

Rehearsing Biological Motion in Working Memory: An EEG Study

Zaifeng Gao¹, Shlomo Bentin², and Mowei Shen¹

Abstract

■ Holding biological motion (BM), the movements of animate entities, in working memory (WM) is important to our daily social life. However, how BM is maintained in WM remains unknown. The current study investigated this issue and hypothesized that, analogous to BM perception, the human mirror neuron system (MNS) is involved in rehearsing BM in WM. To examine the MNS hypothesis of BM rehearsal, we used an EEG index of mu suppression (8–12 Hz), which has been linked to the MNS. Using a change detection task, we manipulated the BM memory load in three experiments. We predicted that mu suppression in the maintenance phase of WM would be modulated by the BM memory load; moreover, a negative correlation between the number of BM stimuli in WM and the degree of

mu suppression may emerge. The results of Experiment 1 were in line with our predictions and revealed that mu suppression increased as the memory load increased from two to four BM stimuli; however, mu suppression then plateaued, as WM could only hold, at most, four BM stimuli. Moreover, the predicted negative correlation was observed. Corroborating the findings of Experiment 1, Experiment 2 further demonstrated that once participants used verbal codes to process the motion information, the mu suppression or modulation by memory load vanished. Finally, Experiment 3 demonstrated that the findings in Experiment 1 were not limited to one specific type of stimuli. Together, these results provide evidence that the MNS underlies the process of rehearsing BM in WM. ■

INTRODUCTION

Holding biological motion (BM), the movements of animate entities, in working memory (WM) is critical for coherent visual perception of dynamic actions, imitating the actions of others and engaging in normal social interactions. However, the mechanisms for retaining BM in WM remain largely unclear. Currently, it is known that BM has a distinct storage buffer in WM from visual objects and spatial locations, and only three to five BM stimuli can be held in WM (Wood, 2007, 2011; Smyth & Pendleton, 1990; Smyth, Pearson, & Pendleton, 1988). Recent studies have also begun to explore issues such as the relationship between an agent's identity and BM (Poom, 2012; Wood, 2008) and the frame of reference for remembering BM (Wood, 2010). Here, we investigated the mechanisms involved in rehearsing BM in WM.

In contrast to our limited knowledge regarding the mechanisms for BM in WM, there is a considerable amount of research on BM processing in visual perception (for reviews, see Troje, 2013; Pavlova, 2012; Thompson & Parasuraman, 2012; Blake & Shiffrar, 2007; Puce & Perrett, 2003). Among these studies, one of the most striking findings is that when an individual observes or imagines another individual performing an action, a set of neurons that encode that action are activated in the observer's

cortical motor system (called the mirror neuron system, MNS). Mirror neurons were initially found in the macaque monkey, and these neurons fire when a monkey performs a particular goal-directed action or simply observes another individual (monkey or human) performing an action (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neurons with mirror-like properties are located primarily in the ventral premotor cortex and around the anterior intraparietal sulcus of the macaque (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; see Rizzolatti, Fogassi, & Gallese, 2001, for a review). Recent evidence further suggest the existence of such neurons in humans based on fMRI (e.g., Gilaie-Dotan, Kanai, Bahrami, Rees, & Saygin, 2013; Gilaie-Dotan, Bentin, Harel, Rees, & Saygin, 2011; Saygin, Wilson, Hagler, Bates, & Sereno, 2004), TMS (e.g., van Kemenade, Muggleton, Walsh, & Saygin, 2012), EEG (e.g., Singh, Pineda, & Cadenhead, 2011; Ulloa & Pineda, 2007), and magnetoencephalography (MEG; e.g., Pavlova, Lutzenberger, Sokolov, & Birbaumer, 2004) studies. If the human MNS is clinically damaged, BM perception is considerably impaired, leading to serious deficits in social cognition (e.g., Pavlova, 2012; Oberman, Ramachandran, & Pineda, 2008; Saygin, 2007). Therefore, it has been suggested that the MNS functions to conduct an off-line internal simulation of BM during BM perception or imagination (e.g., Oberman, Pineda, & Ramachandran, 2007; Rizzolatti et al., 2001; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996).

¹Zhejiang University, ²Hebrew University of Jerusalem

Here, we hypothesized that the MNS also plays a critical role in the rehearsal of BM in WM. This hypothesis is reasonable considering that recent behavioral and neuroimaging studies have consistently demonstrated that visual perception and WM share similar processing mechanisms when processing the same information (e.g., Ester, Serences, & Awh, 2009; Harrison & Tong, 2009). To examine the MNS hypothesis of BM rehearsal in WM, we utilized an EEG index of mu suppression (8–12 Hz) recorded from central brain sites. Mu suppression has been linked to the MNS and is thought to reflect event-related EEG desynchronization induced by the enhancement of neural activity in somato-motor regions and the pFC, leading to asynchronous neural firing (Kuhlman, 1978). Significant mu suppression has been consistently shown in BM perception, action, and imagination (e.g., Singh et al., 2011; Perry, Troje, & Bentin, 2010; Oberman & Ramachandran, 2007; Ulloa & Pineda, 2007).

