Sensitivity of alpha and beta oscillations to sensorimotor characteristics of action: An EEG study of action production and gesture observation

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ABSTRACT

The sensorimotor experiences we gain when performing an action have been found to influence how our own motor systems are activated when we observe others performing that same action. Here we asked whether this phenomenon applies to the observation of gesture. Would the sensorimotor experiences we gain when performing an action on an object influence activation in our own motor systems when we observe others performing a gesture for that object? Participants were given sensorimotor experience with objects that varied in weight, and then observed video clips of an actor producing gestures for those objects. Electroencephalography (EEG) was recorded while participants first observed either an iconic gesture (pantomiming lifting an object) or a deictic gesture (pointing to an object) for an object, and then grasped and lifted the object indicated by the gesture. We analyzed EEG during gesture observation to determine whether oscillatory activity was affected by the observer's sensorimotor experiences with the object represented in the gesture. Seeing a gesture for an object previously experienced as light was associated with a suppression of power in alpha and beta frequency bands, particularly at posterior electrodes. A similar pattern was found when participants lifted the light object, but over more diffuse electrodes. Moreover, alpha and beta bands at right parieto-occipital electrodes were sensitive to the type of gesture observed (iconic vs. deictic). These results demonstrate that sensorimotor experience with an object affects how a gesture for that object is processed, as measured by the gesture-observer's EEG, and suggest that different types of gestures recruit the observer's own motor system in different ways.

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1. Introduction

1.1. Neural mirroring

Our own actions and our perceptions of others' actions are closely linked. There is ample evidence suggesting that our own experiences with action can influence perception in such a way that we become especially sensitive to observing similar actions performed by others (Hecht, Vogt & Prinz, 2001; Schütz-Bosbach & Prinz, 2007) For example, dancers trained in ballet show greater premotor cortex activation when observing ballet dancing than when observing other dances with which they have not had extensive motor experience (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005). This type of evidence has been used to support the idea that action and perception rely on similar neural substrates.

One prominent hypothesis about the relation between perception of action and production of action concerns a putative human mirroring system (Decety & Grezes, 1999), composed of ventral and dorsal premotor cortex, the anterior inferior parietal lobule, somatosensory areas such as BA2, and the middle temporal gyrus (Gazzola & Keysers, 2009). The mirroring hypothesis postulates that, when an action is observed, the brain regions involved in performing that action are activated—as though the observer were performing the action herself (Gazzola & Keysers, 2009); this vicarious simulation of observed action then has the potential to facilitate the interpretation and understanding of others' actions (Rizzolatti & Sinigaglia, 2010). Mirroring processes may also allow for fluid social interactions by enabling social partners to prepare appropriate responses to observed actions (Gallagher, 2008).

1.2. Gesture processing

Evidence suggests that the putative human mirroring system may also be involved in observing gestures (Emmorey, Xu, Gannon, Goldin-Meadow, & Braun, 2010; Goldenberg & Hagmann, 1997;

Hostetter & Alibali, 2008). Gestures are actions, but they do not have a direct effect on the world the way most actions do—instead, gestures are representational. Gestures have been hypothesized to ground thought in action (Beilock & Goldin-Meadow, 2010; Cartmill, Beilock, & Goldin-Meadow, 2012; Goldin-Meadow & Beilock, 2010) and experiments to support this hypothesis have shown that perception of gesture, like perception of action, recruits the observer's sensorimotor system (Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2010; Villarreal et al., 2008). If observed gestures are, at least to some degree, represented as actions, then the neural systems underlying gesture perception should be sensitive to characteristics of the actions represented in those gestures; in other words, observing a gesture representing an action should evoke similar neural responses as executing the action itself.

In the current study, we compared two types of gestures to determine whether they resulted in different patterns of neural activity when observed: (1) deictic gestures, which draw attention to objects (e.g. pointing at an object), and (2) iconic gestures, which display characteristics of action as if the gesturer were performing the action himself (e.g., moving the hand as though grasping and lifting an object, i.e., character viewpoint gestures (Cartmill et al., 2012; McNeill, 1992)). These two gestures were selected because they vary in how closely they mimic action. We hypothesized that observing iconic gestures, which closely mimic an action performed on an object, would result in greater activation of sensorimotor cortex than observing deictic gestures, which are static and serve primarily to indicate the location of an object.

