MODULATION OF NEURAL MIRRORING BY SENSORIMOTOR EXPERIENCES: EVIDENCE FROM ACTION OBSERVATION AND EXECUTION

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ABSTRACT

A recent line of inquiry has examined a specific question about how an observer's own experiences with actions may change how his or her brain processes those actions when they are subsequently observed. In short, how does prior experience with action affect the subsequent perception of others' actions? The current study investigated this question using electroencephalography (EEG) to test the hypothesis that receiving experience with an action would subsequently lead to different activation of sensorimotor cortex depending on the predicted consequences of observed actions. While EEG was recorded, three groups of participants watched video clips showing an actor lifting objects, and then each group received information about the sensorimotor properties (i.e., weight) of the objects. One group received extended sensorimotor experience with the objects (EE group), a second group received brief sensorimotor experience with the objects (BE group), and the third group read written information describing the objects' weights (semantic information, SI group). Following the experience, participants again viewed the video clips. Time-frequency analyses showed that for participants in the EE and BE groups, EEG during the observation of action was sensitive to the predicted sensorimotor consequences of the observed action. This was not found for the SI group. As well, all three groups showed increased alpha and beta suppression following experience. Overall, these results lead to two main conclusions: 1) experience with action facilitates subsequent neural mirroring processes, and 2) sensorimotor experience leads to differential activation of the sensorimotor cortex depending on the predicted consequences of observed action.

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THE EFFECT OF EXPERIENCE ON ACTION OBSERVATION

Background

Understanding others' actions is critical for successful social interactions and in order to learn new skills. By observing others' actions, we can learn a new skill by watching others, comprehend nonverbal communications, or simply appreciate watching a highly skilled athlete compete. One might wonder what allows for the successful understanding of others' actions, and the neural mechanisms involved. By gathering evidence about what brain regions are involved in the processing of other people's actions, we can better understand how different properties of observed actions change neural activity, and the degree to which patterns of brain activation related to others' actions are similar to the activations involved in the production of our own actions.

In recent years, a neural network termed the action observation network (AON) has been identified in the human brain. This network is thought to include brain regions that are especially active during the observation of others' actions, ranging from discrete finger movements to elaborate dance sequences (Caspers, Zilles, Laird, & Eickhoff, 2010). It has been suggested that these neural systems might be involved in the ability to predict, make inferences about, understand, and even feel like one is vicariously experiencing the actions of others (Fadiga & Craighero, 2004; Gallese & Goldman, 1998; Gallese, Rochat, Cossu, & Sinigaglia, 2009; Grafton, 2009). Some of the brain regions of the AON may be involved in strictly perceptual processes, such as the low-level visual processing of observed actions, while some regions may relate to the vicarious simulation of the observed actions. The brain regions thought to comprise the AON, as well as their proposed functions, will be discussed below.

While researchers have made a great deal of progress in understanding action processing at a neural level, many questions remain concerning how the AON functions and what activity in this system may contribute to action processing. There is much debate about whether action processing is subserved by a putative mirror neuron system (MNS), which may be closely tied to the functioning of the AON. The mirror neuron hypothesis postulates that observed actions are to some extent processed as if they were being produced by the observer. More specifically, the hypothesis states that the observer's nervous system may engage in a manner similar to when he is performing the action. Proponents of this hypothesis have suggested that this embodied simulation allows the observer is able to process and understand them by means of their own motor system activation (Fadiga & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001).

The human MNS is proposed as a possible analogue of the neural system described by Rizzolatti and colleagues in macaques (Fadiga, Craighero, & Olivier, 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti et al., 2001). In humans, mirror neurons are thought to fire both during the production of an action, and during the observation of others' similar actions, in a process known as neural mirroring or motor resonance (Umiltà, Kohler, Gallese, & Fogassi, 2001). Mirror neurons are most often thought to be present in the sensorimotor cortex, the inferior frontal gyrus, and the intraparietal lobule (Iacoboni, 2009). It has been proposed that the mirroring properties of these neurons could form the foundation of the embodied simulation of others' actions (Gallese & Sinigaglia, 2011). Neural mirroring involves activation of sensorimotor areas of the brain that is similar to the activation that would occur during the execution of one's own actions. Some work has used brain lesion analysis, or the temporary disruption of cortical functioning, to establish a causal link between the activation of sensorimotor cortex during action observation and the recognition of others' experiences (Avenanti, Candidi, & Urgesi, 2013), supporting the notion that sensorimotor activation is critical for processing others' actions.

Despite recent criticisms of the mirror neuron hypothesis (Dinstein, Gardner, Jazayeri, & Heeger, 2008; Dinstein, Thomas, Behrmann, & Heeger, 2008; Hickok, 2009), and continuing debate concerning the role of neural mirroring in action understanding (Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011), there is substantial evidence for the existence of this type of vicarious processing in the human brain (Keysers et al., 2004; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). The current focus of this debate concerns the extent to which action understanding is subserved by the vicarious activation of sensorimotor cortex. It should be noted that little is known about the mechanisms involved in how individual mirror neurons contribute to action processing in human populations, although researchers have extensively explored the properties of individual mirror neurons in primates (Caggiano, Fogassi, Rizzolatti, Thier, & Casile, 2009; Caggiano et al., 2013).

If observed actions are in some way associated with activation of the observer's sensorimotor cortex, then it could be argued that the observer's own experience with the observed actions might affect the extent of this activation. For example, if someone is watching another person perform a complex, novel dance, the sensorimotor cortex may be involved in a different way than if the observer has a great deal of prior experience with the dance movements. If the observer did have experience with the dance, their own prior sensory and motor experiences with the dancing actions may facilitate the vicarious activation of sensorimotor cortices. In recent years, researchers have investigated the extent to which one's own prior experiences change subsequent processing of observed actions. This paper will present a novel experiment designed to test this question.

The Action Observation Network

A recent meta-analysis of 139 cognitive neuroscience studies identified diffuse bilateral regions of the brain that are involved in observing the actions of others (Caspers, et al., 2010). The following areas are those identified by Caspers *et al*. as consistently being involved in both action observation and imitation: inferior frontal gyrus (IFG), lateral dorsal premotor cortex, the supplementary motor area, inferior parietal lobule (IPL), primary somatosensory cortex, superior parietal cortex, intraparietal cortex, posterior middle temporal gyrus, and the fusiform face and body areas. The IFG (also known as Broca's area) is implicated in semantic processing, which may underlie the verbal processing involved in assigning verbal labels to observed actions (Hamzei et al., 2003). Sensorimotor cortex, comprised of the primary motor cortex, premotor cortex, and primary somatosensory cortex, is a critical component of the putative MNS, thought to underlie vicarious motor simulation during the observation of action (Pineda, 2008). The IPL is involved in processing actions performed with the hands, and interpretation of sensory information (Fogassi, 2005), and the supplementary motor area is implicated in imitating motor actions (Halsband, Schmitt, Weyers, & Binkofski, 2001). The AON contains several areas usually included in the human MNS, like the sensorimotor cortex and the IPL (Iacoboni & Dapretto, 2006; Molenberghs, Cunnington, & Mattingley, 2012), and it also includes areas typically not included in the MNS, such as supplementary motor areas and the medial temporal gyrus (Caspers et al., 2010; Rizzolatti & Sinigaglia, 2010). Thus, while some regions of the AON are likely involved in vicarious simulation of observed actions, some non-mirroring areas of the brain are also particularly sensitive to the observation of action.

Links between Action Experience and Mirroring

The links between action and perception can be considered both in terms of offline and online effects (Schutz-Bosbach & Prinz, 2007). Online modulations occur when action and perception are concurrent, and offline modulations occur when action and perception are temporally separated. Offline, action and perception can modulate each other in both directions: the modulation of action by prior perception, and the modulation of perception by prior action. There is a large body of research suggesting that observation of others' action changes one's own subsequent actions (i.e., offline modulation of action by prior perception as in Gray & Beilock, 2011). While less research has focused on the effect of action experience on subsequent perception, investigation of this phenomenon is a growing field (Salama, Turner, & Edwards, 2011). A better understanding of offline modulation of action perception will help explain how a putative human MNS might link our own action experiences with those of others.

Cognitive Neuroscience Evidence for Effects of Expertise

By identifying the brain networks and regions involved in the effects of experience on action processing, we can understand what characteristics of action experience are particularly important for bringing about these effects. Much of the existing literature concerning this question has used the framework of expertise to look at the effects of experience. For example, high-level experts in a skilled field such as piano playing or sports are compared to people who are novices in the same field. These studies capitalize on long-term experience with actions, as opposed to training studies that look at experiences lasting only minutes or hours. By focusing on long-term expertise, it is not altogether surprising that many of these studies find increased motor resonance during action observation in experts, due to their more elaborate knowledge of the actions (Knoblich, 2008).

In one particularly well-known study in this field, professional ballet dancers, professional capoeira dancers, and non-expert control subjects watched videos of ballet and capoeira dance actions while fMRI scans were collected (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005). Both groups of dancers showed significant premotor cortex, parietal cortex, and superior temporal sulcus activation during observation of all dance moves, but these brain regions were more highly activated during the observation of the familiar dance movements. This experiment is often taken as evidence that observation of action activates the observer's motor system depending on the degree to which they have motor experience with the action.

A similar experiment used EEG to examine differences between expert dancers and non-dancers during observation of dance movements and non-dance movements (Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008). Expert dancers showed greater event-related suppression of alpha and beta frequency bands than did non-dancers during the observation of dance movements. This difference was not seen during observation of non-dance movements. This provides further evidence that motor experience with action facilitates neural mirroring during the perception of others' similar movements, and that the degree of integration of an action into one's own motor repertoire may be especially important.

Studies of musicians have shown similar effects of experience-based modulation of action perception on brain activity during action perception. Expert piano players show greater BOLD responses in frontal, parietal, and temporal brain regions during observation of silent piano playing, compared to a control group of non-musicians (Haslinger, Erhard, & Altenmüller, 2005). Musical expertise may also enhance the processing of more abstract action-related tasks. In another experiment, musicians and non-musicians observed static sheet music while their EEG was recorded (Behmer, Jr. & Jantzen, 2011). The observation of static sheet music elicited greater sensorimotor mu rhythm suppression in musicians than in non-musicians, signifying greater activation of sensorimotor cortex. This suggests that the mere presence of sheet music was activating the associated motor sequences required to play the music, for those musicians who had experience with playing from sheet music.

A recent experiment compared blood-oxygen-level-dependent (BOLD) responses during the observation of archery in both expert archers and non-archers, and found that expert archers showed greater AON activation than non-archers (Kim et al., 2011). As in other studies, these authors argue that the effects of expertise were largely due to the sensorimotor elements of their prior archery experience, rather than visual familiarity with or general interest in the actions.

Contradictory Findings and Limitations

In contrast to the evidence presented thus far, some studies that have used expertise to examine the effects of action experience have found that experts show *decreased* BOLD activation or EEG reactivity during observation of the actions with which they have extensive experience. One experiment compared non-athletes to amateur and expert karate students while they observed video sequences of actors performing karate, and found less cortical activation in participants with greater karate expertise (Babiloni et al., 2010). The same research group found similar effects in elite rhythmic gymnasts (Babiloni et al., 2009). The researchers explain the findings from both of these experiments in terms of "neural efficiency", which posits that as people become more experienced with an action, their brains become more efficient at processing related actions when they see them being carried out (Babiloni et al., 2009; Babiloni et al., 2010). Neural efficiency is thought to result in less neural activation during action observation, based on the idea that sometimes, more diffuse brain activation may compensate for impaired or underdeveloped skills, whereas recruitment of smaller areas reflects more efficient processing. The authors of one study suggest that decreased BOLD signals in expert guitarists during guitar chord formation may be due to decreased supervisory control and great automaticity of action in experts compared to controls (Vogt et al., 2007). However, neural efficiency cannot adequately explain the body of work presented earlier showing increased neural activity following action experience (Behmer, Jr. & Jantzen, 2011; Fadiga et al., 2005; Lyons et al., 2009; Orgs et al., 2008).

Thus, the question arises of why some expertise studies demonstrate increased sensorimotor activation during observation in experts, and some studies seem to show the opposite pattern. One review outlines several reasons that different experiments might find different effects of expertise on brain activity during action performance (Kelly & Garavan, 2005), such as the domain of the experimental task or action (e.g., dance or archery), strategies involved in practice, task instructions or behaviors, and the time window between practice and imaging. Kelly & Garavan (2005) also explore the possibility that practice with action may result in functional reorganization, rather than simply greater or lesser neural activation. Different types of actions may modulate perception in very different ways. Some skills, such as archery or riflery, may require a quieting of sensorimotor involvement in order to not “overthink” the movement, and instead rely more on precision of timing and coordination of small motions. Other types of actions, such as dancing, may produce different cortical patterns as they become more practiced, since the actions require synchrony between distant body parts, larger-scale motor commands, and longer durations. Finally, some recent evidence suggests that with increased sensorimotor expertise with action, gray matter is modulated differentially in areas related to cognitive functioning, compared to areas related to sensorimotor processing (James et al., 2013), suggesting that the link between expertise and brain structure and function is likely nonlinear, and should be examined more closely in future work.

In addition to the possible confounds of familiarity and memory (described in detail in Moreau, 2013), experiments comparing experts to novices fail to show causal links between experience and changes in action processing. These experiments do not experimentally manipulate action experience, thus, we do not know the extent to which the effects are driven by the experiences themselves or another common factor. It may be that people who process actions in certain ways are more likely to become experts in a certain field. Several questions remain to be answered. For example, how much of the effect of experience is due to sensorimotor system involvement and/or mirroring, as opposed to visual experience, familiarity, interest, or different memories of the actions? Vicarious sensorimotor involvement in action observation is the centerpiece of mirror neuron system functioning (Pineda, 2008), but the existing literature concerning the link between sensorimotor experience and action processing has not adequately investigated *how* the somatosensory and motor characteristics of action experience change the neural activity involved in subsequent action processing. This knowledge could explain some of the inconsistencies in the literature, and focus this body of research on the mechanisms that link one's own prior actions with subsequent processing of others' actions.

Sensorimotor Experience

A common theme that can be extracted from the research on experience and action processing is the proposal that sensorimotor experience with action drives the changes seen in action processing. How do sensorimotor experiences change subsequent action processing, separate from visual experience, familiarity, and other things that change with experience? While some of the studies described earlier touch upon the contributions of motor experience with action to action processing as a whole (Calvo-Merino et al., 2005; Orgs et al., 2008), many questions remain regarding precisely what role somatosensory and motor information plays in the effect of experience on action processing (Keysers, Kaas, & Gazzola, 2010; Marshall & Meltzoff, 2011). Somatosensory experiences include the tactile and proprioceptive elements of sensation during action, such as the feeling of an object's texture, or the sensation of pressure on the body while performing an action. Motor experiences encompass the muscular and kinematic elements of action. Both motor systems and somatosensory systems exhibit common activation between action production and action observation (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011;

Ebisch et al., 2011; Gazzola & Keysers, 2009; Keysers et al., 2010; Lamm, Decety, & Singer, 2011), and so both sensory and motor experiences might be thought to affect subsequent action processing.