To test our hypothesis, we manipulated the BM memory load in a change detection task, which is widely used for addressing information maintenance in WM. We predicted that mu suppression in the WM maintenance phase of the change detection task would increase as the BM memory load increased, but would stop increasing when WM reached its capacity. We further predicted a negative correlation between the number of BM stimuli in WM and the degree of mu suppression.

EXPERIMENT 1: MU SUPPRESSION MODULATION BY MEMORY LOAD

Experiment 1 investigated whether the degree of mu suppression was modulated by the BM memory load. The participants were required to remember two to five BM stimuli while conducting a digit rehearsal task. Animated rectangles were used as the control.

Methods

Participants

There were 32 (18 men) participants in Experiment 1. All participants were from Zhejiang University and ranged in age from 18 to 25 years. All participants reported normal or corrected-to-normal visual acuity and had no history of psychiatric or neurological disorders, as confirmed by a screening interview. Individuals were paid for their participation. The study was approved by the Research Ethics Board of Zhejiang University and the granting agency of China.

Stimuli

To have strict control over the BM stimuli (e.g., Perry, Troje, et al., 2010), we adopted point light displays (PLDs; Johansson, 1973) as the stimuli of interest, which have been extensively used in previous BM studies (Troje,

2013; Pavlova, 2012; Thompson & Parasuraman, 2012; Blake & Shiffrar, 2007; Puce & Perrett, 2003). The PLDs depict human activity through a simple set of light points (e.g., 13 points). These lights are placed at distinct joints of a moving human body. Although highly impoverished (e.g., texture and form cues, per se, are absent), once in motion, many aspects of human movement (e.g., gender, performed actions) can be rapidly recognized in these PLDs. Previous fMRI (e.g., Gilai-Dotan et al., 2013), EEG (e.g., Singh et al., 2011), MEG (e.g., Pavlova et al., 2004), and TMS (e.g., van Kemenade et al., 2012) studies have demonstrated that the perception of PLDs activates the human MNS. For instance, Ulloa and Pineda (2007) showed that mu rhythms recorded from central brain sites (e.g., C3, CZ, and C4) were significantly suppressed when participants observed PLDs, and this result has been confirmed by other recent studies (e.g., Perry, Bentin, Bartal, Lamm, & Decety, 2010; Perry, Bentin, Shalev, et al., 2010; Perry, Troje, et al., 2010).

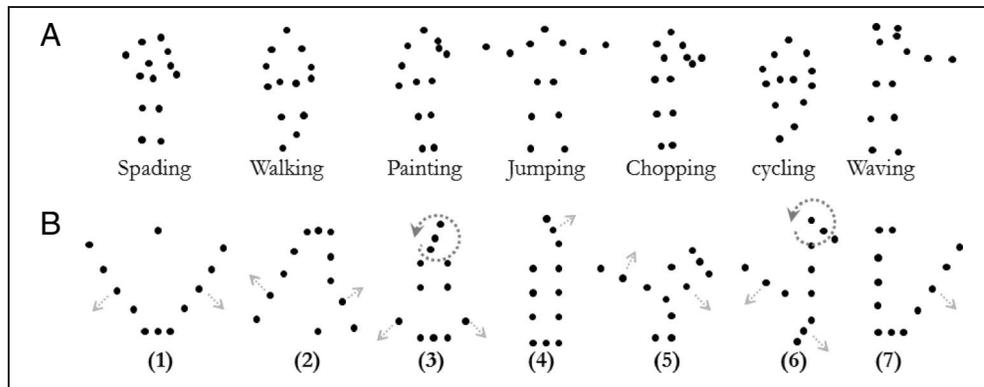
Seven PLDs from the Vanrie and Verfaillie (2004) database were selected as BM stimuli: cycling, jumping, painting, spading, walking, waving, and chopping (see Figure 1A). As a control for establishing a mu activity baseline, we created seven dynamic movements of a rectangle (non-BM; composed of 12 points), which were chosen because PLDs in general exhibited a global appearance of a rectangle (see Figure 1B).

Every animation consisted of 30 distinct frames, and each frame was displayed twice in succession, thus creating a 1-sec animation (refresh rate, 60 Hz). The displays subtended a visual angle of approximately $1.64^\circ \times 1.64^\circ$ from a viewing distance of 60 cm. The stimuli were created and presented via Matlab and Psychophysics Toolbox software (Brainard, 1997) on a gray (128, 128, 128, RGB values) background on a 17-in. CRT monitor. Two to five distinct stimuli were randomly presented during each trial. The spatial locations of the stimuli were evenly distributed on the periphery of an invisible circle with a radius of 4.88° from the screen center.