An important unanswered question with respect to gesture perception is whether an observer's prior experience with the action represented in a gesture changes how that gesture is processed. This question has important implications for observational learning and, more specifically, for how gesture is used in teaching situations. Recent evidence suggests that mirroring in the observer is sensitive to the somatosensory and motor characteristics of the observed action, and also to the amount of prior experience the observer has had with the observed action (Calvo-Merino et al., 2005; Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008; Quandt, Marshall, Bouquet, Young, & Shipley, 2011). In the current study, we extended this line of reasoning to ask whether one's prior somatosensory or motor experiences with specific objects affect the subsequent processing of others' gestures towards those objects.

Alpha- and beta-range rhythms in the electroencephalogram (EEG) have been examined in studies of action processing (Muthukumaraswamy, Johnson, & McNair, 2004; Pfurtscheller, Neuper, & Krausz, 2000). Rhythms in these frequency ranges typically show a regional decrease in power in response to both executing and observing action, suggesting that they may be related to the common neural coding of action and perception (Perry & Bentin, 2009; Press, Cook, Blakemore, & Kilner, 2011). While it is not clear precisely how EEG rhythms relate to specific cognitive processes, it is thought that alpha and beta bands are closely tied to the allocation of visuospatial attention (Mathewson et al., 2011) and the activation of sensory (van Ede, de Lange, Jensen, & Maris, 2011) and/or motor cortex (Perry, Stein, & Bentin, 2011). The primary focus of the current study is using alpha and beta rhythms to explore activation of sensorimotor cortex during action observation and production. We performed separate analyses on the lower alpha (8–10 Hz), upper alpha (11–13 Hz), and beta (14–30 Hz) bands. We were particularly interested in the upper alpha band response during gesture observation, given evidence that this frequency band is sensitive to previous experience with actions (Marshall, Bouquet, Shipley, & Young, 2009; Quandt et al., 2011).

1.3. Current study

To our knowledge, no prior studies have examined the relation between patterns of cortical activity elicited when a communicative gesture is observed and patterns of cortical activity elicited when the corresponding action is executed. We designed an experiment in which participants were first given sensorimotor experience with different objects, after which they observed gestures referring to those objects. We were interested in whether specific experience with a set of objects would change EEG activity elicited when observing gestures referring to those objects. We were also were interested in whether EEG activity would vary as a function of the type of gesture observed (iconic vs. deictic).

At the outset of the experiment, and throughout the experimental session, each participant received sensorimotor experience with one set of objects: either heavy/yellow and light/blue objects OR heavy/blue and light/yellow objects. We collected EEG while participants observed video clips of an actor performing either an iconic or deictic gesture toward the yellow or blue object. Each participant saw four video clips in total: iconic/yellow (i.e., iconic gesture directed toward a yellow object), iconic/blue, deictic/yellow, and deictic/blue. After each video clip, the participant reached for, grasped, and lifted an object of the same color as the object indicated by the gesture. Thus, if they saw an iconic (or deictic) gesture directed toward a blue object, they lifted the blue object that was in front of them. Importantly, the actor in the video clips never touched either object, and the objects remained stationary during the entire video clip, so there was never any information regarding the weight of the objects gestured to in the video clips. This aspect of the design allowed us to relate differences in the EEG during gesture observation to the participants' expectations about the relative weights of the objects (which would be based on their own experience interacting with the objects). We also examined differences in alpha and beta power during participants' execution of the grasping and lifting actions on the same objects.

Our analyses tested three hypotheses: (1) EEG responses elicited when executing an action on objects and EEG responses elicited when observing a gesture referring to those objects will show similar modulation by object weight (light vs. heavy during action execution, and expected light vs. expected heavy during gesture observation). (2) EEG alpha and beta range rhythms will show greater reactivity when observing iconic gestures than when observing deictic gestures. (3) When observing a gesture referring to an object, participants' expectations about the sensorimotor consequences of lifting that object (which are based on their own previous experiences lifting the object) will modulate alpha and beta rhythm activity. If this last hypothesis is supported, it would provide evidence that prior experience producing an action modulates the way a gesture related to that action is processed. This result, in turn, would support the idea that gesture perception is embodied, in the sense that prior experiences with objects modulate how we process gestures referring to those objects.