The literature concerning this question suggests that somatosensory and motor aspects of action experience do indeed afford special contributions to the coupling of action and perception (Calvo-Merino, Urgesi, Orgs, Aglioti, & Haggard, 2010; Shiffrar, 2011; Yee, Chrysikou, Hoffman, & Thompson-Schill, 2013), and some researchers believe that links between sensory and motor experiences during development or action learning actually form the basis of mirroring processes (Catmur, Walsh, & Heyes, 2007). Even if it seems likely that sensorimotor experience is important for action perception, we do not yet know much about the mechanisms involved. For example, precisely what amount of sensorimotor experience with an action brings about changes in subsequent processing of others' actions?

It is likely that the sensorimotor characteristics of one's own experiences with actions explain a portion of the results from the previously discussed expertise studies. However, none of the studies that use the expertise paradigm experimentally manipulate action experience, preventing a comprehensive understanding of which aspects of experience produce changes in subsequent action processing. In contrast, training studies that involve learning novel actions, or the formation of new sensorimotor associations with actions, can better separate out the effects of specific sensorimotor experiences. Attempting to separate these two types of experience can help answer questions about observational learning such as the importance of actually performing the action one is trying to learn rather than simply observing it.

Some existing work suggests that sensorimotor experience may uniquely affect subsequent action processing. Calvo-Merino *et al* (2005) suggest that the differences in BOLD signal between ballet dancers and capoeira dancers while they observe dance actions is a result of motor expertise, and not the visual familiarity which would come about from years of practicing with other dancers and observing one's own dancing from the first-person perspective. This claim is based primarily on the location of the fMRI effects, which were not in areas generally related to visual experience (i.e., the fusiform gyrus). Although this argument is fair, the evidence is still not causal and the observed effects cannot logically be isolated to sensorimotor experience alone.

In two follow-up experiments to their 2005 work, Calvo-Merino and colleagues attempted to further separate out the effects of sensorimotor experience from the effects of visual experience or familiarity (Calvo-Merino, Ehrenberg, Leung, & Haggard, 2010; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). In these studies, experienced ballet dancers viewed videos or point-light displays of gender-specific ballet moves. While a dancer only ever performs their own gender's moves, they see many opposite-gender moves due to intensive hours of practice together. fMRI scans showed greater BOLD activity at premotor, parietal, and cerebellar regions during observation of same-gender moves than during observation of different-gender moves. This lends support to the notion that first-person sensorimotor experience induces greater BOLD activation during action processing that go beyond visual familiarity alone. However, the authors note that visual familiarity with action appears to also have some effect on subsequent observation of action.

Training studies have also provided a more direct link between action experience and subsequent action processing. After five days of training with novel dance sequences, participants showed increased activity in premotor and parietal areas during observation of learned (either through physical practice or observation only), but not unlearned sequences (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2008). Both motor learning (physically performing the dance moves) and observational learning (watching the dance moves) led to changes in neural processing during subsequent observation of the actions. There were many similarities between the activations recorded during the observation of the two different sets of actions in regions throughout the AON, particularly premotor and inferior parietal regions. Some regions of the AON, however, were more highly activated during observation of practiced actions, namely the right precentral gyrus and the right middle frontal gyrus. No brain regions showed greater activation to observed actions than practiced actions. More recent work from the same group suggests that physical experience with knot-tying, as opposed to learning the names of knots, increases activation in intraparietal sulcus during subsequent observation of knot-tying (Cross et al., 2012), which may mean that there is greater facilitation of neural mirroring following sensorimotor experience. However, this study does not explicitly explain what element of experience leads to the effect, since learning the names of knots (the control condition) does not give the participant any information about the sensorimotor aspects of the knot-tying experience, thus the effects following experience with knot-tying may be due to the sensorimotor experiences themselves, or may be due to the more elaborate understanding of the actions, for example.

Another way of conveying information about the sensorimotor characteristics of an object is by means of semantic labeling. For example, in a transcranial magnetic stimulation study, participants viewed actions upon objects that differed in weight (Senot et al., 2011). Some of the objects were transparent, allowing participants to directly see whether the objects were heavy or light. Some of the objects were opaque, but had labels that identified the objects as “heavy” or “light”. Motor evoked potentials (MEPs) recorded during observation of actions upon labeled objects were not sensitive to the labeled weight of the objects, in comparison to MEPs during observation of objects that were known to be heavy or light, which varied depending on the visible weight of the objects. This suggests that semantic information regarding the sensorimotor characteristics associated with performing specific actions might not provide enough information to modulate vicarious motor system involvement during the observation of actions upon those items. It remains relatively unclear to what extent the acquisition of semantic or conceptual knowledge about the sensorimotor consequences of actions may affect subsequent action processing (Zhu, Qian, Yang, & Leng, 2013).

EEG Correlates of Action Processing

The current study will focus on EEG measures in the context of an experiment investigating the impact of action experience on cortical activation during action observation. Analysis of EEG signals provides information about the synchronous voltage changes across neuronal networks in the cerebral cortex that are associated in time with mental phenomena (Pfurtscheller & Lopes da Silva, 1999). By quantifying the power of different frequency bands in the EEG signal, researchers are able to get temporally precise information about the psychophysiological underpinnings of action processing. Additionally, using EEG allows for higher ecological validity than most other cognitive neuroscience methods, since it is feasible to naturally perform actions and interact with others during EEG recording. The most commonly used EEG technique used to study action processing is band-power analysis. Band-power analysis quantifies the degree to which different frequency bands are present in the waveform during discrete epochs of time. Activity in certain frequency bands during the observation of action are particularly sensitive to sensorimotor stimuli, goal-directed actions, and the social relevance of actions (Streltsova, Berchio, Gallese, & Umilta, 2010). In particular, researchers have extensively examined alpha-range rhythms (8-13 Hz) as a way of measuring psychophysiological correlates of action perception (Muthukumaraswamy, Johnson, & McNair, 2004; Pfurtscheller & Neuper, 2000). Alpha-range rhythms, and the slightly higher frequency beta rhythms (14-22 Hz), are uniquely suited for investigating the determinants of action processing because of their relation to somatosensory and motor processes.

The Alpha Rhythm (8-13 Hz)

The alpha rhythm, which oscillates at frequencies between 8-13 Hz, is prominent in the human EEG signal. Research on the alpha rhythm has historically focused on activity in the alpha band over occipital regions during visual processing (Bartley, 1940; Callaway, 1962; Jasper & Cruikshank, 1937). In more recent years, researchers have turned to investigating the involvement of alpha-range activity in the processing of sensorimotor stimuli (Chang, Arendt-Nielsen, & Chen, 2002; Cheyne et al., 2003; Gaetz & Cheyne, 2006; Streltsova et al., 2010; Svoboda, Sovka, & Stancák, 2004). A substantial body of research shows that alpha-range rhythms are sensitive to sensorimotor characteristics of both action production and the observation of others' actions (Hari, 2006; Muthukumaraswamy et al., 2004; Quandt, Marshall, Shipley, Beilock, & Goldin-Meadow, 2012), which makes them ideal candidates for investigating vicarious action processing. Alpha range rhythms can be subdivided into lower alpha (usually encompassing ~8-10 Hz) and upper alpha (usually encompassing ~11-13 Hz) frequency bands (Babiloni et al., 2009; Quandt et al., 2012). The upper and lower alpha bands are often found to have somewhat different involvement in action processing—for example, the upper alpha band may be more sensitive to variations in prior experience with observed actions (Hummel, Andres, Altenmüller, & Dichgans, 2002; Marshall, Bouquet, Shipley, & Young, 2009; Quandt, Marshall, Bouquet, Young, & Shipley, 2011).

The mu rhythm is a term for oscillations within the same frequency range as the classical posterior alpha rhythm (8-13 Hz), but with distinct sources in mirroring-related regions of the AON such as the premotor cortex, somatosensory cortex, and the IPL (Arnstein et al., 2011; Ritter, Moosmann, & Villringer, 2009). Given these sources, the mu rhythm is generally recorded from central electrode sites, which directly overlie the pre- and post-central gyrus, where the sensorimotor cortex is located. The mu rhythm is often measured as an index of sensorimotor cortex activation during the observation of others' actions, as well as during the production of one's own actions (Arroyo et al., 1993; Hari, 2006; Muthukumaraswamy et al., 2004). This rhythm is thought to link perception and action (Pineda, 2005) and reflect activity of the putative human MNS by way of matching between the actions of oneself and the actions of others (Orgs et al., 2008; Perry & Bentin, 2009). Indeed, the precise distinction between the alpha rhythm and the mu rhythm is somewhat unclear, since alpha-range rhythms at non-central sites have also been implicated in action observation and moderated by prior action experience (Marshall et al., 2009; Orgs et al., 2008; Quandt et al., 2011). The extant literature, however, largely considers the central mu rhythm to be functionally distinct from other alpha-range rhythms.

The amplitude of alpha-range rhythms (including the mu rhythm) is traditionally thought to be inversely correlated to underlying cortical activity (Hari, 2006). Historically, the alpha rhythm has been referred to as an idling rhythm—that is, higher alpha power would be associated with inactivity of underlying cortical areas (Pfurtscheller & Lopes da Silva, 1999). Thus, many band power analyses have interpreted the suppression of alpha power with increased cortical activation, and vice versa. More recent evidence, however, suggests that this view of the alpha rhythm may be simplistic and that the alpha rhythm may be reflective of higher cognitive functions (Pineda, 2005). For instance, the lateralization of the alpha rhythm over sensorimotor cortex might reflect preparation of somatosensory systems for upcoming information according to the expected relevance of the stimuli (Haegens, Handel, & Jensen, 2011; Stancak, 2006). There is also evidence that the alpha rhythm reflects active spatial and somatosensory attentional suppression mechanisms (Bauer, Kennett, & Driver, 2012; Foxe & Snyder, 2011; Mathewson et al., 2011), related to stimulus properties and task parameters. Together, these studies suggest that alpha-range rhythms should be considered to reflect a broader range of active cognitive functions involved in the production and observation of action.

A great deal of evidence suggests that alpha-range rhythms are also sensitive to the experience of somatosensory stimulation. For example, a body of research has examined the reactivity of the alpha rhythm to painful stimulation (Babiloni et al., 2005; Babiloni et al., 2006; Stancak, 2006; Svoboda et al., 2004). The amount of force exerted upon an object (Mima, Simpkins, Oluwatimilehin, & Hallett, 1999; Mizelle, Forrester, Hallett, & Wheaton, 2010) and different combinations of sensory and motor stimuli (Svoboda et al., 2004) also modulate alpha-range suppression. Since the alpha rhythm is modulated by many somatosensory experiences, there is reason to believe the rhythm would show a similar pattern during the observation of somatosensory stimulation in others, based on the common neural coding underlying action observation (Pineda, 2005; Quandt, Marshall, Bouquet, & Shipley, under review).

The Beta Rhythm (14-22 Hz)

The beta rhythm in the EEG oscillates between approximately 14-22 Hz (Hari, 2006; McFarland, Miner, Vaughan, & Wolpaw, 2000; Stancak, 2006), and like the alpha rhythm, it is involved in sensorimotor processing. The beta rhythm is also thought to originate in the sensory and motor cortices (Gaetz & Cheyne, 2006; Jensen et al., 2005; Ritter et al., 2009), and its amplitude is modulated by both the production of movement and imagined movement (McFarland et al., 2000), suggesting that modulation of the beta rhythm is indicative of activation of sensorimotor cortex. The beta rhythm is thought to be especially sensitive to somatosensory aspects of action (Mizelle et al., 2010; van Ede, de Lange, Jensen, & Maris, 2011; van Ede, Jensen, & Maris, 2010). Recent research suggests that beta rhythm activity may be useful in the study of action mirroring, since the rhythm is sensitive to both the production and observation of action (Puzzo, Cooper, Cantarella, & Russo, 2011; Quandt et al., 2012).

EEG Evidence for the Effect of Experience on Action Processing

In recent years, EEG has been used to examine the effects of sensorimotor experience during action observation, aside from the effects of visual experience or other confounding factors. Marshall *et al* (2009) used EEG to look at how brief imitative performances of novel drawing actions influenced subsequent observation of another person performing the same actions. They found that brief imitation of novel actions led to suppression of alpha-range rhythms in frontal areas during the subsequent observation of an actor performing the actions. Additionally, there was a positive correlation between the accuracy of the imitative performances and the amount of alpha-range suppression over central electrodes. By training participants with novel actions, this experiment controls the amount and type of experience that participants receive with actions, and shows that differences in action processing emerge after only very brief sensorimotor experience. Furthermore, this experiment points to the involvement of sensorimotor experience in changing subsequent vicarious action processing.

A follow-up experiment examined the role of somewhat more experience with novel actions, and further dissociated visual and visuomotor experience from one another (Quandt et al., 2011). On the first day of the experiment, participants viewed two sets of novel drawing actions—one set they learned via observation only; one set they saw and then practiced, learning the actions through both visual and motor experience. On the following day, participants saw videos of both sets of actions learned the day before, as well as another previously unseen set of actions. EEG was recorded while they observed and executed all actions—those learned through visual experience, visual and motor experience, and novel actions. Analyses showed that the actions trained with visuomotor experience resulted in the greatest alpha suppression at frontal sites, followed by the visual-only actions, followed by the completely novel actions. This study, in combination with Marshall *et al* (2009), suggests that during observation of action, the alpha rhythm is sensitive to the type of experience with the observed action—specifically to what extent the action has been motorically performed. This benefit of motor experience over visual-only experience reflects findings from some behavioral studies (Casile & Giese, 2006; Shea, Wright, & Wulf, 2000). Interestingly, in these EEG training studies, these effects emerged after a relatively small amount of experience with the actions, in contrast to the years-long experience seen in most of the expertise literature.

Another experiment showed that sensorimotor experience with heavy or light objects modulated the alpha and beta suppression during the observation of gestures directed to similar-looking objects (Quandt et al., 2012). Participants experienced blue and yellow objects as being either light or heavy (i.e., blue is heavy and yellow is light). They then saw an actor perform gestures directed towards blue or yellow objects. Results showed that the participant's expectations regarding the weight of the object (based on its color and their own prior experience with objects of that color) modulated alpha and beta power during gesture observation. Alpha and beta power were suppressed during observation of gestures toward objects expected to be light, compared to objects expected to be heavy. Prior research has demonstrated that alpha rhythms are modulated by object weight during the execution of actions (Mizelle et al., 2010), so these findings suggest that this effect of sensorimotor variation on alpha may extend to the observation of actions as well.