Design and Procedure

Previous WM studies, which demonstrated a WM capacity of three to four visual objects, revealed that the most distinct difference in neural activity emerged between loads 2 and 4 (e.g., Gao et al., 2009; Drew & Vogel, 2008; Xu & Chun, 2006; Vogel, McCollough, & Machizawa, 2005; Vogel & Machizawa, 2004). Moreover, a significant correlation is consistently observed between individual WM capacity and the difference in neural activity between loads 2 and 4 (e.g., Drew & Vogel, 2008; Vogel et al., 2005; Vogel & Machizawa, 2004). Using BM as the stimuli of interest, we also found that three to four BM stimuli could be kept in WM (Shen, Gao, Ding, Zhou, & Huang, in press). Consequently, we decided to use memory loads 2 and 4 as the main conditions of interest. Furthermore, to examine the suppression changes across the different memory load

Figure 1. Example frames for BM stimuli (A) and rectangle animations (B) used in Experiments 1 and 2. For each rectangle animation, they started as a static dotted rectangle. When a rectangle began to move, the rectangle did the following movements (from left to right in turn; and gray arrows in Figure 1B were used to illustrate the moving direction of the sides, which did not appear in the experiment): (1) The left and right sides moved downward 60° relative to their vertical position and returned back. (2) The left side moved upward 45° relative to its original position and returned, whereas the right half-side moved upward 45° relative to its original position and returned. (3) The left and right half-sides moved downward 90° relative to their original positions and returned, whereas the top side rotated around the middle dot once. (4) The top side moved upward 90° relative to its horizontal position and returned. (5) The upper 50% of the rectangle rotated 90° clockwise relative to its vertical position, whereas the left bottom half-side moved upward 90°. (6) The top side rotated 180° around the top-dot in the right side, whereas both the left and bottom sides moved downward 90°. (7) The right side moved downward 45° and returned.



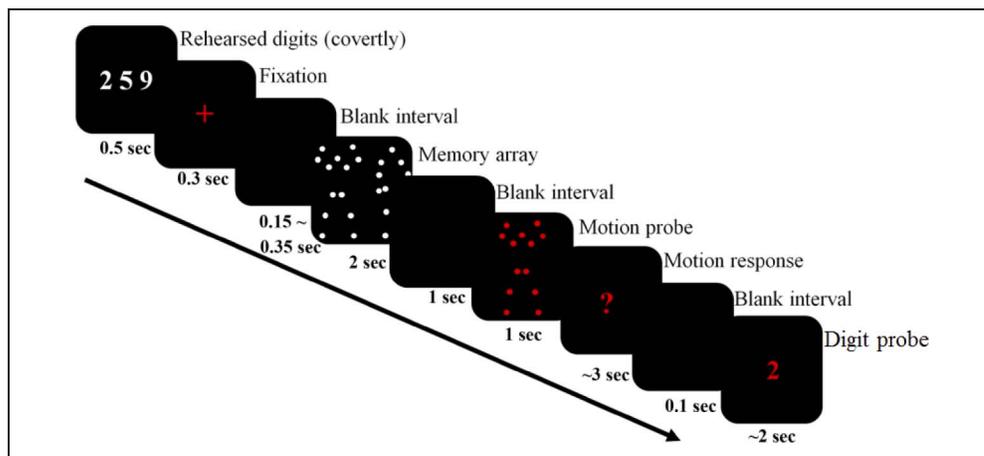
conditions, we also included memory loads 3 and 5 into the test. Load 3 was within the WM capacity for BM, whereas load 5 was beyond the capacity.

Each trial began by requiring the participants to covertly rehearse three numerical digits throughout the trial (see Figure 2) to prevent verbal coding of the stimuli (e.g., Vogel, Woodman, & Luck, 2001). The digits were presented in white in the center of the screen for 500 msec. Then, a red fixation cross appeared for 300 msec to inform the participants of the upcoming BM memory task. After a blank interval of 150–350 msec, the memory array was presented for N (memory load of motions; either 2, 3, 4, or 5) seconds to ensure participants had enough encoding time. After a 1-sec blank interval, a red motion probe was presented for 1 sec in the center of the screen. When a red question mark appeared on the screen, participants made a button response to indicate whether the previous BM had appeared in the memory array. After the button response or if no response was made within 3 sec, a blank

interval appeared for 100 msec followed by a digit judgment task, in which participants had 2 sec to make a button response indicating whether the red digit was one of the digits they had seen at the beginning of the trial (see Figure 2). All participants performed the task while seated in a dark and sound-shielded room. Before starting the task, participants were instructed to press “J” on the keyboard if they thought a BM stimulus or digit had appeared in the memory array and “F” if it had not. Response accuracy was emphasized and analyzed.