2. Materials and methods

2.1. Participants

Thirty-seven right-handed (Oldfield, 1971) undergraduates (19 females; mean age=21.7, SD=3.8) took part in the study in exchange for course credit. All participants gave their informed consent prior to the experimental session, and the university Institutional Review Board had approved the study protocol.

2.2. Stimuli

Two pairs of objects were created out of opaque, identically-sized cylindrical metal containers (15.5 cm tall × 7.0 cm diameter) that varied in weight (heavy, 1150 g,
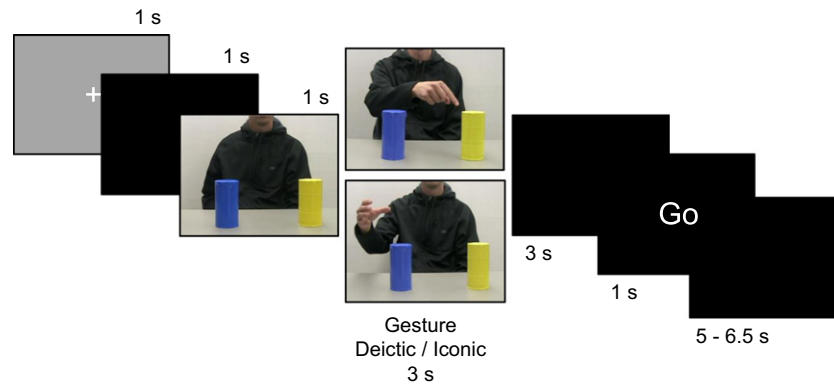
Fig. 1. Schematic depicting the structure of each trial. Participants viewed a video screen which showed a clip of an actor performing an iconic or deictic gesture for a yellow or blue object. After a brief delay, participants were instructed by the prompt "Go" to then reach for and lift the object represented in the gesture. Each participant was assigned to one pair of objects: heavy blue/light yellow or heavy yellow/light blue. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

or light, 125 g) and color (yellow or blue). One pair consisted of the heavy yellow object and the light blue object; the other pair consisted of the heavy blue object and the light yellow object.

Video clips (recorded at 30 frames per second/NTSC) showed an actor performing an iconic gesture (moving his hand as though grasping and lifting the object) or a deictic gesture (producing a point) toward either a yellow or a blue object (see Fig. 1). In each of the four video clips (deictic/blue, deictic/yellow, iconic/blue, iconic/yellow), the blue object was always to the viewer's left. The actor in the video never held or came into contact with either of the objects, ensuring that no explicit information about object weight was given in the videos at any time during the experiment.

Each trial began with a 1 s fixation point, followed by a 1 s black screen. The video clip then began, showing the two objects sitting next to each other on a table, with an actor sitting behind them facing the video camera. After 1 s, the actor used his right hand to either produce an iconic or deictic gesture toward the yellow or blue object (duration of movement was approximately 3 s). A black screen was shown for 3 s, and then the word "Go" appeared on the screen for 1 s, followed by 5–6.5 s of black screen. A total of 120 trials were presented, divided into five blocks of 24 trials each; each block contained six instances of each of the four video clips. Upon arrival, participants were assigned to one of three randomized trial orders.

2.3. Experimental procedure

Each participant was assigned to one of the two object pairs (heavy yellow and light blue, or light yellow and heavy blue). The other pair of objects was neither touched, nor seen, by the participant at any time. After the EEG cap was prepared, the two assigned objects were set in front of the participant, who was seated comfortably at a table. The blue object was always on the participant's left side. Participants were told how to reach for, grasp, and lift the objects approximately 8 in. into the air using a whole-hand grip. They were then told to watch the video clips and, after seeing the word "Go" at the end of each trial, to reach for, grasp, and lift the object that the actor had indicated with either a deictic or iconic gesture. Participants were asked to keep their hands still when they were not reaching for and lifting the objects. The entire experimental session was recorded on video.