This line of questioning was followed to ask whether somatosensory experiences alone (aside from motor experiences) would facilitate engagement of mirroring processes during action observation (Quandt et al., under review). Participants performed reaches into yellow and blue boxes that varied in their tactile consequences (i.e., one box was filled with feather brushes, the other was empty). EEG was recorded during execution of the actions, and during observation of videos depicting an actor reaching inside similar-looking boxes. Analyses revealed that during the observation of action, alpha and beta rhythms were more suppressed when the actor was reaching into the box that was expected to contain somatosensory stimulation, compared to the boxes expected to be empty. This supports the idea that somatosensory (in this case, tactile) experiences with action also play a unique role in how we process the actions of others.

Motivation for the Current Study

Together, these research studies suggest that the oscillations involved in neural mirroring processes are affected by the observer's own prior sensorimotor experiences. However, several questions remained unanswered. For example, existing research has not adequately explored *how much* sensorimotor experience is necessary to change our processing of others' actions. It may be that very brief sensorimotor experience is sufficient, as suggested by Marshall *et al* (2009), or it may be that extensive sensorimotor training is most facilitative to mirroring processes as in the work of Calvo-Merino *et al* (2005) and others, but it is impossible to say given what is currently known. Another gap in the existing research concerns how different types of experience with action might affect subsequent action processing. For example, we do not have an adequate explanation for how knowledge gained by sensorimotor experience (i.e., that object is heavy because I just lifted it) differs from knowledge gained by semantic or verbal means (i.e., that object is heavy because I was told about its weight). The current study set out to examine 1) whether activation of the sensorimotor cortex during action observation is increased by action experience, and 2) whether more sensorimotor experience with action would lead the activation of sensorimotor cortex to be sensitive to the predicted consequences of observed action.

CHAPTER 2

METHODS

The current study was designed to provide answers to questions concerning the relation between sensorimotor experience and action processing, specifically what amount of sensorimotor experience with action is necessary to change neural activation patterns during subsequent observations, and how different ways of learning about actions may differently affect subsequent action processing. Building on some elements from previous experiments from our laboratory, the current study provides a comprehensive view of how action experiences change action processing.

In order to explore these questions, EEG activity during action observation was collected before and after the acquisition of information about the sensorimotor characteristics of actions. At the beginning of the experiment, each participant observed video clips of an actor reaching for, grasping, and lifting objects that were visually identical except for color (yellow or blue). Each group then received a different type of experience that revealed information about the objects' weights (i.e., yellow is heavy, blue is light). The participants received either a) brief experience that indicated the different weights of the two objects; b) extended experience that indicated the different weight of the two objects; or c) written information about the weights of the two objects. Then, each participant again viewed video clips depicting an actor acting upon the objects and changes in EEG activity during this second observation epoch were assessed.

Participants

Undergraduate participants were randomly assigned to one of three groups (Brief Experience, BE; Extended Experience, EE; Semantic Information, SI). Each group included 20 undergraduate students for a total of 60 participants. Participants were between 18 and 29 years of age (mean and SD by group: BE = 22.57 [2.63]; EE = 21.80 [2.46]; SI = 21.70 [2.94]) and received class credits in exchange for participation. Left-handed participants were excluded, as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). There were no significant differences in age or handedness between groups. All participants had normal or corrected-to-normal vision, and reported no history of neurological abnormality. One participant (in the Brief Experience group) was excluded from execution analyses due to failure to record video during the execution portion of the experiment, leaving a total of 59 participants for the execution analyses.

Stimuli

Objects

Four objects were created which varied by both color (yellow or blue) and weight (1300 g or 130 g) such that there was one of each possible color and weight combination. The objects were organized into two sets containing one of each color and one of each weight: e.g., heavy yellow and light blue. Gaining information about these objects (during the experience block) created an association for each participant between the object's color and its weight, and therefore, the somatosensory and motor characteristics associated with acting upon each object. This type of color-weight association has been used successfully in past studies (Quandt et al., 2012).

Two distracter objects were also included in the experiment—a small plastic cup, and a small rubber bath toy. Both objects were easy to grasp and lift. These objects were placed on the table during the experience phase of the protocol, and were used to control for the amount of activity performed by the participant (see pages 27-30 for more details). Every participant in the study performed a total of 20 actions, divided between the assigned objects and the distracter objects. Thus, every participant was engaged in the experience portion of the experiment for approximately the same amount of time, and performed the same total number of lifting actions.

Videos

Video clips showed a yellow or blue object resting on a table with a small platform nearby (see Figure 1). After 2 seconds of viewing the static scene, an actor's hand entered from the right side of the screen and reached toward the object as if to grasp it (reach duration = 1 s). At the frame in which the fingers made contact with the object, the video clip froze and the still image of the hand in contact with the object remained visible for 1 s. A still image then showed the hand transporting the object towards the platform (duration = 1 s). Next, a still image showed the hand placing the object on the platform (duration = 1 s). Following this image, the video resumed and the hand retracted away from the object and off the screen, leaving the object on the platform. Together, the video clip and images depicted an actor reaching for, grasping, lifting, and placing the object on the platform. Due to the use of still images rather than video clips to depict the lifting and grasping, the videos contained no kinematic information regarding the actual weight of the objects used in the videos, such as variation in the speed of the lifting action.

Though there were no kinematic clues as to the weight of the objects, it is possible that the grip force required to lift the object could be visible to the participant in the still images, so the weight of the objects used in the video was carefully controlled for. The objects used during creation of the video clips were a third set of objects (never available to any participant) that were mid-weight—i.e., their weight was exactly halfway between

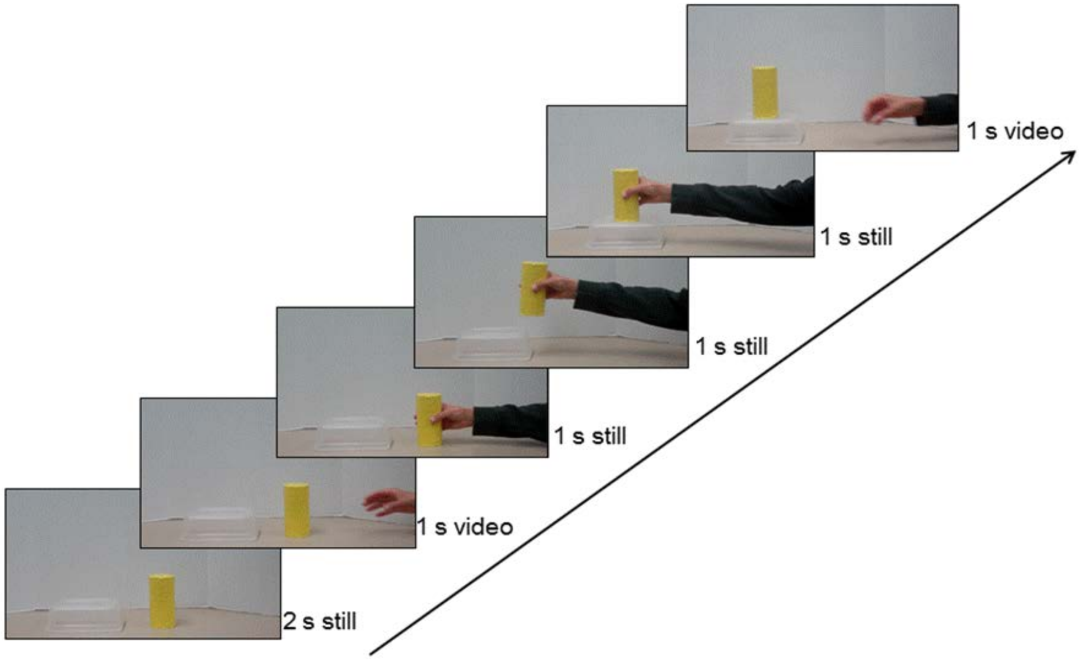

Figure 1. Video Stimuli. Schema depicting the time course of video stimuli. Starting at the bottom left of the image, the video showed a still image of an object on a table, a video of an actor's hand reaching for the object, three still images together depicting the grasping, transport, and placement of the object, and finally a video showing the hand retracting away from the object.

the weights of the "heavy" and "light" objects. Thus, the yellow and blue objects depicted in the videos had identical weights, so any differences in EEG between observation of yellow and blue objects were based on color-weight associations and were not contaminated by variation in the actual weight of the objects in the videos.

A task was embedded in the experimental protocol to maintain participants' attention toward the reaches during observation of the video clips, and to avoid a context of passive viewing. An additional 2-4 trials were included in each observation block that served as "distracter trials". The EEG from these trials was not included in analyses, since their purpose was solely to provide a task for the participant. On these distracter trials, the video clip froze for an additional 2 seconds when the fingers came in contact with the object. During the breaks following each sub-block, the participant was asked to verbally report how many of these freeze-frame reaches they observed. This task ensured that participants focused on the reaching and grasping actions, rather than losing attention or becoming distracted from watching the video stimuli.

Experimental Protocol

Upon arrival, each participant was randomly assigned into one of three groups, and was randomly assigned to one pair of objects: either heavy yellow and light blue; or heavy blue and light yellow. The unassigned pair of objects was not seen or touched by the participant at any time. Each experimental session included observation blocks and experience with objects (see Table 1). The instructions given to the participants are available in Appendix B. EEG and video were recorded during the entire experiment. Each group participated in the following segments of the experiment, in one continuous experimental session:

1. *Part 1*: participants observed 60 trials of videos depicting actions directed toward yellow or blue objects (30 of each color; ~10 min total). The trials were organized into three groups of 20 trials. Each trial started with a fixation cross, and then showed a video clip depicting the actor reaching for, grasping, and lifting one object as described (see Figure 1). The participant saw 2-4 distracter trials, as described above. EEG was collected during this portion of the experiment.

Figure 2. Experimental Setup. During the Experience portion of the experiment, four objects (one blue, one yellow, and two distracter items) were placed in front of the participant. Here, the participant lifts the yellow object in response to a prompt on the computer screen.

2. *Experience*: participants received experience depending on which group they were assigned to. For all groups, the experimenter placed the two assigned objects on the table in front of the participant, next to the two distracter objects (see Figure 2). Following the acquisition of information regarding the objects' weights, each participant was asked by the experimenter which object was heavy and which was light, to confirm that they understood and remembered which color was associated with which weight.
    a. The Brief Experience (BE) group lifted the distracter objects nine times each, then lifted each assigned object one time.

b. The Extended Experience (EE) group lifted the assigned objects ten times each. Participants in this group did not lift the distracter items at all.

c. The Semantic Information (SI) group first lifted the distracter objects ten times each. They then received written information regarding the sensorimotor characteristics of the assigned objects. The computer screen displayed the words “The blue object is heavy. It weighs about 3 pounds. It is filled with concrete.”, “The yellow object is light. It weighs about one third of a pound. It is filled with air.”, and “The blue object is 10 times heavier than the yellow object” (depending on the color-weight association to which they had been assigned).

3. *Part 2*: all participants saw 60 randomized trials (three blocks of 20) depicting the same reaching, grasping, and lifting actions. EEG was collected during this portion of the experiment. 2-4 distracter trials were included in each block.

Table 1

Experimental Protocol

Group	Observation—Part One	Experience	Observation—Part Two	Execution
Brief Experience (BE)	Observe 60 reaches	Lift each distracter 9 times Lift heavy 1 time Lift light 1 time	Observe 60 reaches	Perform 20 heavy reaches, 20 light reaches
Extended Experience (EE)	"	Lift heavy 10 times Lift light 10 times	"	"
Semantic Information (SI)	"	Lift each distracter 10 times Read written information about assigned object weights	"	"

4. *Execution*: the two assigned objects were set on a table in front of the participant. They followed on-screen instructions directing them to reach for, grasp, and lift each object 20 times in a random order. EEG was collected during this portion of the experiment.

Data Acquisition and Processing

EEG was collected from 28 electrodes using a custom-made Lycra stretch cap (Electro-Cap, Eaton, OH) in combination with Electro-Gel conducting gel. The sites included were Fp1, Fp2, F3, F4, Fz, FC1, FC2, FC5, FC6, F7, F8, C3, C4, CP1, CP2, CP5, CP6, T7, T8, P3, P4, Pz, P7, P8, O1, O2 and the left and right mastoids. The EEG signal and was amplified by optically isolated, high input impedance (>1 GΩ) bioamplifiers from SA Instrumentation (San Diego, CA). The signal was digitized at a sampling rate of 512 Hz onto the hard drive of a PC running Snap-Master data acquisition software from HEM Data Corp. (Southfield, MI) using a 16-bit A/D converter (±5 V input range). Scalp electrode impedances were kept under 25 kΩ. Bioamplifier gain was 4000 for the EEG channels, and the hardware filter settings were .1 Hz (high-pass) and 100 Hz (low-pass), with a 12 dB/octave rolloff. The EEG signal was collected referenced to Cz with an AFz ground, and was re-referenced offline to the average of left and right mastoids. Eye blink artifacts were removed using independent component analysis, based on extraction and removal of the characteristic signal produced by movement of the eyes (Hoffmann & Falkenstein, 2008).

The time-frequency analysis was computed using complex Morlet wavelets. In order to assess changes in EEG power relative to baseline, the event-related spectral perturbation (ERSP; Delorme & Makeig, 2004) was computed for frequencies ranging from 8-22 Hz, encompassing the alpha (8-13 Hz) and beta (14-22 Hz) rhythms. ERSP indicates whether power at a certain time, and a certain frequency, is increased or decreased compared to the baseline. ERSP is calculated by means of the equation ERSPft = 10*log10(pft/pbasef), where pft is the mean wavelet estimate for frequency bin f and time point t averaged over trials, and pbasef is the wavelet estimate in frequency bin f and time point t averaged over trials and sample points from the baseline period (Jantzen et al., 2012). ERSP is computed over a sliding time window for each epoch, with a window length of 512 data points. ERSP calculations can reveal that power within a certain frequency band at a particular time is higher than the baseline power—a state known as synchronization. Alternately, power during the time of interest can be lower than at baseline, which is known as suppression.

EEG analyses for the two observation blocks (Part 1 and Part 2) were time-locked to the moment at which the actor's hand made contact with the object (time 0 ms). The analysis epoch encompassed a period of time starting at -2000 ms, when the object was visible on the table but the hand had not yet entered the screen. The epoch included the hand entering the screen, the reach toward the object, and continued until the end of the video clip (+5000 ms). This epoch of interest, -2000 to 5000 ms, was analyzed in comparison to a baseline period defined as -4000 to -2050 ms. The baseline included the display of a black screen and part of the time the object was resting on the table (see Figure 1), in order to compute changes in band power relative to the observation of the static object. There were two types of observation epochs, based on the color of the object seen in each trial. For analyses of the first observation block, prior to gaining experience with the objects, the two trial types were based only upon the color of the object. For the second observation block, the trial types were based on the participant's expectations concerning the sensorimotor characteristics of each object. For example, during the second observation block, a participant may expect yellow objects to be heavy and blue objects to be light.