The probed motion and the probed digit were changed independently with a probability of 50%. When a change occurred, a new BM stimulus or digit that was not used in the memorized/rehearsed array was adopted as a probe. A within-subject design was adopted with the set size (2, 3, 4, or 5 movements) of the memory array and stimulus type (BM vs. non-BM) as the within-subject factors. The BM and non-BM stimuli were tested in two different blocks, the orders of which were counterbalanced across participants.

Figure 2. A schematic illustration of a single trial in Experiment 1.



There were 72 trials in each set size condition, resulting in 288 randomly presented trials for each block. Each block was divided into six sessions with a 5-min break in between each session, lasting about 1 hr for a block. Before the formal experiments, at least 16 practice trials were given to ensure the participants understood the instructions.

Electrophysiological Recording

EEG recordings were made at 62 scalp sites using Ag/AgCl electrodes mounted on an elastic cap. All recordings were made using a left mastoid reference, and then the data were re-referenced off-line to the algebraic average of the left and right mastoid voltages. Vertical and horizontal EOGs were recorded using two pairs of electrodes. One pair was placed above and below the left eye, and the other pair was placed at the outer canthus of the two eyes. All interelectrode impedances were maintained below 5 k Ω . The EEG and EOG signals were amplified by a SynAmps 2 amplifier (Compumedics NeuroScan, Charlotte, NC) using a 0.05- to 100-Hz band-pass filter and were continuously sampled at 500 Hz/channel for off-line analysis.

Analyses of Behavioral and EEG Data

Because the digit task was used to prevent participants from verbally coding the BM stimuli and participants performed this task close to ceiling levels, we analyzed the behavioral and EEG data from the memory task regardless of their accuracy on the digit task.

For the behavioral results, we first analyzed the accuracy as a percentage. Then, we estimated the WM capacity of BM and non-BM separately by adopting Cowan's formula, $K = S \times (H - F)$, because a partial probe method was used (Rouder, Morey, Morey, & Cowan, 2011). In this formula, K is WM capacity, S is the number of displayed stimuli, H is the hit rate, which refers to the successful detection of a new stimulus, and F is the false alarm rate, which refers to an incorrect response. We calculated K for each set size in each participant and set the largest K value (K -max) as the estimated capacity of WM for each participant.¹

As for the EEG analysis, we used a combination of Neuroscan software, Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011), and EEGLAB toolbox (Delorme & Makeig, 2004). The data were first preprocessed by correcting the EOG artifacts including blinks by using a regression procedure (Semlitsch, Anderer, Schuster, & Presslich, 1986). Remaining artifacts exceeding $\pm 75 \mu\text{V}$ in amplitude at central (C3, Cz, and C4) and occipital (O1, OZ, and O2) sites were rejected from further analysis. The data were then segmented into 1-sec epochs ranging from the offset of the memory array to the onset of the probe for all conditions, which corresponded to the maintenance phase of WM.² For each segment, the integrated power in the 8–12 Hz range was computed using a fast Fourier transform (FFT) based on 500 data points per segment, using a Hanning window. Following previous studies (e.g., Perry,

Troje, et al., 2010; Oberman et al., 2007; Pineda & Oberman, 2006), a mu/alpha suppression index was calculated as the logarithm of the ratio of the power of the BM condition relative to the power of the non-BM condition at the same memory load level. A negative log ratio indicated suppression in the EEG amplitude, whereas a positive ratio indicated enhancement. The mu suppression at sites C3, Cz, and C4, and the alpha suppression at sites O1, Oz, and O2 were analyzed.

A repeated-measures ANOVA with Set size and Stimulus type as the within-subject factors was conducted on the participants' performance accuracy for each experiment. Two separate ANOVAs with Set size as the within-subject factor were conducted on mu suppression and alpha suppression, because they are suggested to have distinct cognitive meanings (e.g., Klimesch, 2012; Perry, Stein, & Bentin, 2011). For factors with more than two levels, the degrees of freedom were corrected when necessary using the Greenhouse–Geisser epsilon. Significant main effects and interactions were followed by post hoc contrasts or by subsequent dependent t tests for each level of the memory load condition.

In addition, because loads 2 and 4 were our main conditions of interest (see the first paragraph in the Design and Procedure section for details), we conducted two additional planned analyses between loads 2 and 4, regardless of the ANOVA analysis on mu suppression. First, we compared the mu/alpha suppression between loads 2 and 4 by running a paired t test. Second, we calculated Pearson correlations between the WM capacity (K -max) of each participant and the mu difference between loads 4 and 2, which could help us further illustrate the difference between loads 2 and 4 and understand the role of mu in the rehearsal of BM stimuli. The correlation was estimated using the capacity estimates (K -max) of BM and non-BM stimuli, separately.