2.4. Electroencephalographic recordings

EEG was collected from 20 scalp sites using a Lycra stretch cap (Electro-Cap, Eaton, OH, USA) with Electro-Gel conducting gel. The sites recorded from were Fp1, Fp2, F3, F4, Fz, F7, F8, C3, C4, T7, T8, P3, P4, Pz, P7, P8, O1, O2 and the left and right mastoids. Vertical electrooculogram (EOG) activity was collected from electrodes placed above and below the left eye. The EEG signal was amplified by optically isolated, high input impedance (> 1 GΩ) bioamplifiers from SA Instrumentation (San Diego, CA, USA) and was digitized onto a PC using a 16 bit A/D converter (± 5 V input range). Scalp electrode impedances were kept under 25 kΩ and were typically much lower than this upper limit. Bioamplifier gain was 4000 for the EEG channels, 1000 for the EOG 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. Eyeblinks in the EOG signal were identified and propagation factors were computed for the blink-induced voltage

changes at each scalp site. The eyeblinks where then regressed out of the EEG signals (Lins, Picton, Berg, & Scherg, 1993; Miller & Tomarken, 2001). An artifact detection algorithm flagged and rejected epochs containing artifact (samples outside ± 100 μV). The EEG was spectrally analyzed by means of a Discrete Fourier Transform using a Hanning window (50% overlap), and power was computed in μV^2 for the lower alpha (8–10 Hz), upper-alpha (11–13 Hz), and beta (14–30 Hz) frequency bands.

EEG analyses focused on two main epochs: (1) observing a video clip of the actor producing a gesture toward an object, and (2) lifting the object that the actor had indicated. For observation epochs, analyses were time-locked to the beginning of the gesture. Specifically, the 1 s following gesture onset was analyzed as the observation epoch, with two conditions: observing a gesture referring to an object known (on the basis of previous sensorimotor experience) to be light vs. an object known to be heavy. For execution epochs, we used the Video Coding System (James Long Company, Caroga Lake, NY) to visually identify the video frames (30 frames per second/NTSC) showing the onset and offset of the grasping and lifting phases, again with two conditions: lifting a light object vs. a heavy object.

3. Results

3.1. Execution of action

For the action execution condition, we performed repeated-measures ANOVAs for lower-alpha, upper-alpha, and beta power using the factors of Weight (heavy, light), Region (mid-frontal F3/F4, lateral frontal F7/F8, central C3/C4, mid-parietal P3/P4, lateral parietal P7/P8, temporal T7/T8, and occipital O1/O2), and Hemisphere (left, right). Probability values reported for all main effects and interactions have been adjusted using the Greenhouse–Geisser correction factor (epsilon).

3.1.1. Lower alpha power (8–10 Hz)
For the lower alpha band, there was a significant main effect of Region, $F(6,216)=6.29$, $p < .001$, with the highest power values at mid-frontal sites (F3/F4), followed by occipital sites (O1/O2). Band power was lowest at lateral parietal electrodes (P7/P8). Analysis of lower alpha power during action execution revealed no other significant main effects or interactions.