For analysis of the execution epochs that occurred at the end of the experimental session, the Video Coding System (James Long Company, Caroga Lake, NY) was used to identify the video frames showing the onset and offset of the participants' grasping and lifting actions, again with two conditions: lifting a light object vs. a heavy object. The Video Coding System allowed for the EEG signal to be matched with the corresponding time codes from the video recording, at the level of one NTSC frame, or $1/30^{th}$ of one second. The epochs of interest for action execution were time-locked to the frame in which the participants' fingers came in contact with the object (time 0 ms). The EEG corresponding to the reach (~-500 ms to 0 ms) and the grasping/lifting action (0 ms to offset of grasp, as coded from the video) was then analyzed, in comparison to a baseline period defined as -1999 to -1000 ms, which was prior to the onset of the participant's reach. The duration of participants' actions was also analyzed to compare the timing of actions performed on heavy and light objects.

Hypotheses

Planned statistical analyses tested the following hypotheses:

Observation:

(1) There will be greater alpha and beta rhythm suppression during the second block of observation trials for all three groups, due to greater visual experience

and familiarity with the objects, as well as increased knowledge of the sensorimotor characteristics of the objects (whether in the form of sensorimotor experience or semantic information).

(2) During the first block of observation trials, there will be no difference in alpha or beta ERSP during observation of reaches toward the different-colored objects, since participants will have no expectations regarding the sensorimotor characteristics of the objects.

(3) During the second block of observation trials, the extended experience group will show a significant difference in alpha and beta power depending on the expected weight of the object, such that objects expected to be lighter will elicit lower alpha or beta power than objects expected to be heavier. These effects will be evident primarily over central electrode sites, due to the likelihood that sensorimotor experience affects processes in somatosensory and motor cortices (e.g., Calvo-Merino et al., 2005; Cross et al., 2008).

(4) The effect of weight will be present in the same direction for the brief experience group, but may be a weaker effect than for the extended experience group.

(5) The semantic information group will show no effect of expected weight during the second observation epoch.

(6) The greatest effects of expected weight will be seen in the upper alpha range (11-13 Hz), relative to the lower alpha band (8-10 Hz).

(7) Modulation of alpha-range rhythms will occur during the reaching epoch (before the hand contacts the object) and during the transport phase (when the

object is being lifted and placed on the platform). Beta rhythm modulation will be more closely tied to the transport phase and will not be present during the reach toward the object, based on prior findings (e.g., Quandt et al., under review).

Execution:

(8) During the execution of action, alpha and beta ERSP will be modulated depending on the object's weight. Lighter objects will elicit greater alpha and beta suppression than heavy objects (Mizelle et al., 2010; Quandt et al., 2012).

(9) The beta rhythm will show the strongest effects of weight during execution (Quandt, et al., 2012).

Statistical Analysis

A MATLAB (Mathworks, Natick, MA) plug-in, EEGLAB, was used to statistically compare the ERSP at alpha and beta frequencies within the epoch of interest. Time-frequency decompositions were created for each condition (e.g., heavy and light), and then grand averages were calculated across all participants. Time-frequency analysis allows for the examination of data that differs between conditions at certain points in time and frequency (McGarry, Russo, Schalles, & Pineda, 2012). For example, ERSP was computed for the epoch during which the participants were viewing a reach toward an object expected to be light, and this epoch was statistically compared to those trials when the reach was towards an object expected to be heavy. ERSPs were calculated throughout the epoch (as defined on page 31), compared to a baseline epoch. In order to compare this epoch (observation of light object) with another epoch (observation of heavy object), bootstrap significance tests were performed between the two conditions, based on random re-sampling of the data. These tests compared ERSPs across time and frequency between conditions, and produced time-frequency plots indicating at what points in time and at what frequencies significant differences arose.

Based on the hypotheses being tested, planned comparisons were performed to assess whether ERSPs differed between conditions, for each group. A limited number of statistical significance tests were conducted in order to test the specific hypotheses, and to avoid spurious findings as a result of performing a large number of tests. Specifically, since particular effects were hypothesized for each of the three groups (as in Hypotheses 3-5), the effect of Weight (heavy vs. light) was analyzed for each Group (Extended Experience, Brief Experience, and Semantic Information groups), as was the effect of Part (Part 1 vs. Part 2).

A scalp Region of Interest (ROI) for the EEG analyses was defined as the electrodes overlying sensorimotor cortex. The ROI was made up of seven electrodes: FC1, FC2, C3, C4, Cz, CP1, and CP2. Data were also analyzed at frontal electrodes (F3, F4, and Fz) and parietal electrodes (P3, P4, and Pz) adjacent to the ROI, to provide more information about the topographical distribution of any significant effects (see Figure 3). The hypotheses only concerned activity in the central ROI, so analyses performed at frontal and parietal electrodes served as a control to see whether any effects were specific to central regions, which would imply that underlying sensorimotor cortex might be uniquely sensitive to the task manipulations. In order to correct for comparisons across multiple electrodes and lower the risk of committing a Type I error (Kilner, 2013), all

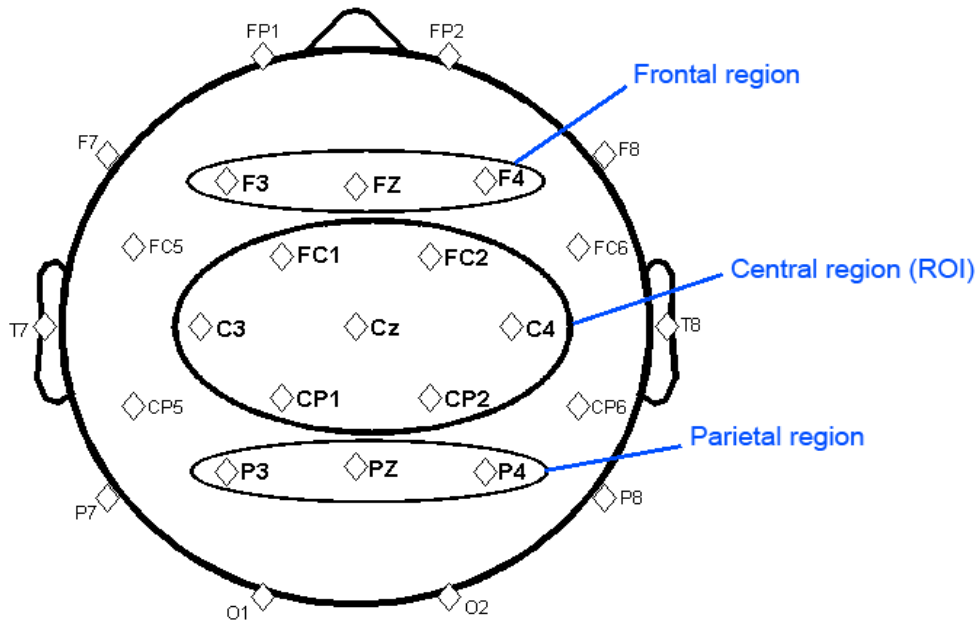

Figure 3. Electrode array. The electrodes from which EEG was recorded. The middle ellipsis defines the central region of interest (ROI). The ellipses above and below indicate the frontal and parietal regions, which were analyzed to assess the topographic specificity of any significant effects. The view is from above the scalp, with the nose at the top of the figure.

statistical tests were held to a Bonferroni corrected p-value threshold (.05 / 7 =~ .007). In addition, in order to correct for comparisons across thousands of time and frequency points, all ERSP results were corrected using the False Discovery Rate correction, as originally described by Benjamini and Hochberg (1995) and implemented in EEGLAB.

SPSS (IBM, Armonk, NY) was used to compare the duration of the participants' actions from the execution portion of the experiment. The time codes generated using the Video Coding System were used to calculate the duration of each action, and these were averaged across conditions to derive an average duration for each participant, for each condition (Heavy vs. Light).

CHAPTER 3

RESULTS

Action Observation

Part One vs. Part Two

The behavioral distracter task embedded within the experimental protocol ensured that participants were paying attention to the videos and watching the reaching actions. At the end of each of the six observation blocks, participants were asked to report how many freeze-frame reaches they had seen. Participants performed well on the distracter task (mean correct responses out of six: BE group = 5.05, EE group = 5.10, SI group = 5.10), and there were no significant differences in accuracy between groups ($F(2,59) = .023$, $p = .977$). Initial time-frequency analyses compared alpha and beta power during action observation before and after experience (Part 1 vs. Part 2) for each Group (Extended Experience, Brief Experience, and Semantic Information groups), regardless of whether the object being viewed was expected to be heavy or light. This analysis, as described in Hypothesis 1, tested whether participants' experience with the objects changed overall alpha or beta suppression during action observation over the course of the experiment.

For the EE group, the analysis indicated that during various time points within the observation epoch, there was significantly more alpha and beta suppression at six central electrode sites during observation of the actions in Part 2 compared to Part 1 (ps < .007). Similar alpha-range effects were seen at parietal electrodes, and beta suppression was significantly greater at one frontal electrode (F3) for the EE group throughout the epoch of interest ($p < .007$). Figure 4 depicts the distribution of these significant effects, and

Figures 5 and 6 show the time-frequency plots for electrodes C3 and C4 respectively, which overlie the hand areas of the sensorimotor cortex.

For the BE group, there was significantly greater alpha suppression at the left central electrode (C3) during Part 2 compared to Part 1 during observation of reaching, grasping, and lifting ($p < .007$).

For the SI group, the analysis indicated that at one central electrode, and several frontal and parietal electrodes, there was significantly greater alpha suppression during Part 2 compared to Part 1 at various time points throughout the observation epoch (ps < .007). The SI group also showed significantly greater beta-range suppression at one central electrode and one parietal electrode during Part 2 compared to Part 1.

Expected Heavy vs. Expected Light

During Part 1, all participants viewed the reaching/grasping video clips. Analysis of the data from Part 1 tested the hypothesis that prior to receiving experience with acting upon the objects, there would be no differences in ERSP based on Weight (heavy vs. light, based on random assignment for each participant) or Group, as in Hypothesis 2. This hypothesis was confirmed. There were no effects of Group or Weight on alpha (8-13 Hz) or beta (14-22 Hz) ERSP at any frontal, central, or parietal electrode sites during Part 1 of the experiment, for any Group.

Time-frequency analyses of EEG collected during Part 2 of the experiment tested whether ERSPs in the alpha and beta frequency ranges were sensitive to the expected weight of the objects, within each of the Groups (Hypotheses 3-5), and, if these differences existed, during what times and at what frequencies (Hypotheses 6-7).

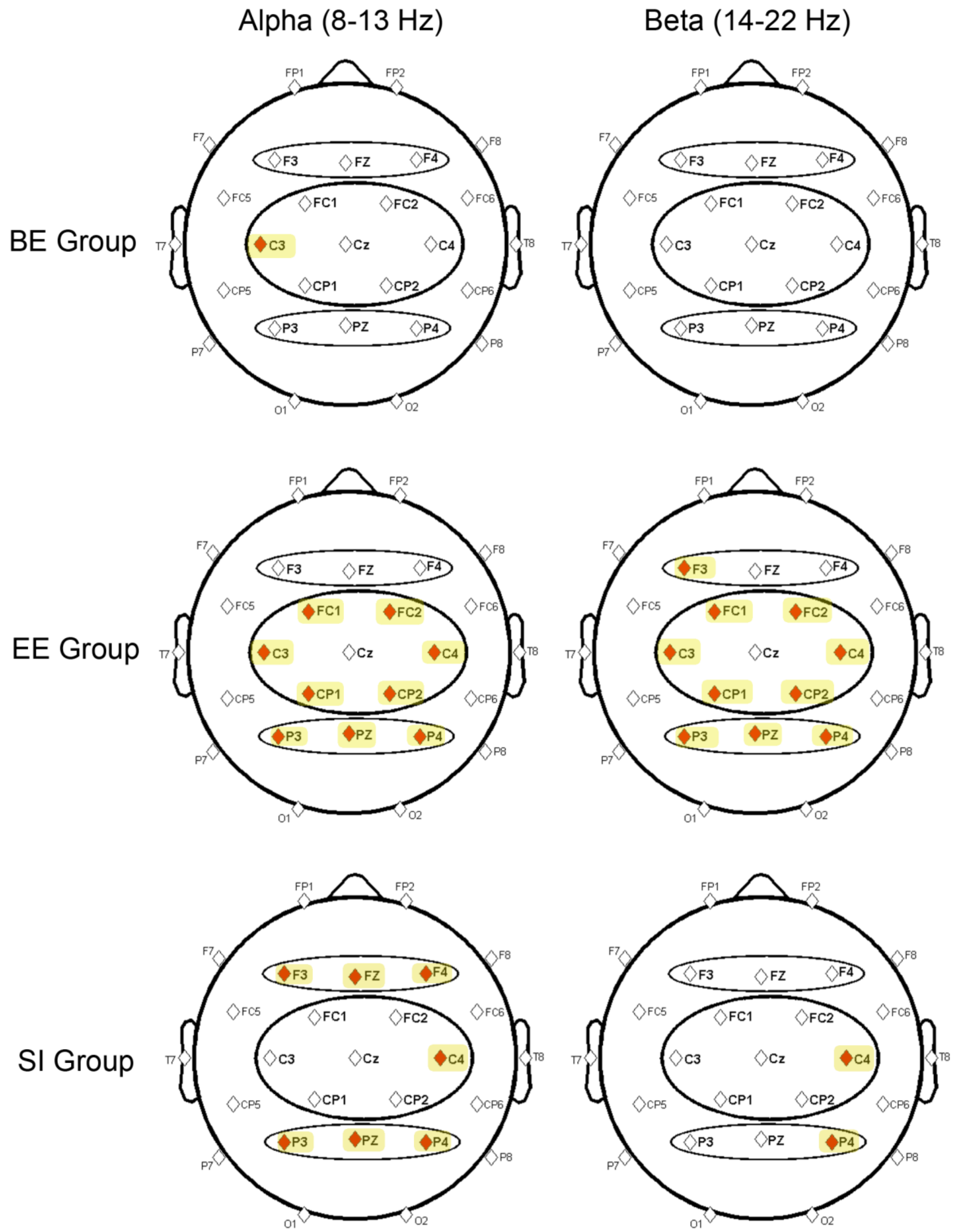

Figure 4. <u>Distribution of Effect of Part for each Group</u>. Highlighted electrodes indicate that there was a significant difference in alpha (left) or beta (right) suppression during the observation of actions in Part 1 and Part 2. Electrodes are highlighted if the time-frequency analysis revealed significant (p < .007, FDR corrected) differences between Part 1 and Part 2 at any point during the epoch of interest (-2000 to 5000 ms). The primary central ROI, as well as the frontal and parietal regions, are indicated.