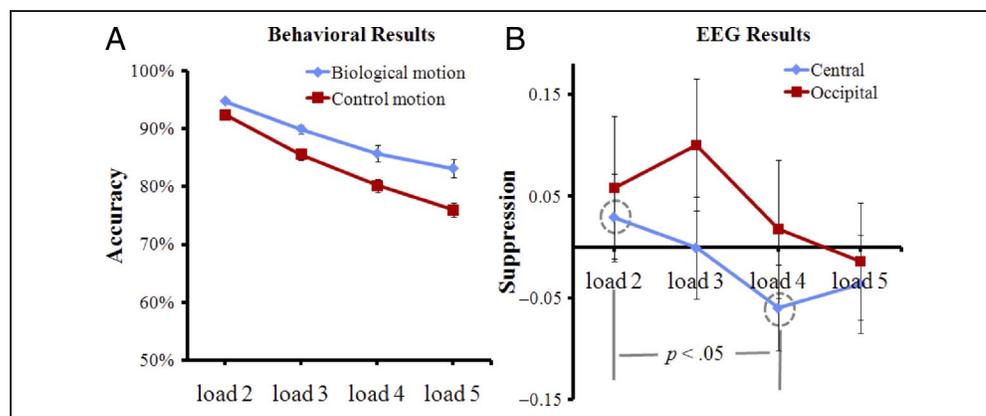
Results

Behavioral Results

The ANOVA on accuracy (Figure 3A) revealed a significant main effect of Set size [$F(3, 93) = 117.85, p < .001, \eta_p^2 = 0.79$], suggesting that the performance declined as the memory load increased. Post hoc contrasts revealed that the difference between each pair was significant ($ps < .01$; Bonferroni-corrected). The main effect of Stimulus type was also significant [$F(1, 31) = 18.93, p < .001, \eta_p^2 = 0.38$], indicating that accuracy was higher for BM (86%) than for non-BM (81%) stimuli. Finally, a significant interaction between Set size and Stimulus type was revealed [$F(4, 93) = 4.01, p = .01, \eta_p^2 = 0.12$]. Further post hoc analysis revealed the accuracy was significantly higher for BM than for non-BM in all four load conditions ($ps < .01$).

The capacity estimate (K -max) for BM stimuli was 3.42, and the K -max for the rectangle animations was 2.78.

Figure 3. Results of Experiment 1. (A) Analysis of behavioral data. (B) Analysis of EEG recordings showed a significant difference in mu suppression (central; calculated as \log [BM power/control power]) between loads 2 and 4 (gray circles; $p < .05$). Error bars indicate standard error.



EEG Results

As shown in Figure 3B, mu suppression (calculated as the \log [BM power/control power]) at central brain sites increased as the memory load increased, but leveled off when participants had to remember four BM stimuli. Moreover, similar to previous studies on WM capacity (e.g., Xu & Chun, 2006; Vogel & Machizawa, 2004), the mu suppression was weaker for load 5 than for load 4. However, the occipital alpha suppression (calculated as the \log [BM power/control power]) did not exhibit such a pattern.

The ANOVA on mu suppression did not reveal a significant main effect of Memory load [$F(3, 93) = 2.03, p = .12, \eta_p^2 = 0.06$]. However, in line with previous WM studies (e.g., Drew & Vogel, 2008; Vogel & Machizawa, 2004), our planned paired t test revealed a significant difference between loads 2 and 4 [$t(31) = 2.61, p < .025$, Cohen's $d = 0.37$]. Neither the main effect of Memory load [$F(3, 93) = 1.95, p = .13, \eta_p^2 = 0.06$] nor the difference between loads 2 and 4 [$t(31) = 0.91, p = .37$, Cohen's $d = 0.11$] reached significance for the occipital alpha suppression.

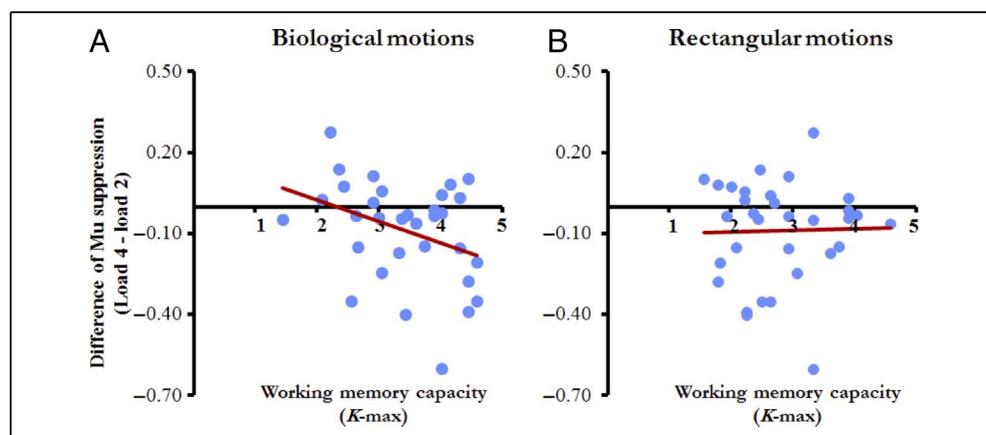
We further calculated the Pearson correlation (r) between individual WM capacities and the differences in