3.1.2. Upper alpha power (11–13 Hz)
For the upper alpha band, there was a significant main effect of Region for upper alpha, $F(6,216)=17.67$, $p < .001$, driven by highest power at occipital sites (O1/O2) and lowest at lateral frontal (F7/F8) and temporal (T7/T8) sites. Band power in the left hemisphere was significantly lower when lifting light objects than when lifting heavy objects, as indicated by a significant Weight × Hemisphere interaction, $F(1,36)=4.13$, $p=.049$ (see Fig. 2).
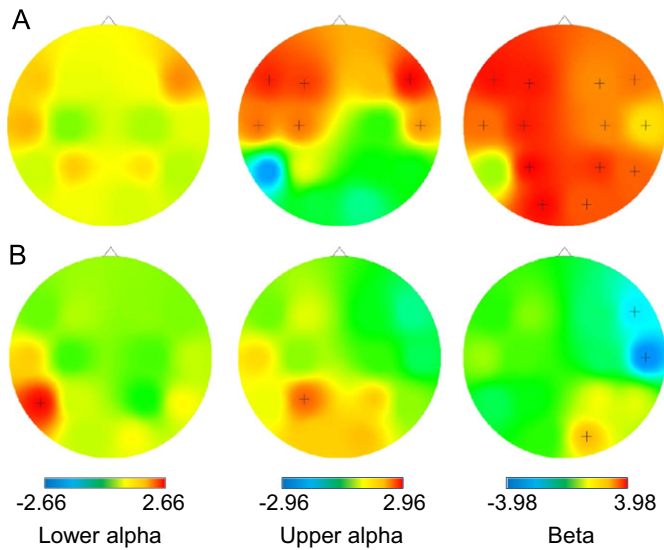
Fig. 2. Scalp maps show subtractions between conditions of interest, analyzed within the following frequency bands: lower alpha (8–10 Hz), upper alpha (11–13 Hz), and beta (14–30 Hz). Electrode marks are shown if a paired t test results in $P < .05$ at that site. (A) Colors represent t values for heavy–light during the execution of action. (B) Colors represent t values for expected heavy–expected light during the observation of gestures. Expected weights are based on the experiences participants had with the object (e.g., blue objects are heavy and yellow objects are light). The scale for each frequency band was the absolute value of the greatest t statistic within that frequency band across all paired t-test analyses, in order to clearly identify the location of the effects within each band. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1.3. Beta power (14–30 Hz)

For the beta band, there was also a significant main effect of Region, $F(6,216)=7.59$, $p < .001$, driven by the highest power at occipital sites (O1/O2) and the lowest power at lateral parietal sites (P7/P8). Beta power was significantly lower in response to lifting light objects, indicated by a significant main effect of Weight, $F(1,36)=14.04$, $p=.001$ (see Fig. 2). This effect of object weight was significantly stronger over left hemisphere electrodes, as evidenced by a significant Weight × Hemisphere interaction, $F(1,36)=10.47$, $p=.003$.

3.2. Observation of gesture

For observation epochs, repeated-measures ANOVAs were computed for lower alpha (8–10 Hz), upper alpha (11–13 Hz), and beta power (14–30 Hz), with the factors of Expected Weight (heavy or light, based on the participants' experience with objects of the same colors), Gesture (iconic, deictic), Region (mid-frontal F3/F4, lateral frontal F7/F8, central C3/C4, mid-parietal P3/P4, lateral parietal P7/P8, temporal T7/T8, and occipital O1/O2) × Hemisphere (left, right).

3.2.1. Lower alpha power (8–10 Hz)

For lower alpha power, there was significant main effect of Region, $F(6,216)=9.10$, $p < .001$, with highest power at mid-frontal (F3/F4), mid-parietal (P3/P4), and occipital sites (O1/O2) and lowest power at temporal (T7/T8) and lateral parietal sites (P7/P8). There was a significant interaction between Expected Weight, Region, and Hemisphere, $F(6,216)=3.87$, $p=.023$, reflecting decreased power for lifting light objects over left parietal electrodes (see Fig. 2).

Band power was significantly decreased during the observation of iconic gestures, compared to deictic gestures, and this effect was significant at central and parietal sites, as shown by a significant Region × Gesture interaction, $F(6,216)=3.25$, $p=.019$ (see Fig. 3). Lower alpha power was significantly decreased in response to iconic gestures, compared to deictic gestures, over the right hemisphere, as shown by a significant interaction between Gesture and Hemisphere, $F(1,36)=9.65$, $p=.004$. We also observed a significant interaction between Gesture, Expected Weight, and Region, $F(6,216)=3.74$, $p=.016$, driven by lower power during observation of deictic gestures referring to light objects. Finally, we observed a significant four-way interaction between Gesture, Expected Weight, Region, and Hemisphere, $F(6,216)=9.37$, $p=.021$. Upon further investigation, the effects driving this interaction were unclear; moreover, we did not clearly predict any effects at this level, so this four-way interaction will not be further discussed.