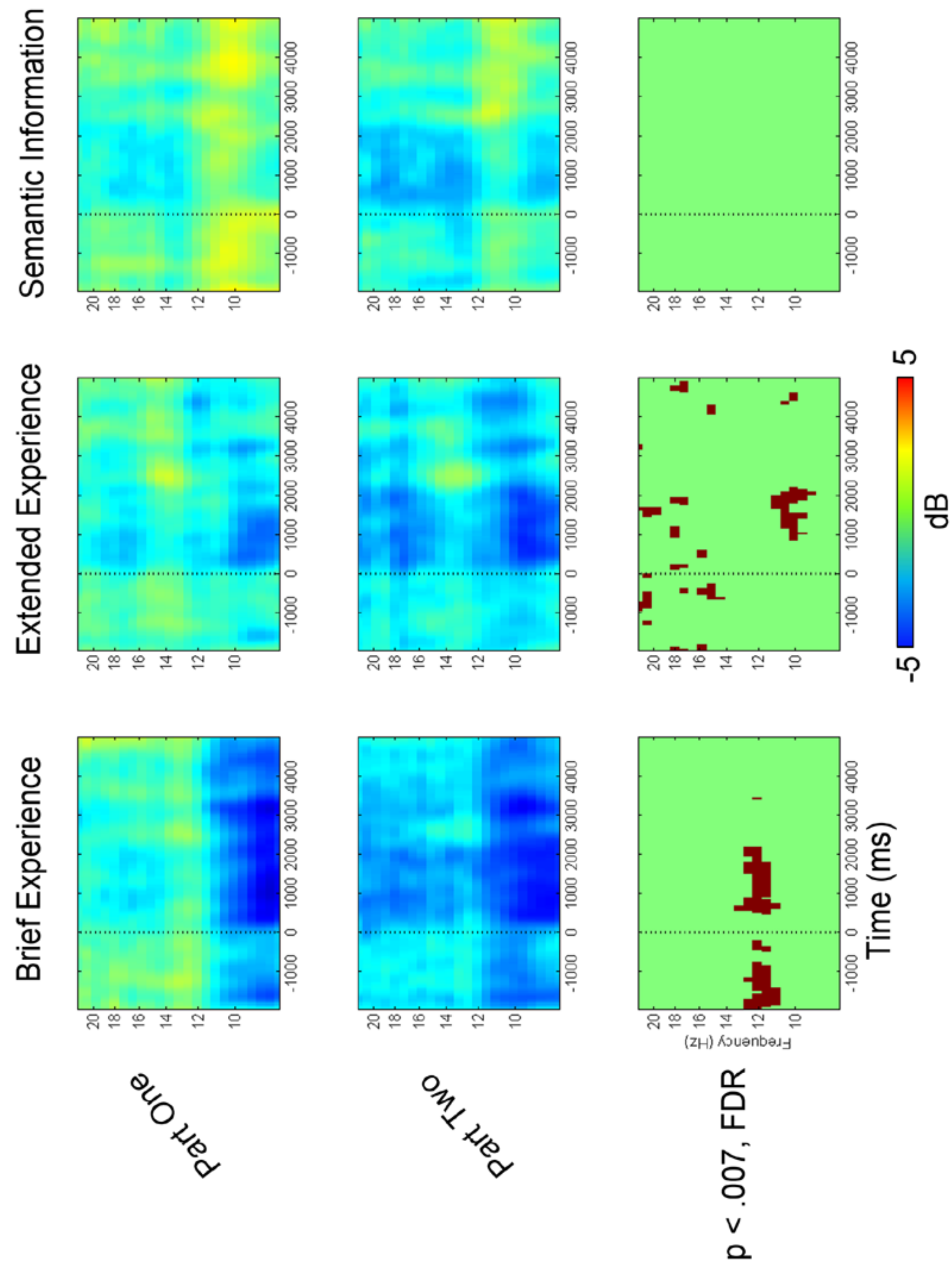

Figure 5. Differences in ERSP by Part for each Group at Electrode C3. Time-frequency analysis showing ERSPs at C3 for each condition during the observation of actions before (Part 1) and after experience (Part 2). Cooler colors indicate suppression of power; warmer colors indicate increase in power. Bottom panels show significant ($p < .007$, FDR corrected) differences between ERSPs in alpha (8-13 Hz) and beta (14-22 Hz) frequency bands (dark red = Part 2 < Part 1).

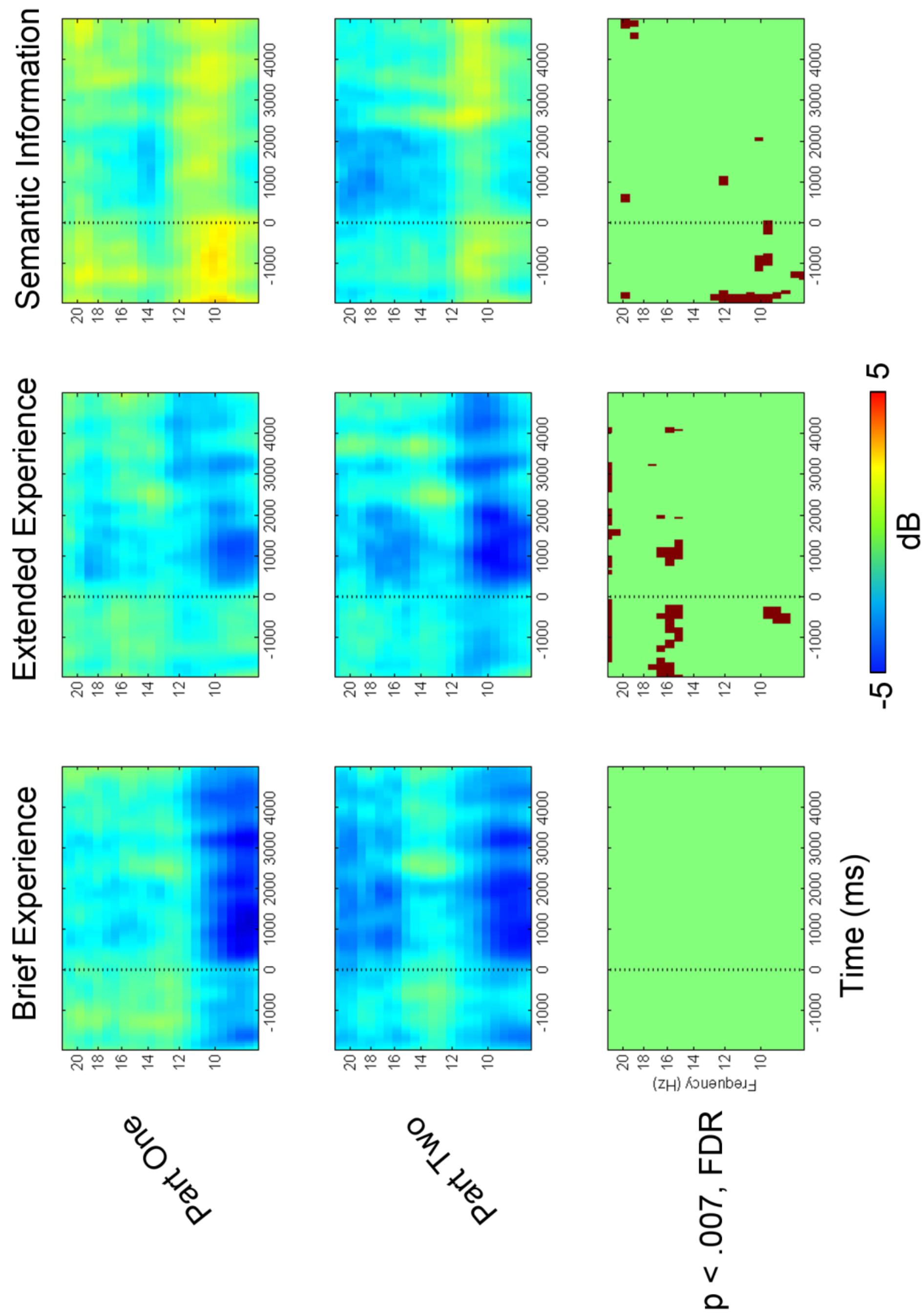

Figure 6. <u>Differences in ERSP by Part for each Group at Electrode C4</u>. Time-frequency analysis showing ERSPs at C4 for each condition during the observation of actions before (Part 1) and after experience (Part 2). Cooler colors indicate suppression of power; warmer colors indicate increase in power. Bottom panels show significant (*p* < .007, FDR corrected) differences between ERSPs in alpha (8-13 Hz) and beta (14-22 Hz) frequency bands (dark red = Part 2 < Part 1).

The expectation of weight during this portion of the experiment would be based on the color-weight associations formed during the acquisition of experience with the objects. During Part 2, no significant effects within each Group were found for expected Weight at frontal or parietal electrodes. The results outlined below therefore concern electrodes within the central ROI.

In the extended experience (EE) group, significant differences between the conditions were apparent throughout the analysis epoch. Figure 7 depicts the distribution of these significant effects, and Figures 8 and 9 show the time-frequency plots for electrodes C3 and C4 respectively, which overlie the hand areas of the sensorimotor cortex. The time-frequency analyses indicated that at frequencies above 10 Hz, there was significantly greater alpha and beta suppression at the left central mid-electrode (C3) during observation of trials showing objects expected to be light, compared to objects expected to be heavy ($p < .007$). In the lower alpha range, between 8-10 Hz, there was a significant effect in the opposite direction—greater alpha suppression during the observation of trials showing objects expected to be heavy ($p < .007$).

For the brief information (BE) group, time-frequency analysis showed that throughout the observation epoch, there was significantly more alpha and beta suppression at the left fronto-central electrode (FC1) during observation of an action directed toward a light object compared to a heavy object ($p < .007$). These effects were particularly evident in the 8-10 Hz range.

The semantic information (SI) group showed no significant differences for expected object Weight following experience.

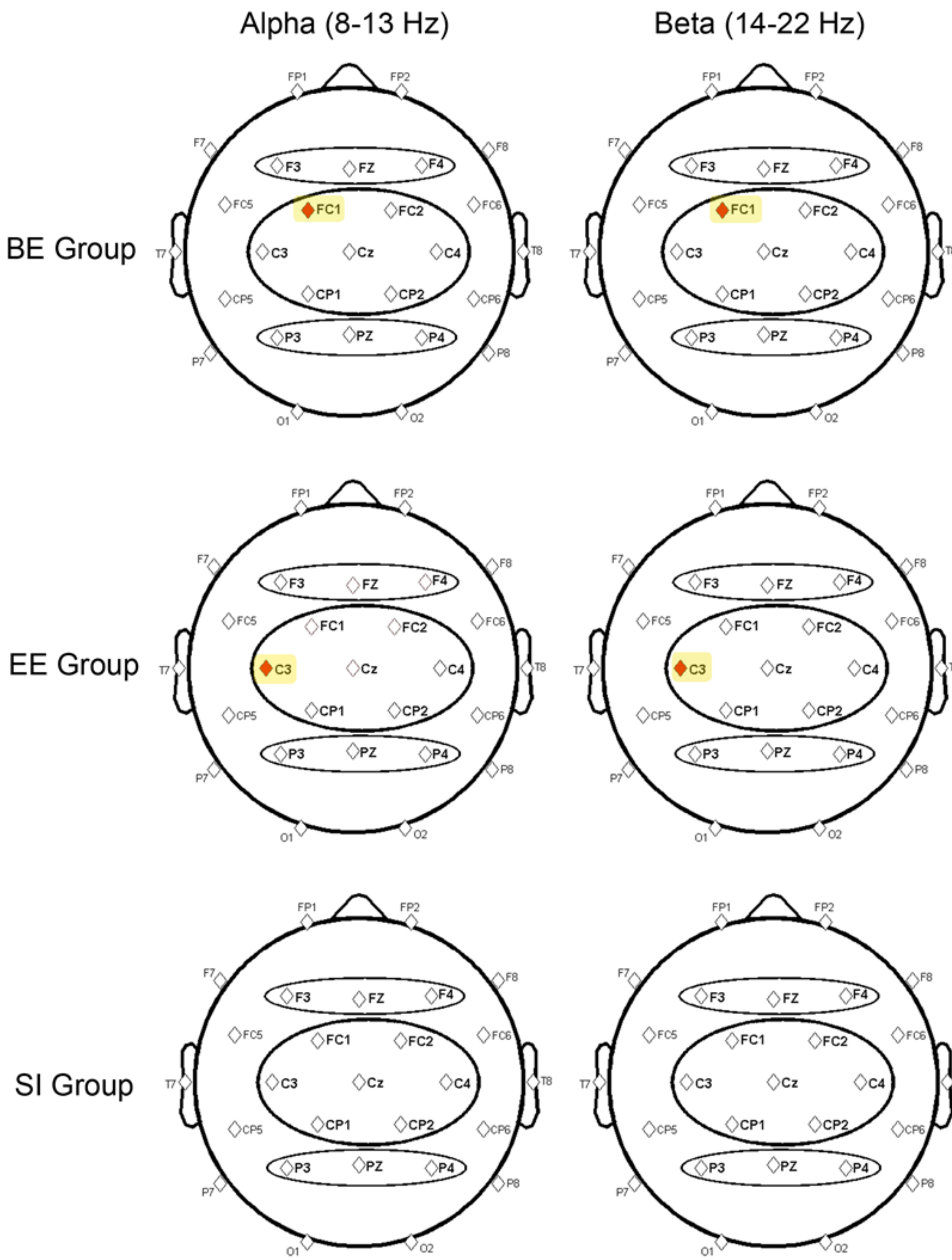

Figure 7. <u>Distribution of Effects of Weight for each Group</u>. Highlighted electrodes indicate that there was a significant difference in alpha (left) or beta (right) suppression during the observation of actions upon heavy or light objects. Electrodes are highlighted if the time-frequency analysis revealed significant (*p* < .007, FDR corrected) differences between Heavy and Light at any point during the epoch of interest (-2000 to 5000 ms). The primary central ROI, as well as the frontal and parietal regions, are indicated.