mu suppression between loads 4 and 2 (e.g., Drew & Vogel, 2008; Vogel & Machizawa, 2004). We found that the difference in mu suppression increased as the number of BM stimuli stored in WM increased ($r = -.35, p < .05$; Figure 4A). However, this negative correlation vanished when using the WM capacity estimates of rectangle animations ($r = .03, p > .1$; Figure 4B).

Discussion

Congruent with previous behavioral studies (e.g., Wood, 2007, 2011; Smyth & Pendleton, 1990; Smyth et al., 1988), the current behavioral results suggest that the participants could remember three to four BM stimuli, at most. More importantly, the mu suppression results revealed a pattern that supported the behavioral findings, in that the mu suppression rose as the memory load increased, and stopped rising after more than four BM stimuli were presented (paired t test between loads 4 and 5: $t(31) = -0.67, p = .51$, Cohen's $d = 0.09$). Although the main effect of memory load did not reach significance, perhaps because differences in task difficulty weakened the mu suppression, our planned contrast revealed considerably stronger mu suppression at load 4 than at load 2. This

Figure 4. The Pearson correlations (r) between WM capacity (K -max) of the memorized stimuli and the difference in mu suppression (load 4 – load 2) for (A) BM and (B) rectangle animation.



finding is meaningful for two reasons. First, it is in line with previous studies showing that the greatest difference usually occurs between loads 2 and 4 (e.g., Gao et al., 2009; Drew & Vogel, 2008; Vogel & Machiwaza, 2004). Second, a significant correlation was identified between individual WM capacity and the corresponding mu difference between loads 2 and 4.

It could be argued that the current finding on mu suppression does not reflect rehearsal mechanisms because the 8–12 Hz suppression in nature develops over time (referred to here as the natural increase explanation). In other words, the current results were contaminated by the exposure time of the memory array. We agree that the mu suppression developed over time during the encoding phase (see footnote 1) of WM because participants had to encode the motion stimuli into WM in sequence during the encoding phase. However, our MNS hypothesis was different from the natural increase explanation, in that it predicted that, once the WM reached capacity, the mu suppression would stop increasing. In contrast, the natural increase explanation predicted that the mu suppression would increase as the memory load or exposure time increased regardless of WM capacity. In addition, the natural increase explanation did not have any specific predictions regarding the relationship between individual WM capacity and the differences in mu suppression between loads 2 and 4 (see Experiments 1 and 3). Therefore, the natural increase explanation does not describe the current results.

However, although the results of Experiment 1 dovetailed well with our prediction, the nonsignificant main effect of memory load on mu suppression raised questions regarding the solidity of the conclusion. To this end, we ran two additional experiments to examine whether the statistical difference between loads 2 and 4 indeed reflected rehearsal mechanisms for BM stimuli in WM. Experiment 2 investigated whether the significant difference between loads 2 and 4 would be eliminated in the absence of MNS rehearsal. Experiment 3 attempted to replicate the core findings of Experiment 1 by adopting a new set of control stimuli, with whom the task difficulty of the two change detection tasks was comparable.

EXPERIMENT 2: MU SUPPRESSION MODULATION WITHOUT REHEARSAL

Experiment 2 examined whether the participants indeed rehearsed BM stimuli in WM via the MNS. If true, then the significant difference between loads 2 and 4 in Experiment 1 would be eliminated in the absence of MNS rehearsal. Our initial pilot experiment revealed that without the verbal task, participants tended to verbally code the BM stimuli (Z. Gao, unpublished observations). Consequently, we removed the digit rehearsal task in Experiment 2 and predicted that the significant difference between loads 2 and 4 in Experiment 1 would vanish.

Methods

There were 32 (17 men) new participants in Experiment 2. The digit rehearsal task was removed from the procedure. Participants had to memorize either two or four stimuli in each trial. There were 108 trials in each set size condition (2 vs. 4 motions), resulting in 216 randomly presented trials for each motion block (BM vs. non-BM). Each block lasted about 45 min. The other aspects were the same as Experiment 1.