3.2.2. Upper alpha power (11–13 Hz)

Upper alpha power was the highest at central (C3/C4), parietal (P3/P4), and occipital electrode sites and the lowest at lateral frontal (F7/F8) and temporal sites (T7/T8), reflected in a significant main effect of Region, $F(6,216)=19.61$, $p < .001$. These different levels of upper alpha power across the scalp also varied significantly by hemisphere, as shown by a significant Region × Hemisphere interaction, $F(6,216)=5.77$, $p=.001$. A significant Expected Weight × Region interaction was driven by decreased upper alpha power during observation of gestures referring to light objects over parietal and occipital electrode sites, $F(6,216)=4.71$, $p=.005$ (see Fig. 2). Furthermore, a significant Expected Weight × Region × Hemisphere interaction reflected the specificity of the effect of weight over the left hemisphere, $F(6,216)=3.65$, $p=.013$.

Parietal and occipital electrodes showed significantly decreased upper alpha power for iconic gestures, as shown by a significant Gesture × Region interaction, $F(6,216)=5.32$, $p=.006$ (see Fig. 3). This effect of gesture type was significantly stronger over the right hemisphere than the left hemisphere, indicated by a significant Gesture × Hemisphere interaction, $F(1,36)=7.29$, $p=.011$. A significant Gesture × Region × Hemisphere interaction, $F(6,216)=4.33$, $p=.003$, was driven by significantly stronger effects of gesture type over right parietal and occipital electrodes. Finally, there was a significant Gesture × Expected Weight × Region × Hemisphere interaction, $F(6,216)=3.66$, $p=.013$. As in the lower-alpha band, we did not have clear predictions about interactions at this level and thus will not discuss them further.
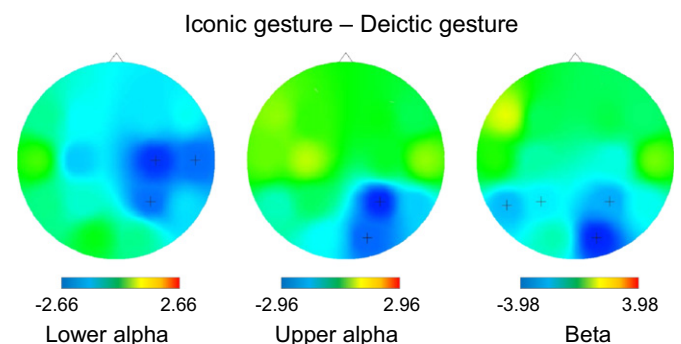
Iconic gesture – Deictic gesture

Fig. 3. Scalp maps show subtractions between observation of iconic and deictic gestures, analyzed within the following frequency bands: lower alpha (8–10 Hz), upper alpha (11–13 Hz), and beta (14–30 Hz). Colors represent t values of paired t tests (iconic–deictic). Electrode marks are shown if the paired t test results in $P < .05$ at that site. The scales for the color ranges were determined as in Fig. 2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2.3. Beta power (14–30 Hz)

For the beta band, there was also a significant main effect of Region, $F(6,216)=7.01$, $p=.002$, driven by higher power at frontal (F3/F4) and occipital sites (O1/O2), and lower power at lateral parietal sites (P7/P8). Beta power was lower over parietal and occipital electrodes during observation of gestures referring to light objects than to heavy objects, indicated by a significant Expected Weight × Region interaction, $F(6,216)=3.00$, $p=.024$ (see Fig. 2). In addition, iconic gestures elicited lower power than did deictic gestures, as shown by a significant main effect of Gesture, $F(1,36)=4.23$, $p=.047$ (see Fig. 3). This effect was the strongest at parietal and occipital electrodes, indicated by a significant Gesture × Region interaction, $F(6,216)=4.39$, $p=.008$. The effect of gesture type was also significantly stronger over the right hemisphere, as shown by a significant Gesture × Hemisphere interaction, $F(1,36)=6.98$, $p=.012$.

4. Discussion

4.1. Action execution

The lower alpha frequency band showed little reactivity to the weight of the objects during action production. However, power in the upper alpha and beta frequency bands was clearly modulated by object weight. Upper alpha power decreased when the participants lifted the light object, compared to when they lifted the heavy object. Beta power across the scalp was also reduced when lifting the light object, with this effect being particularly strong over the left hemisphere. This lateralization is consistent with literature supporting greater modulation of EEG during action production in the hemisphere contralateral to the hand used to perform the action (Hatfield, Haufler, Hung, & Spalding, 2004). These results add to the previous literature showing that alpha and beta rhythms are reduced during action production (McFarland, Miner, Vaughan, & Wolpaw, 2000; Pfurtscheller, 1981; Ritter, Moosmann, & Villringer, 2009; Svoboda, Sovka, & Stancák, 2004) and show that specific characteristics of action (i.e. weight) can modulate EEG band power. Related evidence has also shown that varying the force required to perform a hand action modulates upper and lower alpha band power (Mima, Simpkins, Oluwatimilehin, & Hallett, 1999).