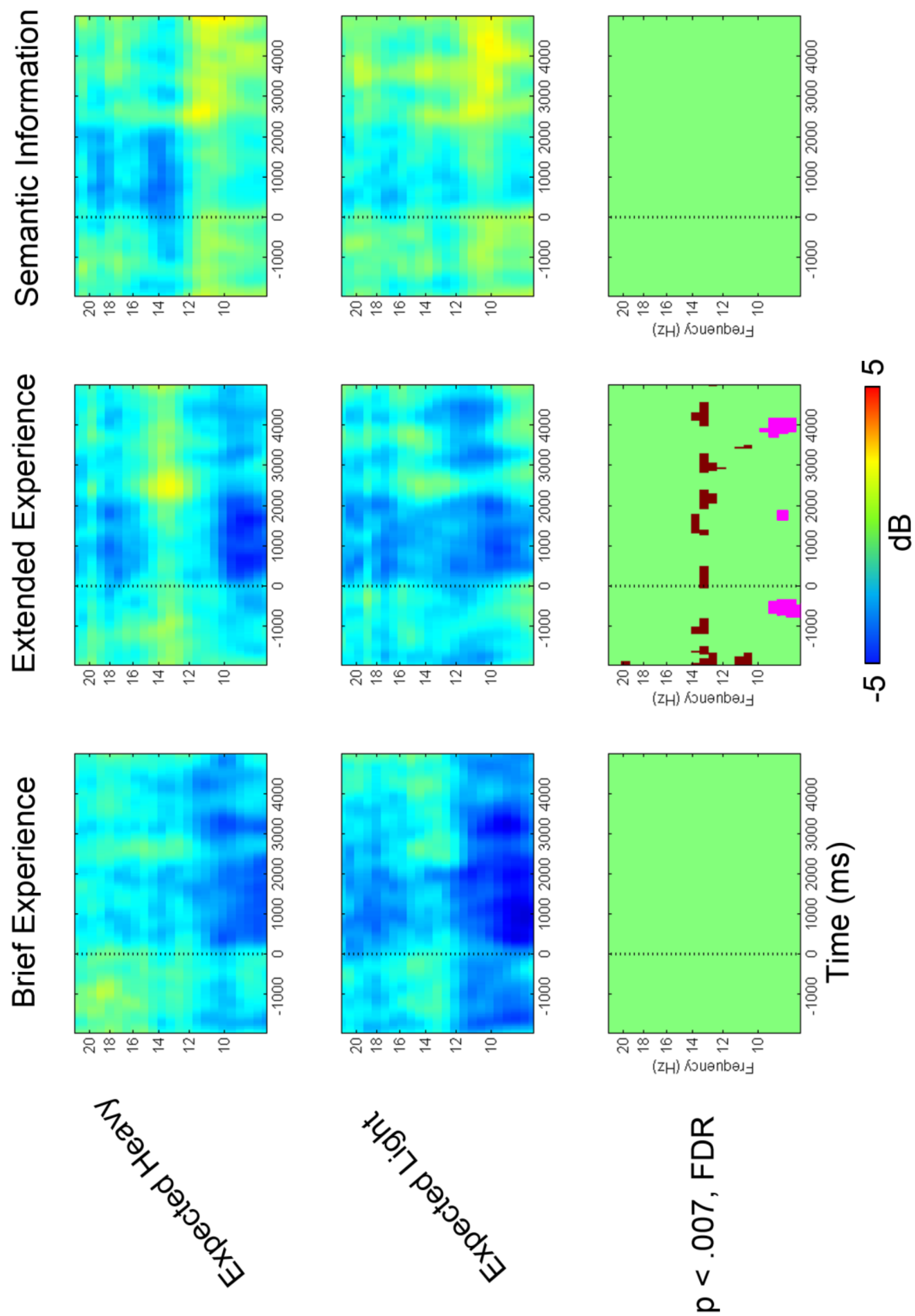

Figure 8. Differences in ERSP by Weight for each Group at Electrode C3, Part 2 Only. Time-frequency analysis showing ERSPs for each condition during the observation of actions upon objects expected to be Heavy or Light. Cooler colors indicate suppression of power; warmer colors indicate increase in power. Bottom panels show significant (*p* < .007, FDR corrected) differences between ERSPs in alpha (8-13 Hz) and beta (14-22 Hz) frequency bands (dark red = Light < Heavy; pink = Heavy < Light).

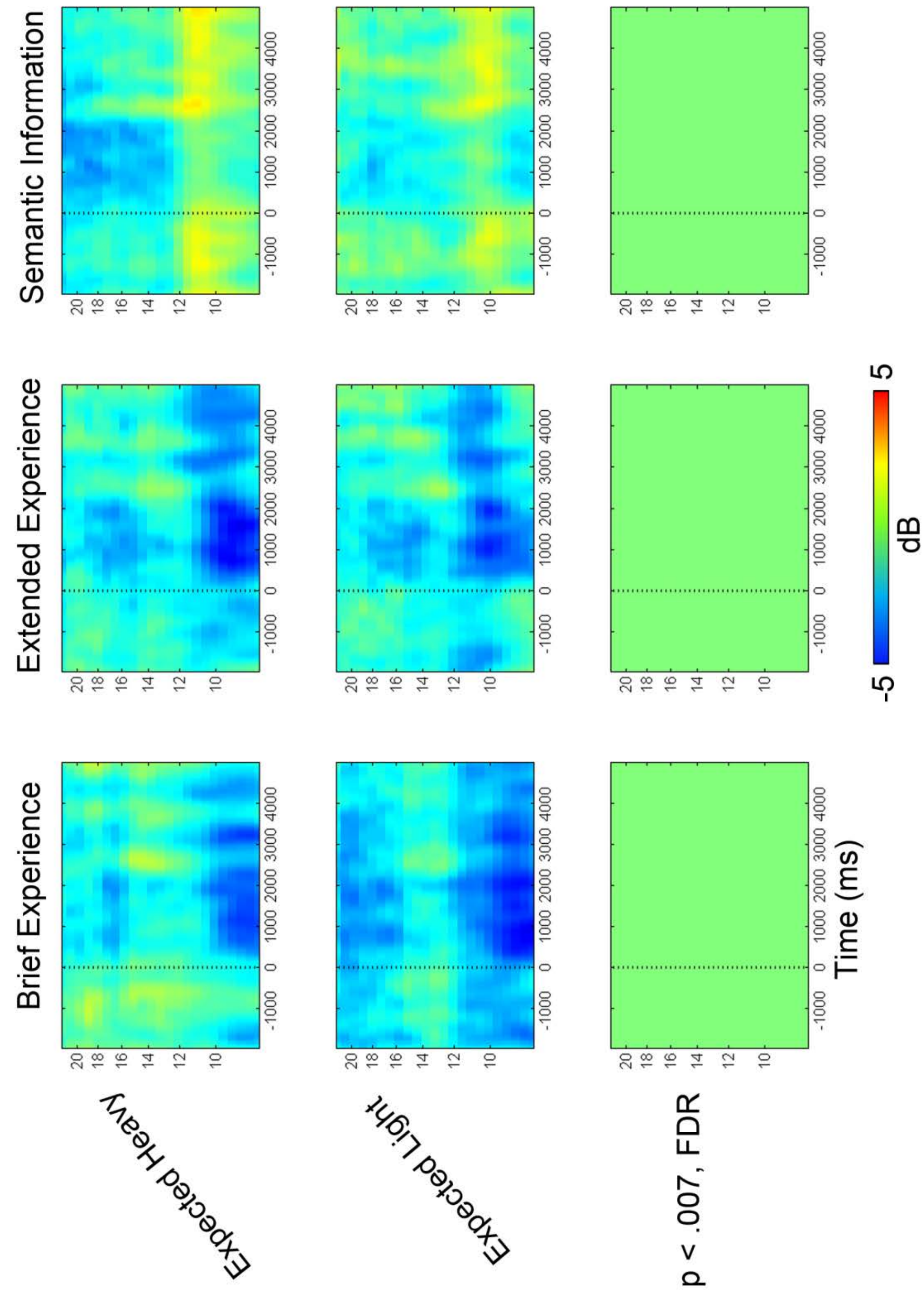

Figure 9. <u>Differences in ERSP by Weight for each Group at Electrode C4, Part 2 Only</u>. Time-frequency analysis showing ERSPs at C4 for each condition during the observation of actions upon objects expected to be Heavy or Light. Cooler colors indicate suppression of power; warmer colors indicate increase in power. Bottom panels show no significant (*p* < .007, FDR corrected) differences between ERSPs in alpha (8-13 Hz) and beta (14-22 Hz) frequency bands.

Action Execution

An analysis of action execution compared ERSPs during the production of reaching, grasping, and lifting actions, by Weight (heavy or light; Hypotheses 8 and 9). At all central electrode sites in the region of interest, there was no significant difference between alpha or beta power while acting upon heavy or light objects. Figure 10 shows time-frequency plots at electrodes C3 and C4, overlying the hand areas of the sensorimotor cortex. Additionally, there was no significant effect of Weight on alpha or beta power at frontal or parietal electrode sites.

Three exploratory post-hoc follow up analyses were performed to see if alpha power during execution might differ by Group membership.

For the EE group, the time-frequency analyses showed that there was significantly greater alpha suppression while acting upon light objects, compared to heavy objects, at frontal and central electrodes, at various time points during the observation epoch (all *p*s $< .007$; see Figure 11 for the distribution of these effects). Additionally, the EE group showed significantly more beta suppression during lifting of light objects at the left central electrode ($p < .007$).

There were no significant effect of Weight for the BE group during execution of actions.

For the SI group, time-frequency analyses showed that at various time points throughout the epoch, there was significantly greater alpha and beta suppression while acting upon light objects compared to heavy objects at three central electrodes (all *p*s $<$ .007; see Figure 11). These effects for the SI group were also present at frontal and parietal electrode sites.

The duration of participants' actions upon the heavy and light objects was compared to see whether the timing of the actions was similar. Duration of action was defined as the amount of time during which the participants' fingers were in contact with the object—i.e., grasping and lifting. The duration of actions upon heavy objects (mean = 2.58 s, SD = .71 s) was significantly longer than the duration of actions upon light objects (mean = 2.16 s, SD = .54 s; $t(58)=10.60$, $p < .001$).

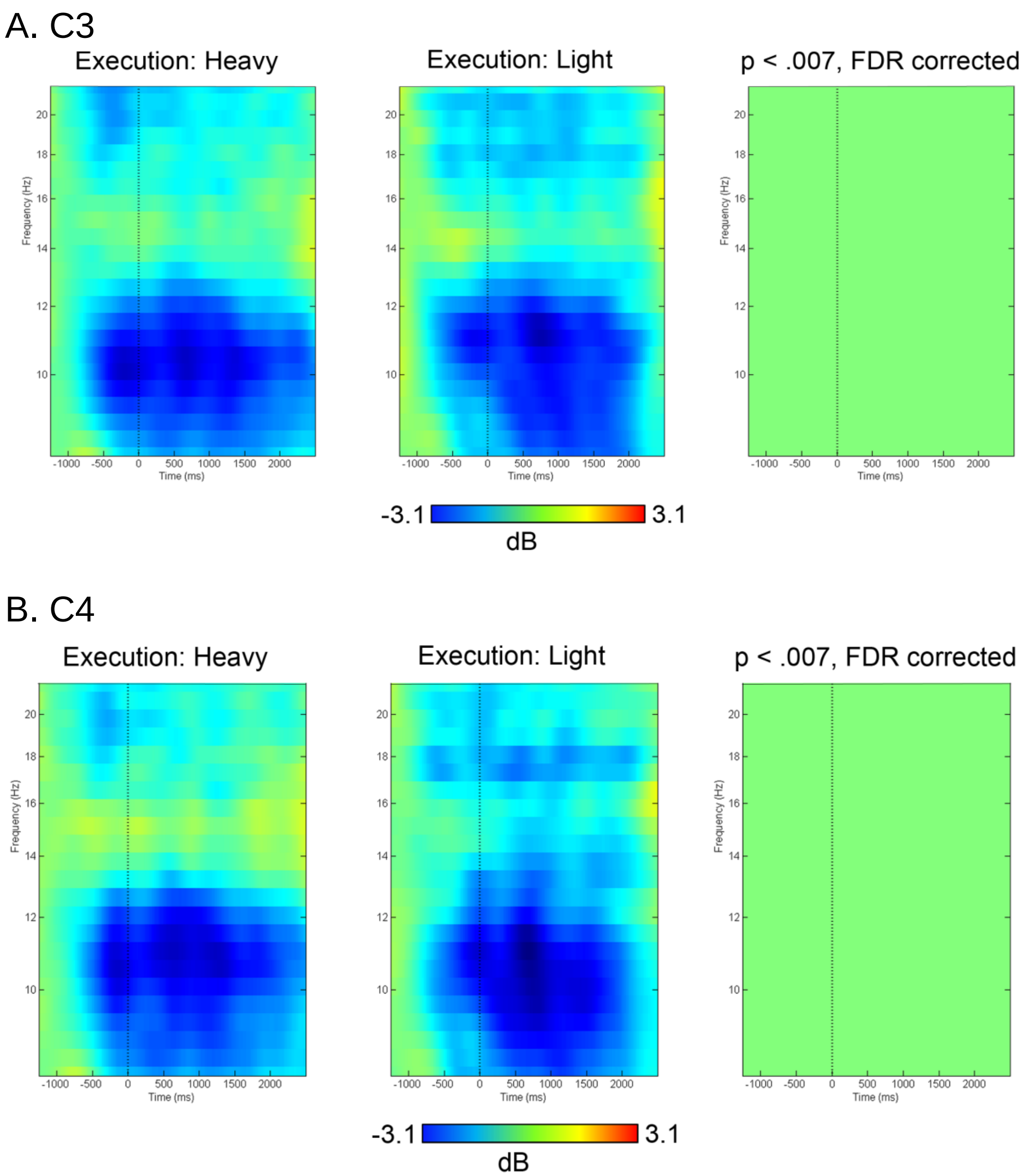

Figure 10. Overall ERSP during Action Execution at Electrodes C3 and C4. Time-frequency plots depicting alpha and beta ERSP during execution of actions, at C3 (panel A) and C4 (panel B). Cooler colors indicate suppression of power, measured in dB, and warmer colors indicate an increase in power. Time 0 is the moment at which the participants' hand came in contact with the object. The right panel indicates that there were no significant difference exists between the two conditions.