Results

Behavioral Results

The ANOVA on accuracy (see Figure 5A) revealed a significant main effect of Set size [$F(3, 31) = 158.06, p < .001, \eta_p^2 = 0.84$], suggesting that the accuracy was significantly higher at load 2 than at load 4. Similarly, the main effect of Stimulus type was significant [$F(1, 31) = 19.01, p < .001, \eta_p^2 = 0.38$], indicating that the accuracy was higher for BM (91%) than for control motion (85%) stimuli. Finally, a significant interaction between Set size and Stimulus type was revealed [$F(1, 31) = 23.86, p < .001, \eta_p^2 = 0.44$]. Further analysis revealed that the accuracy was significantly higher for BM than for non-BM in both load conditions ($ps < .05$).

Figure 5. Results of Experiment 2. (A) Analysis of behavioral data. (B) Analysis of EEG recordings showed no suppression (calculated as $\log[\text{BM power}/\text{control power}]$) of either central mu or occipital alpha. Error bars indicate standard error.

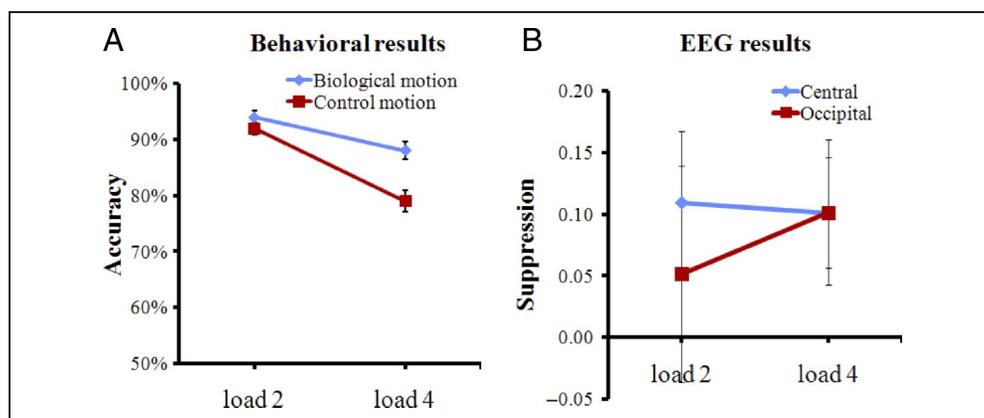
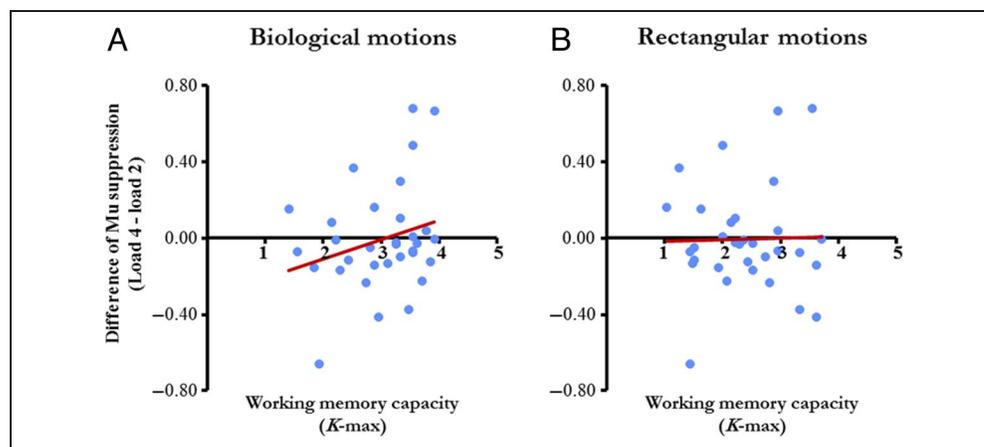


Figure 6. The Pearson correlations (r) between WM capacity (K -max) of the memorized stimuli and the difference in mu suppression (load 4 – load 2) for (A) BM and (B) rectangle animation.



The capacity estimate (K -max) for BM stimuli was 3.01, and the K -max for the rectangle animations was 2.39.

EEG Results

As demonstrated in Figure 5B, instead of being suppressed, the mu rhythm was enhanced, and this enhancement was not modulated by the memory load [$F(1, 31) = 0.02, p = .89, \eta_p^2 = 0.001$]. In addition, although the alpha rhythm exhibited a slight enhancement from load 2 to 4, in line with the results of Experiment 1, it did not reach significance [$F(1, 31) = 0.85, p = .36, \eta_p^2 = 0.03$].

The Pearson correlation (r) between individual WM capacities and the mu-suppression differences between loads 4 and 2 did not reach significance for either the BM stimuli ($r = .26, p > .1$; Figure 6A) or rectangle animations ($r = .03, p > .1$; Figure 6B).