One might have expected that the greater demands of lifting the heavy object would produce greater suppression of alpha and beta rhythms—our results across all three frequency bands go in the opposite direction (i.e., lower power in alpha and beta bands in response to lifting the light object). However, our findings are consistent with work showing that moving one finger recruits more cortical activity than moving the whole arm (Schieber, 1990), suggesting that motor control has as much to do with inhibition as it does with excitation (Mathewson et al., 2011). In addition, attentional involvement in sensorimotor processing has been shown to modulate alpha-range rhythms (Foxe & Snyder, 2011; Haegens, Handel, & Jensen, 2011; Palva & Palva, 2007) and it is possible, at least in principle, that higher-level processes differ when acting on objects of different weights.

4.2. Observation of gesture

EEG responses elicited when observing gestures differed as a function of the type of gesture observed. At central, parietal, and occipital sites, particularly over the right hemisphere, lower and upper alpha power and beta power were decreased in amplitude when observing a mimetic gesture pantomiming lifting an object (iconic gesture), compared to observing a pointing gesture directed toward the object of interest (deictic gesture). Although there were slight variations between frequency bands in the topographical distribution of this effect, the effect of gesture type was overall stronger over the right hemisphere. This lateralization of gesture discrimination is generally consistent with functional neuroimaging research showing a right-sided bias in processing object-related actions (Weiss et al., 2006) and gestures (Chaminade, Meltzoff, & Decety, 2005).

In the lower alpha band, the effect of gesture type was particularly evident over central electrodes. A variant of the alpha rhythm, known as the mu rhythm, oscillates within the upper and lower alpha frequency ranges and is strongest over central electrodes. The mu rhythm reflects the involvement of primary sensory and motor cortices (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Hari, 2006); as a result, a decrease in alpha-range frequencies over central sites suggests that observing iconic gestures recruited sensorimotor cortex more extensively than observing deictic gestures. Specifically, in the lower alpha band, observing iconic gestures resulted in decreased power at central electrodes, compared to observing deictic gestures. This finding is consistent with our second hypothesis, which predicted that observing iconic (as opposed to deictic) gestures would preferentially engage neural mirroring processes. Iconic gestures may have elicited greater vicarious motor system activation than deictic gestures because the dynamic aspects of the iconic gesture engage more richly descriptive motion than the relatively static aspects of the deictic gesture. The upper alpha band showed the effect of gesture particularly at parietal electrode sites and in the beta frequency band, the effect was the strongest over occipital electrodes, suggesting that the three frequency bands are sensitive to cognitive processes that occur over different areas of cortex. These results demonstrate, for the first time, that EEG rhythms (including the mu rhythm) are sensitive to different types of observed gestures—some gesture types (i.e., iconic gestures) result in greater sensorimotor engagement in the observer's brain than others (i.e., deictic gestures).

Our third hypothesis was that, when observing a gesture referring to an object, expectations about the sensorimotor consequences of lifting that object would modulate the observer's EEG. It is important to reiterate here that the video clips contained no information about the objects' weight since the objects did not move and were not handled in any way. Thus, any differences based on weight had to be due solely to the participant's prior experiences with the objects pictured in the video. We did find support for the third hypothesis—we found decreased power across all frequency bands when observing gestures referring to objects expected to be light, compared to gestures referring to objects expected to be heavy. In the lower and upper alpha bands, these differences were noted primarily over left parietal electrode sites. The left-hemisphere specificity of this effect in the alpha band in response to observing actions using only the right hand is consistent with the existing literature showing greater alpha desynchronization over the hemisphere contralateral to the observed hand (Perry & Bentin, 2009; Perry et al., 2011; Quandt et al., 2011). Parietal brain regions are known to be involved in the association of somatosensory stimuli (Keysers, Kaas, & Gazzola, 2010), and the prediction of sensorimotor input (Blakemore & Sirigu, 2003), each of which could be responsible for the effect that expectances about weight (based on prior experiences) have on gesture observation. In addition, the effects seen at left posterior locations in the lower and the upper alpha bands may reflect involvement of the left inferior parietal lobule in processing hand movements (Buxbaum, Kyle, Tang, & Detre, 2006; Chaminade et al., 2005; Kalénine, Buxbaum, & Coslett, 2010).

These findings also support the hypothesis that observers are sensitive to the outcomes of actions even before they occur

(i.e., anticipated outcomes) or, in the case of gesture, to the actions that are represented in gesture (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Kilner, Friston, & Frith, 2007; Michael, 2011). Predictive coding of this sort is thought to be a key function of mirroring, potentially allowing observers to infer the outcome of another's action as it unfolds. Our results demonstrate that, when observing gesture, the observer's brain is sensitive to the somatosensory and motor consequences of the action represented in the gesture. Furthermore, it is likely that mirroring processes during gesture observation involve a dynamic flow of information from premotor areas to temporal and parietal areas during observation, as in the forward and inverse models of motor control (Schippers & Keysers, 2011). The frequency bands that we analyzed may be sensitive to different stages of this flow, resulting in each frequency band having a different spatial topography for the effects consequences of expected weight.

Given the interactive and imitative nature of our task, the weight-related effects seen during gesture observation in our study must be considered in the appropriate context. Specifically, participants had just lifted one of the objects and were also planning their own response when they observed the gestures. As a result, their prior experiences with lifting the objects, either on the immediately preceding trial or on a trial earlier in the block, along with their intention to perform the upcoming action, may both be modulating EEG activity during gesture observation. In this sense, we cannot say whether the effects of anticipated weight are based primarily on prior experience, or on the intent to move. Indeed, both may be acting in concert to change how gestures are processed, particularly since there is evidence that previous experience (Behmer Jr. & Jantzen, 2011; Calvo-Merino et al., 2005; Marshall et al., 2009; Quandt et al., 2011) and anticipation of upcoming action production (Babiloni et al., 2006; Kilner et al., 2007) can both modulate action perception. Our findings thus complement the existing literature, while at the same time extending it from action observation to gesture observation. Encoding the somatosensory and motor characteristics of the action represented in a gesture may have been useful for planning the upcoming action in response to the observed gesture.

Overall, our results demonstrate that the neural systems underlying gesture perception are sensitive to characteristics of the actions represented in those gestures—that observing a gesture representing an action evokes similar neural responses as doing the action itself. The similarities we found in EEG patterns for action production and gesture observation support the notion that our own sensorimotor systems are active when we observe other people gesture. The topographic differences in sensitivity to weight between gesture observation and action execution are consistent with the work suggesting that information related to self and other is represented differently in the brain (Walla, Greiner, Duregger, Deecke, & Thurner, 2007). In addition, it is clear that there are differences in the associations of activity in each frequency band with weight-related information between action execution and observation. For example, it seems that while the beta band is highly sensitive to sensorimotor characteristics of action production, it is not nearly as reactive in response to observed gesture.

All three frequency bands (lower alpha, upper alpha, beta) that we examined were found to be sensitive to the type of gesture observed (deictic or iconic), suggesting that EEG oscillations are broadly sensitive to the type of information conveyed in gesture. Moreover, the right-lateralized, parieto-occipital location of this effect in the three frequency bands suggests that underlying cortex may be particularly important for interpreting and processing different types of gestures. Our results illustrate the sensitivity of alpha and beta range rhythms to different types of

experience with actions, and demonstrate that somatosensory and motor experiences with action change neural processing of others' gestures for that action. This work suggests that our own sensorimotor experiences affect how we process others' actions, strengthening the idea that on a neural level, the actions of others are perceived through the lens of the self. Future research in this area should examine how sensorimotor experiences influence not only EEG band power but also other electrophysiological measures related to action processing (e.g., readiness potentials), as well as further investigating the embodied nature of gesture.

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