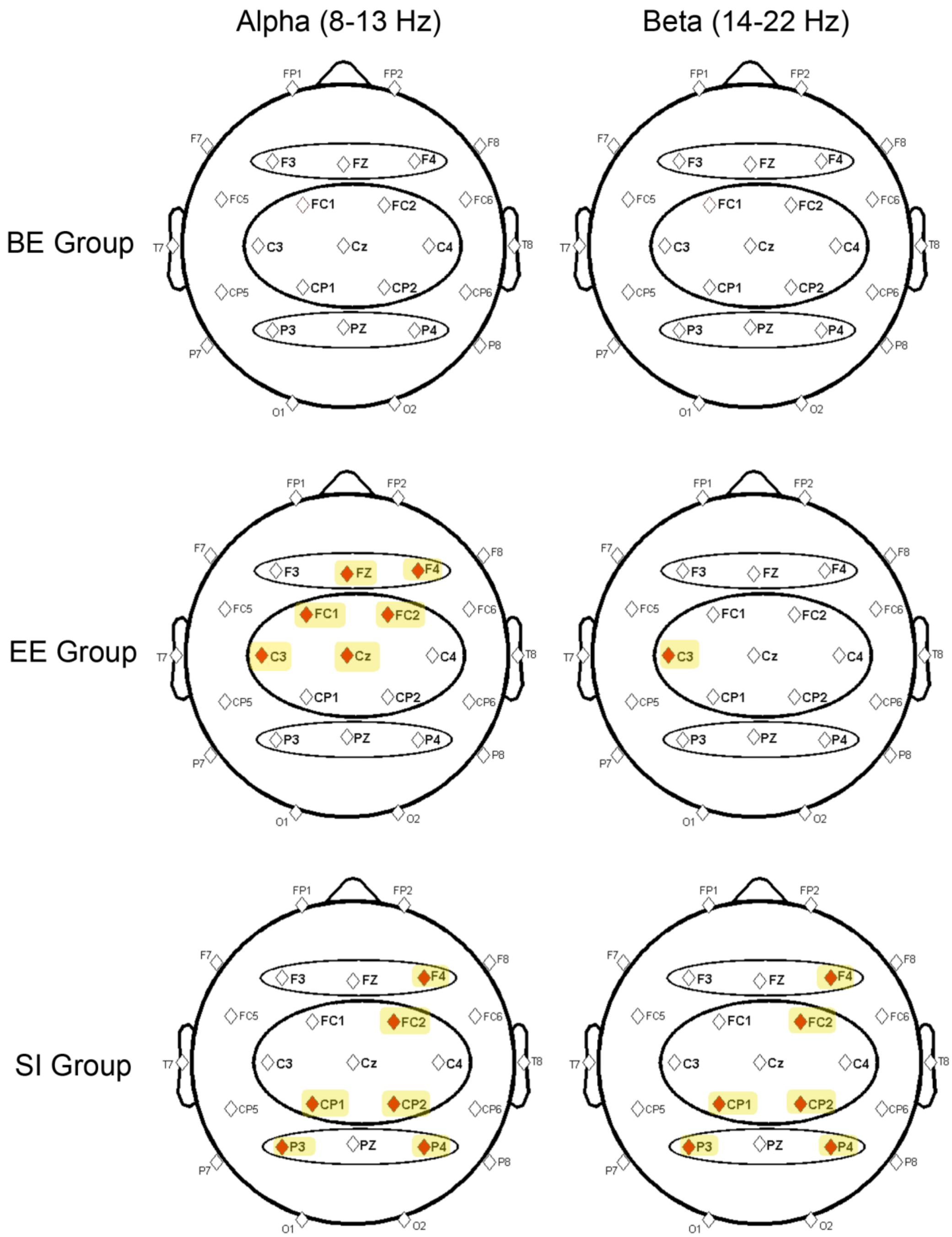

Figure 11. Execution: Differences in ERSP by Weight for each Group. Highlighted electrodes indicate that there was a significant difference in alpha (left) or beta (right) power during the execution of reaching and grasping actions upon heavy or light objects. Electrodes are highlighted on this map if the time-frequency analysis revealed any significant (p < .007, FDR corrected) differences between heavy and light at any point during the epoch of interest (-1250 to 2500 ms). The primary central ROI, as well as the frontal and parietal regions, are indicated.

CHAPTER 4

DISCUSSION

Prior research suggests that the activity of neural mechanisms associated with action observation may be modulated by the prior experience an observer has with the action he or she is observing. However, it has until this point been unclear *how much* and *what kind* of experience is necessary to modulate neural aspects of action processing. In addition, it is debated whether increased experience with action will facilitate neural mirroring, or alternatively whether it would introduce efficiency into the system, reducing motor resonance. The current study was designed to test whether different amounts of sensorimotor experience with actions, or the acquisition of semantic knowledge about actions, would alter the neural oscillations involved in action observation. The results of this study suggest that after sensorimotor experience with action, the action observation network (AON) is more sensitive to the predicted sensorimotor consequences of the observed action. The findings presented here make a case for the facilitation of neural mirroring activity following sensorimotor experience, which has important implications for the field of mirror neuron research.

What Kind of Experience Modulates Neural Mirroring?

As discussed in the Introduction, there is an active debate concerning whether experience with action results in greater or lesser activation of the sensorimotor cortex during subsequent action processing. The results of the current study support Hypothesis 1, in that experience with action leads to greater sensorimotor cortex activation, as measured by more alpha- and beta-range suppression. In particular, the results of the time-frequency analysis comparing Part 1 and Part 2 for each Group show that to some extent, all three types of experience led to greater alpha and beta suppression during subsequent action observation. These findings support the previous work suggesting that action experience leads to greater AON activation (Behmer, Jr. & Jantzen, 2011; Calvo-Merino et al., 2005; Cross et al., 2012; Cross et al., 2008; Haslinger et al., 2005; Kim et al., 2011; Marshall et al., 2009; Orgs et al., 2008; Quandt et al., 2012), and contradict the suggestions of neural efficiency following sensorimotor experience in experts (Babiloni et al., 2009; Babiloni et al., 2010; Vogt et al., 2007). This increase in alpha and beta suppression in Part 2 was present at a number of electrodes for the EE and SI groups, while the BE group showed this effect only at one central electrode. The indistinct topography of these effects suggests that other functions of the alpha rhythm, aside from sensorimotor activation alone, may be affected by prior experience with action. It is possible that the widespread changes in alpha and beta suppression reflect not only the acquisition of knowledge about the sensorimotor consequences of acting upon the objects, but also increased visual experience, familiarity with the objects, and possible changes in attention to the stimuli.

One primary goal of this study was to examine the amount of sensorimotor experience with action that is needed to induce changes in subsequent neural mirroring activity. In the existing research, most studies have given participants one particular amount and type of sensorimotor experience. Previous studies have looked at very brief imitative drawing experience (Marshall et al., 2009), moderate imitative drawing experience (Quandt et al., 2011), multiple days of training with dance actions (Orgs et al., 2008), or moderate amount of knot-naming or tying experience (Cross et al., 2012), for example. A major limitation of these studies is that they presented subjects with one type of action experience, often compared to a control condition receiving no experience, but they did not compare different amounts of experience (e.g., brief vs. extensive) or types of experience (e.g., sensorimotor vs. semantic). The current study aimed to include both of these variables, and the results suggest that both amount and type of experience significantly increase subsequent neural mirroring processes.

The most important finding in support of the current hypotheses is that alpha- and beta-range suppression over the left sensorimotor cortex was sensitive to the predicted sensorimotor consequences of acting upon different objects, following sensorimotor experience with those objects. Specifically, after participants' experience with the objects, those participants in the extended experience (EE) group showed significant differences in ERSP depending on whether the object they were seeing was expected to be heavy or light. Since this effect was significant at C3 only, it is likely that the difference is due to different involvement of the underlying sensorimotor cortex in processing the actions toward heavy objects or light objects, and it is likely that the effect is specific to the mu rhythm. Additionally, the brief experience group (BE) showed significant differences in expected light vs. expected heavy during Part 2 at electrode FC1 over left fronto-central cortex, which suggests that the brief sensorimotor experiences received by those participants were enough to change how actions upon heavy and light objects were processed. In short, it appears that sensorimotor experience with action (whether brief or extensive) facilitates AON activation, and more sensorimotor experience may, as predicted, lead to the greatest sensitivity to the expected sensorimotor characteristics of action.

Hypotheses 6 and 7 predicted the specific times and frequencies at which the effects of sensorimotor experience would be seen. First, it was predicted that the upper alpha range EEG (between 11-13 Hz) would be particularly sensitive to prior experience during the observation of action. For the EE group, significant differences between expected heavy and expected light occurred throughout the alpha range, and into the beta frequency range, with the most sustained effect occurring from 12-14 Hz, a slightly higher frequency band than predicted (see Figure 8). Hypothesis 7 predicted that alpha-range effects would be apparent during the observation of reaching and transport. For the EE group, significant effects were seen during essentially the entire epoch, from when the object was visible resting on the table at -2000 ms, to when the hand was retracting away from the object at +4500 ms. Thus, we see no temporal specificity and conclude that the sensitivity to predicted sensorimotor consequences of action occurs in anticipation of upcoming action, as well as during the observation of the unfolding action. Similarly, for the BE group, significant differences were apparent throughout the epoch. However, the differences found in the BE group were present at a lower frequency band, with most effects in the 8-10 Hz range. The differences in frequency band sensitivity between groups suggest that the brief and extended experience conditions may be affecting different aspects of subsequent action processing, but it remains unknown exactly what those might be.

There was no effect of predicted weight during observation in Part 2 for the semantic information (SI) group, meaning that the participants who learned about the objects' weights by means of written material did not subsequently show any sensitivity to the predicted sensorimotor consequences of observed actions. This is consistent with the work of Senot and colleagues (2011), in which labeling objects as "heavy" and "light" did not affect motor evoked potentials during observation of an actor lifting the objects. In the current experiment, members of the SI group received relatively rich information concerning the sensorimotor characteristics of the yellow and blue objects--learning, for example, that a blue object weighed three pounds and was filled with concrete, whereas the yellow object weighed 1/3 of a pound and was filled with air. Even with these elaborate descriptions of weight, alpha and beta suppression was not significantly affected during Part 2 of the experiment. One might wonder if an even more detailed description might induce changes in subsequent action observation, or whether the acquisition of semantic information is simply not sufficient to significantly facilitate neural mirroring processes. The current results, taken together with the work of Senot and colleagues, suggest the latter may be more likely.

Sensitivity of Neural Oscillations to Sensorimotor Characteristics of Action

The sensorimotor experiences that the participants received concerned the weights of two objects of different colors—they learned that blue was heavy and yellow was light, or vice versa. This manipulation allowed us to investigate everyday naturalistic grasping and lifting actions (as opposed to studies in which novel or unusual actions are learned), and focus on the association of a specific sensorimotor characteristic (weight) with a particular object. The study design meant that any differences in Part 2 between Weights were solely based on their prior experiences, and not due to any intrinsic or generalized knowledge (e.g., blue objects are always heavy).

It is notable then, that this experience did, in the case of the EE and BE groups, change the way the participants processed the actions—it seems that mirroring processes are not simply sensitive to the presence of an action in a binary (on/off) fashion, but rather that AON activation is sensitive to the specific sensorimotor characteristics associated with that acting upon an object (Marshall, Saby, & Meltzoff, 2013; Quandt et al., 2012). This implies that neural mirroring is sensitive to detailed information about the feeling of the action another person is performing. Thus, if you see someone lifting to pick up a box, aspects of your perception of their action are different if you expect the box to be empty or full (Alaerts, Senot, et al., 2010; Alaerts, Swinnen, & Wenderoth, 2010; Hamilton, Wolpert, Frith, & Grafton, 2006).

We hypothesized that the observation of an action directed toward a light object would result in greater mu suppression. One may wonder why, then, the EE group showed significant results going in two opposite directions (see Figure 8). In the lower alpha band (8-10 Hz), the observation of action toward an object expected to be heavy led to greater mu suppression—a brain state traditionally associated with greater activation of the underlying sensorimotor cortex. It is possible that this finding reflects greater involvement of the sensorimotor cortex during the observation of a more physically demanding action such as lifting a heavy weight (Alaerts, Senot, et al., 2010; Alaerts, Swinnen, et al., 2010). At higher frequencies, encompassing upper alpha and, to some extent, the beta band, the significant results went in the opposite, and predicted, direction. At these frequencies, there was greater suppression during the observation of actions directed to light objects. In the 12-14 Hz range particularly, these significant differences were sustained throughout the epoch. Importantly, these results in the upper alpha and beta bands are consistent with the results from a previous study from our lab concerning the acquisition of experience regarding the weight of objects during action observation

(Quandt et al., 2012). In this previous study, during both the observation of gesture and the execution of action upon blue/yellow heavy/light objects, light objects were associated with more alpha and beta suppression than were heavy objects.

Increased alpha and beta suppression during the observation of actions upon objects with lighter weights may be due to the observer mirroring the increased motor control needed to lift a light object. Lifting a heavy object (in this case, a relatively heavy weight of around three pounds) requires more brute force, whereas lifting the lighter object may require more delicate control of one's action, in order to avoid over-shooting and thrusting the object high into the air. This hypothesis is supported by other research showing that alpha suppression decreases as weight-bearing load increases (Mizelle et al., 2010), and that this pattern may take a U-shaped form, with greatest suppression for mid-weight objects. Other research also found a non-linear relation between inertial load and EEG measures of sensorimotor activation (Kristeva, Cheyne, Lang, Lindinger, & Deecke, 1990). The authors of this study hypothesized that this effect may be largely due to the higher-order control mechanisms activated when performing a highly demanding task, such as lifting a heavy object. Taken together, the results of the current study, in combination with prior research, suggest that the relation between sensorimotor characteristics of action and the activation of sensorimotor cortex is not entirely straightforward. In particular, the current findings suggest that lower and upper frequency bands may be differentially sensitive to variations in expected weight. Future research should continue to explore this topic, perhaps by parametrically varying weight to more fully describe how neural activity is modulated by the force required to perform an action.

Oscillatory brain activity often shows asymmetries between the left and right hemispheres. The results presented here are consistent with some prior findings regarding hemispheric differences in action processing. While we had no specific hypotheses about how the two hemispheres of the brain might be differentially involved in action processing, and our experiment was not designed to explicitly test for them, the results do show a general pattern of sensitivity to the predicted sensorimotor consequences of action at electrodes over the left hemisphere (see Figure 7). This may be due to increased sensitivity of action processing over left sensorimotor cortices, or it may be due to the fact that the video stimuli depicted an actor's right hand, that consistently entered from the right side of the screen, in which case we might expect to see greater activation over contralateral brain regions (Perry & Bentin, 2009; Quandt et al., under review). This would be consistent with the fact that each hemisphere generally processes the sensorimotor information associated with the opposite side of the body (Graziano & Gross, 1998). The effects of Part, however, do not appear to have as much topographic specificity, since the electrodes at which there were significant differences were diffusely spread out across the scalp. The lack of specificity may mean that following experience, activation in the sensorimotor cortex, and throughout widespread cortical networks, was increased.

Action Execution

Many neural mirroring studies only report data from observation conditions. In the current study, it was a priority to see how the dynamics of neural oscillations were sensitive to variation in sensorimotor characteristics (i.e., weight) during the production of actions, in order to provide a more complete picture of how weight (or expected weight) and action processing might relate to one another. This analysis was somewhat exploratory, since only a small number of studies have collected similar data from both the observation and the execution of similar actions (Avanzini et al., 2012; McGarry et al., 2012; Muthukumaraswamy et al., 2004). In our previous work, we found that execution of action upon heavy or light objects, and observation of gestures directed toward similar objects, resulted in similar suppression of alpha and beta rhythms, but that the topography of these effects differed depending on whether the participant was seeing or doing the actions (Quandt et al., 2012). We predicted a similar effect in the current study.