Discussion

Supporting our prediction, we found that both the mu suppression and the difference between loads 2 and 4 vanished after removing the digit rehearsal task, and there was no significant correlation between the mu suppression differences and the number of BM stimuli in WM. These results were in line with our pilot observation, suggesting that participants did not rehearse BM via the MNS but may have used verbal coding instead. In addition, because the BM stimuli depicted common daily activities, whereas the rectangle animations were novel to the participants, the task difficulty was lower for the BM condition relative to the non-BM condition. Confirming this explanation, the alpha rhythm showed clear enhancement.

EXPERIMENT 3: MU SUPPRESSION MODULATION BY MEMORY LOAD: A DIFFERENT CONTROL

Experiment 3 was designed to examine whether the core findings of Experiment 1 could be generalized to other

types of control stimuli, while balancing the task difficulty. Particularly, we replaced the rectangle animations from Experiment 1 with circle animations, which have been used in previous mu studies (e.g., Perry, Bentin, Bartal, et al., 2010; Perry, Bentin, Shalev, et al., 2010; Perry, Troje, et al., 2010). The participants were required to remember two or four stimuli.

Methods

There were 18 (12 men) participants in Experiment 3. Two participants were removed from analysis because of poor EEG waveforms. Distinct animations of a circle were created as the control motions. The circle animations were composed of 13 points, which were evenly distributed around the periphery of an invisible circle with a radius of 1.15° . The circle could inflate, shrink, move down, move up, roll left, or roll right.

Participants had to memorize either two or four stimuli in each trial. There were 72 trials for each set size (2 vs. 4 motions), resulting in 144 randomly presented trials in each motion block (BM vs. non-BM). Each block was divided into four sessions with a 5-min break in between and could be completed in about 40 min. The other aspects were the same as Experiment 1.

Results

Behavioral Results

The ANOVA on accuracy (see Figure 7A) revealed a significant main effect of Set size [$F(1, 15) = 54.28, p < .001, \eta_p^2 = 0.78$], indicating that the accuracy was significantly lower at load 4 than at load 2. Neither the main effect of Stimulus type [$F(1, 15) = 0.12, p = .12, \eta_p^2 = 0.08$] nor the Set Size \times Stimulus Type interaction [$F(1, 15) = 2.50, p = .14, \eta_p^2 = 0.14$] reached significance, suggesting that the accuracies for BM and circle animations were comparable.

The capacity estimate (K -max) for BM stimuli was 2.76, and the K -max for the circle animations was 2.81.

mu suppression was significantly correlated with the number of BM stimuli, but not with the number of non-BM stimuli in WM (Experiments 1 and 3), and this correlation was not restricted to one specific type of control motion.

The current study is the first to provide direct evidence that the MNS is involved in BM rehearsal in WM. Previous studies have demonstrated that imagining an action can evoke activation of the MNS (see Grezes & Decety, 2001, for a meta-analysis; Neuper, Scherer, Wriessnegger, & Pfurtscheller, 2009; Pfurtscheller, Brunner, Schlogl, & Lopes da Silva, 2006; Pineda, Allison, & Vankov, 2000). This implies that the MNS may play a role during WM processes because imagining an action, at least partially, requires the involvement of WM. However, it remains unknown whether the MNS is involved in rehearsing BM stimuli in WM. In addition, the “theory of event coding” (TEC) proposes that perception and action share common representations (Hommel, Musseler, Aschersleben, & Prinz, 2001; see Prinz, 1997, for a similar claim), which are suggested to be fulfilled by the MNS (Jeannerod, 2001). This theory predicts that the same mental representations are employed when perceiving/memorizing an action as when executing the same action. Although there has been ample evidence supporting the shared representation between perceiving and executing an action, to our knowledge, no study has examined whether perceiving and memorizing an action obeys the same rule. The current study closes this gap by demonstrating clear-cut evidence that the MNS, as indexed by mu suppression, plays a critical role in BM maintenance, and hence confirms the prediction of the TEC.

Congruent with the TEC, the current study adds to the accumulated evidence that visual perception and visual WM share similar processing mechanisms (e.g., Gao, Gao, Li, Sun, & Shen, 2011; Gao, Li, Yin, & Shen, 2010; Ester et al., 2009; Harrison & Tong, 2009). These previous WM studies used static and simple stimuli (e.g., orientated Gabor patches), which require low-level processing in the visual cortex. The results of these studies revealed, for instance, that brain regions in charge of processing orientation perception are also involved in holding orientation in WM (e.g., Ester et al., 2009; Harrison & Tong, 2009). Here, we used PLDs, which are animated sets of dots that form a compelling impression of a human action. Such stimuli are far more complex than the stimuli used in previous WM studies, and they convey social information. Furthermore, these complex stimuli are processed by high-level visual cortices such as the STS and premotor cortex (e.g., