adult literature, the N400 is found overwhelmingly in studies in which the kind of structural, modifiable meaning defined as "semantics" above is modulated, and to argue that it indexes another process is difficult (Kutas & Federmeier, 2011). Conversely, in infancy, without a similarly strong array of evidence it is difficult to argue that N400 homologues definitively indexes semantic processing in infancy.

5.4.2 General limitations in the field

When the work in this thesis commenced, many studies of mirror system function in infancy emphasised how the mirror system worked in relation to "goal-directed" action, with ambiguous gestures or non-causally-generated end-states used as a foil (Nyström et al., 2011; Southgate et al., 2010). Some literature on the N400 potential as a marker of semantic processing of action in infancy existed (Pace et al., 2013; Reid et al., 2009) as did much research on infant encoding of conceptual elements of action (e.g. Daum et al., 2009; Träuble & Pauen, 2011). The mirror system or motor activation work did not explicitly refer to its connections to conceptual elements of action processing despite the differences in conditions being driven by what could be considered a conceptual or semantic aspect – goal-directedness. This thesis was written and the experiments herein conducted with the intent of making these links more explicit.

There are a number of discontinuities in our knowledge of the mirror system as a developing neural network. The overarching question is that of whether its function develops along predetermined trajectories or whether the formation of visuomotor associations supports ideomotor responses during observation of predictable actions (see e.g. Cook et al., 2014). Although mu desynchronization can be measured from across the infant's scalp, it is not clear to what extent this correlate of motor activation is driven or modulated by the superior temporal and parietal modules of the mirror system network. This relates to the previously identified question, derived from the two-stage (Gallese & Goldman, 1998) and predictive coding models (Kilner, Friston & Frith, 2007), of how the mirror system can function without semantic processing of action. Within the latter model, it is possible that the premotor and motor areas of cortex could be responsive to observed action without extensive conceptual understanding but the results of developmental mirror system studies indicate that mirror responses in the first post-natal year distinguishes between incidental arm movement and goal-directed action (Southgate et al., 2010).

The potentiality that the mirror system is functional before semantic processing emerges in infancy points to the possibility that the precise correlates used for detection of both semantic processing (the N400) and mirror system function (mu desynchronization) might have developmental precursors that have not yet been detected or specified. There are additional possible neural correlates of mirror system function measured via ERPs (Nyström, 2008) or NIRS (Shimada & Hiraki, 2006). For semantic processing, few possibilities currently exist in the literature. Although terms like “congruence” are used in the action P400 literature (e.g. Bakker et al., 2015), this refers specifically to the congruence between the orientation of a grasping hand and a previously displayed object. This is a spatial relationship and supports rather than questions or broadens the communicative function of the P400.

Other possible precursor neural correlates exist and could be explored further. These include the positive slow wave ERP (seen in 4-month-olds; Hoehl et al., 2008), alpha desynchronization (seen by 9 months; Hoehl et al., 2014) and gamma oscillatory activity (present at 8 months; Reid et al., 2007). The first of these is associated with memory encoding, the second with activation of networks for semantic retrieval, and the third with action parsing. In conjunction with one another, these components could illustrate how conceptual aspects of action are encoded in memory, how they are recruited to differentiate distinct conceptual stages within action, and how these concepts are retrieved in order to generate predictions about how an action will continue along semantically congruent parameters.

Another area within infant action perception and processing research that restricts how conclusions can be drawn from the work in this thesis and indeed from other work in the field is the discontinuity between results based on overt infant behavior and looking patterns, and results deriving from neural measurement. The neural components underlying infant perception and encoding of action are not fully elucidated. One key example is that the work of Daum and colleagues (2011; 2009) that shows, from measurements of infant looking time, that infants look longer at grasps on objects that do not match the shape of the hand as it reached for the object, and that six-month-olds who can perform thumb-to-finger grips show this distinction in looking time more so than peers who do not perform thumb-to-finger grips. In the work presented in Chapter 3, we see that although nine-month-olds perceive differences in hand-object relationships, the relationship between pincer grip performance and attentional processes is not seen. There must be another neural component that supports the abilities shown by the infants in the Daum et al. (2011; 2009) work that is not the Nc, P400 or N400 component.

In investigating the relationship between semantic and motor processing of action, and the neural correlates involved in each system, the work in this thesis has attempted to bridge many of the discontinuities in the field's conceptions of the mirror and semantic processing systems. In addition to demonstrating the function and development of these systems in relation to tool-use actions of varying complexities (grasping, Chapter 3; grasping to act, Chapter 4; using dual-function tools, Chapter 2), the work indicates that although there are conceptual similarities between semantic processing and some aspects of mirror system activation, differences in neural manifestation remain. Thus the systems can be considered as distinct, although semantic processing also functions as a component of the mirror system that modulates motor activation. From the literature review in Chapter 1 onwards, the contribution of this thesis to the field has been to examine the conceptual similarities between and hierarchies in processing of action from social, semantic and motor perspectives.

5.4.3 Future directions – specific and general

In addition to the expansion of the paradigms in this study to further age groups and the adoption of new measures of motor experience and representation described in section 5.4.1, there are some more specific questions arising from the work in this thesis. The first is whether the results found in Chapters 3 and 4 arise from familiarity with the implicated objects – cups and spoons – or whether perceptual, semantic and motor processing of grasping actions is more general. Given the presence of specific cues that a sequence of movement is an action, such as agency or animacy (Hofer, Hauf & Aschersleben, 2005; Pauen & Träuble, 2007) and the achievement of a goal (Southgate et al., 2010; Southgate & Begus, 2013; Woodward, 1998), infants may apply general expectancies to the sequence. This could be investigated by showing 9-month-olds an actor grasping an unfamiliar object with specific structural features that indicate how it should be held, and analysing the neural response for the same differences in Nc and P400 components seen in Chapter 3, Experiment 2. In addition, the paradigm used in Chapter 4 could be adapted for an older age group, sensitive to grasp orientation, to determine if infants generally expect that a handled object will be held with a radial rather than an ulnar grasp.

The precise relationship between the developmental trajectories of semantic processing and motor activation remains to be found, although work in this thesis shows that they are not the same means of processing. The correlations found in Chapter 3 promote further work to establish if predictive differential processing of congruent and incongruent grasps emerges later in infancy, and if there remains a relationship between differential motor activation in response to such grasps and motor planning. It could be found whether the semantics of these manual aspects of action become incorporated into mirror system representations along a similar timeline to the emergence of semantic processing of grasp appropriateness, as measured in Chapter 2. Such a relationship would add credence to the possibility that semantic and motor processing of action are strongly linked, that they operate teleologically once overall semantic processing of action goals emerge, and that as motor or manual minutiae of actions are incorporated into semantic representations they are differentiated in measures of motor activation.

The re-emergence of infant sensitivity to minutiae of grasping after eleven-and-a-half months (Chapter 3), and sensitivity to nuanced motor differences in how actions are performed (Chapters and 4) remains to be investigated. The ability to use one's hands in precise configurations allows for expert manipulations of tools employed by adults in everyday life. From stirring to writing to sewing to eating with forks or chopsticks, specific and precise means of altering the degrees of freedom of the hand in relation to one another that are challenging for infants become necessary and natural in adulthood. The exact means of holding and employing a tool for use can change its associated function. Just as different orientations of the tool altered its intended function in Chapter 2 (despite these orientation differences not being encoded by the 16-month-olds), different means of holding a hammer can convey delicate or powerful means of hammering, or a different function such as pulling nails out of a wall. Without sensitivity to the means or minutiae of performing an action with an object, the ability to use tools is diminished and, in relation to action observation, social cues such as when someone is handing an object over or performing an action in relation to you may be missed. The work in this thesis indicates that although a (narrowly interpreted) teleological stance and focus on action end-states may dominate infant action processing in the first post-natal year, the ability to process the motor subcomponents of actions is important for both performance and observation of action and its development ought to be studied further.

5.5 Conclusions

The research conducted as part of this thesis links behavioural measures of action performance, neural measures of motor activation, semantic processing and attentional processing, and eye-tracking measures of associations between actors and the tools and tool parts they use to perform their preferred actions. Results show that incorporating information about grasp and hand-object relationships into semantic and mirror representations of tool function, grasp appropriateness and congruence of action conclusions is challenging for infants. It is possible that as infants begin to form semantic or meaningful representations of action, and as these representations become strongly linked to motor activation of observed actions, as in the mirror system, infants attend only to the most salient, most meaningful aspect of the action – the goal. By adulthood, motor minutiae of actions are identified as congruent or incongruent with the objects they are executed upon. This is likely driven by the strongly entrenched semantic and motor representations of action present in adulthood. With greater experience of manipulating objects and planning actions, semantic elements of action can be incorporated into motor representations, and motor elements into semantic representations. Although infants are adept at forming associations between tools, targets, actors and action conclusions, the robust processing of precise manual elements of tool-mediated actions must emerge in later development.

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