It is important to note that the production of actions upon both heavy and light objects resulted in the expected pattern of EEG responses—alpha suppression, and to a lesser extent, beta suppression, during the reach (approximately -750 ms to 0 ms), and during the grasping and lifting of the objects (0 ms to approximately 2000 or 2500 ms; see Figure 10). Contrary to our hypotheses, however, the weight of the two objects had no significant effect on alpha and beta suppression during the production of action. It is possible that, as some previous research indicates, the relationship between weight and sensorimotor oscillations is not entirely straightforward (Kristeva et al., 1990), and so there may simply not be significant differences in action processing for the specific weights that the participants were lifting (130 vs. 1300 g). Another way of thinking about this is that during the execution of lifting actions, the difference between the light and heavy objects may not have been sufficient to significantly alter alpha suppression. If this is the case, it is interesting to consider why weight-related effects would then arise during subsequent action observation.

Additionally, the timing differences between lifting heavy and light objects may have contributed significantly to our failure to find differences between alpha or beta suppression during action execution. Unlike in the observation analyses, where all reaches, regardless of color or expected weight, were precisely the same duration, participants' actions upon heavy objects were significantly longer in duration than their actions upon light objects. Since EEG signals are responsive to actions on a very short time scale, it is possible that this difference in action timing introduced too much variability into the comparison and prevented the discovery of any significant differences in alpha or beta suppression between conditions. In order to avoid this issue, future studies could consider entraining participants' actions onto a fixed time scale, with the use of a metronome, for example. However, variation in timing may be considered an inherent difficulty in studying larger-scale actions (compared to button-presses or other more constrained actions, which are commonly used in studies of action execution).

While there was no overall significant difference in alpha or beta suppression between heavy and light during action execution, exploratory analyses showed a difference in Weight for certain Groups during the execution of action. The EE group showed more alpha suppression during execution of actions with light objects, compared to actions with heavy objects, which suggests that for this group, lifting the light objects may have resulted in greater activation of sensorimotor cortex, a finding that echoes some prior work (Mizelle et al., 2010; Quandt et al., 2012). The SI group showed this same pattern at a number of frontal, central, and parietal electrodes, whereas the BE group showed no sensitivity to weight during action execution. It seems likely that the context of the action execution differed between groups, leading to different activation of sensorimotor cortex (Molenberghs, Hayward, Mattingley, & Cunnington, 2012). Since this effect was not predicted, it is difficult to ascertain what exactly led to these differences. However, the context of the reaching and lifting actions was substantially different between the three groups. The EE group had already performed the same reaching and lifting actions several times by the time they started the experience block. For them, the performance of the actions at the end of the protocol was not a novel experience. In contrast, for the SI group, these ten trials of execution were the first time that these participants had ever interacted with the objects. Thus, it seems that the extent and type of prior experience with the objects may have affected EEG responses during actions carried out upon those objects. This is a potentially important and novel finding, suggesting that contextual influences might affect the oscillatory processes associated with executing action.

Broader Implications

The work presented here suggests the neural activity involved in processing others' actions is modified by the way in which we learn about the actions. In fact, it seems that after gaining sensorimotor experience with an action, the processing of others' similar actions becomes more reliant on the observer's sensorimotor cortex—one might even say, more embodied. Others have proposed this idea, but the current study adds to this literature by specifying differences before and after learning about actions, by looking at the effects of both sensorimotor experience and the acquisition of semantic information, and by varying the amount of experience with actions (one trial vs. ten trials). Taken together, these points are a valuable addition to both the investigation of the human mirror neuron system, and research concerning learning.

Over the past 20 years, research on human neural mirroring processes has demonstrated that our sensorimotor cortices are active during the processing of other people's actions. But the field has, as a whole, struggled with defining what is added (if anything) to the basic perception of action by means of this vicarious motor simulation (Borg, 2012; Csibra, 2007; Gallese et al., 2011; Hickok, 2012; Jacob, 2008; Michael, 2011; Rizzolatti & Sinigaglia, 2010; Sinigaglia, 2012). While some recent research has identified a causal relationship between sensorimotor activation and successful recognition of action, it is still undetermined how and when mirroring processes play a critical role in the understanding of others' experiences (Avenanti et al., 2013). The current study can, in some small way, inform this question, by demonstrating that mirroring processes are sensitive to not only the inherent properties of the observed actions, but also to the prior experiences of the observer himself. The unique aspect of the current study, in which multiple modes of learning about actions are explored, is that brief or extended sensorimotor experience with action leads to different patterns of neural activity during the observation of actions that have different predicted sensorimotor consequences (i.e., force required to act upon objects of different weights). The results from this study suggest that the vicarious activation of the sensorimotor cortex is sensitive to the expectation of the sensorimotor demands of observed actions, and that past action experience is closely linked to future action observation.

The other related field of study for which the current study is particularly applicable lies in learning, since multiple methods of learning about actions were examined. Recent research into how people learn most effectively has focused on whether embodiment may play an important role in learning (Alibali & Nathan, 2012;

Kiefer & Trumpp, 2012; Kontra, Goldin-Meadow, & Beilock, 2012). There is a growing interest in how receiving sensorimotor experiences may uniquely contribute to learning, and how embodied learning might facilitate successful learning of novel concepts. For example, when physics students were learning about torque, students performed better on tests if they participated in demonstrations in which they feel the force of torque pulling on their body, compared to if they watched someone else in the demonstration (Kontra et al., 2012). The results presented in the current study suggest that learning about actions via the acquisition of semantic information is not sufficient to induce subsequent increases in embodied processing. It may be that, especially for scientific concepts such as physics, using embodied learning techniques that integrate sensorimotor experiences into the learning experience will improve understanding of those concepts. While this remains to be explicitly demonstrated in the context of learning educational content, we do know from the current study that embodied processing may be facilitated by the acquisition of sensorimotor experience. Future work should test the application of the results presented here in the context of embodied learning.

Limitations

Like any research study, there are questions that are raised by our findings that cannot be definitively answered. One limitation concerns the amount of experience given to participants, and also the weights of the objects. Since the current study included both parameters, it was not feasible to compare a large number of different weights and many different types of experience. However, future work on the effect of experience upon action processing should consider varying these factors parametrically. In the case of weight, having only one heavy and one light weight does not allow for a complete understanding of how this sensorimotor variation is represented in the brain. For instance, we do not know whether adding much heavier or lighter weights to the experiment would provide a more complete picture of how weight and EEG relate to one another (Kristeva et al., 1990). This information would be especially valuable given the current evidence showing that different EEG frequency bands are sensitive to expected weight in different ways. Additionally, any future work comparing differing amount of sensorimotor experience with action should consider adding greater variability to the design. The use of one trial of experience vs. ten trials of experience was relatively arbitrary, and with the results presented here as a starting point, it would be interesting to compare how subsequent action processing might be affected by no experience, compared to one trial, two trials, or one hundred trials of sensorimotor experience. Without these added parametric variables, it is impossible for the current study to demonstrate precisely how the alpha and beta rhythms of the brain react to variations in these parameters.

Another topic that should be more thoroughly examined concerns the added value of mirroring processes. The current study is unable to explicitly link the facilitation of neural mirroring processes to any specific behavioral or experiential benefit. An important next step in this line of research is to collect a behavioral measure in tandem with the neurophysiological correlates of action processing, to allow measurement of whether changes in brain functioning might lead to improvements in accuracy or prediction of actions. For example, eye tracking could be used to assess whether participants were better or worse at predicting the outcome of the actions following their increased experience. Or, as in the earlier example of embodied learning, it would important to know whether participants' understanding of a concept would be improved by sensorimotor experience with related actions. One recent study found that experience with figure skating resulted in better accuracy with and faster prediction of others' figure skating actions (Diersch, Cross, Stadler, Schütz-Bosbach, & Rieger, 2012). Ideally, performance measures such as these could be collected as part of a training study, in tandem with a psychophysiological measure or hemodynamic imaging, so that the effect of experience could be measured from multiple converging levels. In short, it seems necessary to more deeply consider what it is that the facilitation of neural mirroring contributes to action processing, and more broadly, social cognition as a whole.

Conclusion

The human sensorimotor cortex is involved in processing actions that are carried out by other people, and it is thought this activation might be sensitive to the types of experiences an observer has had with the observed actions. The EEG study presented here demonstrates two particular ways that one's prior experiences with actions can change subsequent action processing. First, over the course of receiving more experience with observed actions, alpha and beta suppression was increased, suggesting that underlying sensorimotor cortex is more activated. Secondly, the analysis of neural oscillations during action observation following experience showed that brief or extended sensorimotor experience is associated with sensitivity to the predicted sensorimotor consequences of observed action. Taken together, these results inform how neural mirroring processes link our own past experiences with our perception and processing of the world around us.

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APPENDIX A: LIST OF ABBREVIATIONS

- AON – Action Observation Network
- BE – Brief Experience
- EE – Extended Experience
- EEG – Electroencephalography
- ERSP – Event-Related Spectral Perturbation
- FDR – False Discovery Rate
- IFG – Inferior Frontal Gyrus
- IPL – Intraparietal Lobule
- fMRI – Functional Magnetic Resonance Imaging
- MNS – Mirror Neuron System
- MEP – Motor Evoked Potential
- SI – Semantic Information

APPENDIX B: INSTRUCTIONS TO PARTICIPANTS

Training

"We are interested in how people perceive the actions of others. We are going to show you some videos of people performing actions, and have you do some actions with your hands as well. We will collect EEG while you watch the videos and do the actions. We will be collecting EEG data from you while you watch the videos. EEG is electrical activity generated by your brain that can be detected from the surface of your head. The cap will pick up the signals that your brain is giving off. In order to get a good signal, we will put a little bit of gel in between each of these electrodes and your scalp. It washes out very easily with shampoo or water, and we can help you get cleaned up afterwards [show them the sink]. We will also put electrodes behind your ears and above and below your left eye. Getting you set up should take about 20 minutes, and you can watch an episode of Big Bang Theory, the Simpsons, or Seinfeld while we do it. What would you like to watch?"

"We're interested in how people see different parts of actions. You will see videos of someone reaching for objects of different colors. Watch the videos very closely. Most of them will be similar, but some of them will be a little different. Your task is to keep track of how many special "freeze frame" videos you see. We will show you examples of those in just a moment. You will see three short blocks of videos clips. At the end of each block, we will ask you how many "freeze frame" trials you saw, so remember to watch out for them and keep count of them in your head. Each block will last about 3 minutes. While you watch the videos, keep your body and arms as still as possible. You can move or stretch in between blocks. We will start the practice now and you'll see the different types of video clips."

- Show the first three normal trials, "These first trials are normal trials showing different parts of an action. You will see many of these trials." PAUSE.
- Before fourth trial: "This next trial is a freeze frame trial. It looks different because when the hand touches the object, it freezes for a few seconds—much longer than in the normal trials. These are the ones you need to count. After each block, you will have to say how many freeze frame trials you saw." Ask if they notice the difference.
- Finish the practice trials. "Okay, we are going to start block one. Remember to count in your head how many freeze frame trials you see. There will be just a small number of them in each block, so watch carefully. Are you ready?"

Begin Part 1. At the end, pause on the "How many freeze frames?" image, and ask the participant "How many freeze frame trials did you see?". Politely correct them if they are wrong, and explain more if they have trouble with the task. "Ready to start the next block?"

[First observation]

Experience

BRIEF
"For now, please do not touch these objects. In a moment, you will see some instructions on the screen asking you to lift some of them. You will lift the cup and the bear a few times each, and at the end you will be asked to lift the blue and yellow objects. Every time you lift, use your right hand to lift the object and put it back down in the same place. Make sure not to touch any of the objects at any time, except for when you are instructed to. The instructions will come up kind of fast, so make sure you lift the objects as soon as you see the directions on the screen. Any questions?"

EXTENDED
"For now, please do not touch these objects. In a moment, you will see some instructions on the screen asking you to lift the yellow and blue objects several times each. Every time you lift one, use your right hand to lift it and put it back down in the same place. Make sure not to touch any of the objects at any time, except for when you are instructed to. The instructions will come up kind of fast, so make sure you lift the objects as soon as you see the directions on the screen. Any questions?"

SEMANTIC
"For now, please do not touch these objects. In a moment, you will see some instructions on the screen asking you to lift some of them. You will lift the cup and the bear several times each, and then you will see some information on the screen about the blue and yellow objects. You will not be lifting the yellow or blue objects, just the cup and the bear. Every time you lift them, use your right hand and put the object back down in the same place. Make sure not to touch any of the objects at any time, except for when you are instructed to. The instructions will come up kind of fast, so make sure you lift the objects as soon as you see the directions on the screen. And, pay close attention to the information you receive about the blue and yellow objects. Any questions?"

[Experience block]

"I just need to ask you two questions before we continue. Is the blue object heavy or light?" If correct, proceed. If incorrect, ask again. "Is the yellow object heavy or light?" If correct, proceed. If incorrect, ask again.

"Now you will see more videos like ones you saw before. Again, you need to count the number of times you see the freeze frame videos in each block. Remember to watch carefully. There will be another three blocks, and we will ask you to report how many freeze frames you see after each block. Ready?"

[Second observation]

Execution

"You will now see some instructions on the screen telling you to lift these two objects, one at a time. Wait until you see the instructions before you do anything. Each time you pick an object, use your right hand to lift it a few inches into the air, and put it back down in the same place. [lift one object to demonstrate correct lift] Once you are done with this part, you will be all finished for today. Ready to start?"

[Execution]

Debrief them: "We are studying the brain activity underlying the observation of action. The main question concerns how your experience with the objects changed how you processed the actions you saw in the videos. This allows us to see whether experience with a particular action affects how we process that action when we see it again."

APPENDIX C: IRB APPROVAL

TEMPLE UNIVERSITY

Office for Human Subjects Protections
Institutional Review Board
Medical Intervention Committees A1 & A2
Social and Behavioral Committee B
Unanticipated Problems Committee

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Certification of Approval for a Project Involving Human Subjects

Protocol Number:	**20821**
PI:	**MARSHALL, PETER**
Review Type:	EXPEDITED
Approved On:	02-Aug-2012
Approved From:	02-Aug-2012
Approved To:	01-Aug-2013
Committee:	B BEHAVIORAL AND SOCIAL SCIENCES
School/College:	LIBERAL ARTS (1800)
Department:	CLA:PSYCHOLOGY (18110)
Project Title:	Modulation of Neural Mirroring by Sensorimotor Experiences: Evidence from Action Production and Execution

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The IRB approved the protocol **20821**.

If the study was approved under expedited or full board review, the approval period can be found above. Otherwise, the study was deemed exempt and does not have an IRB approval period.

Before an approval period ends, you must submit a "Continuing Review Progress Report" to request continuing approval. Please submit the form **at least 60 days before the approval end date** to ensure that the renewal is reviewed and approved and the study can continue.

Finally, in conducting this research, you are required to follow the Policies and Procedures, the Investigator Manual, and other requirements found on the Temple University IRB website: http://www.temple.edu/research/regaffairs/irb/index.html

Please contact the IRB at (215) 707-3390 if you have any questions.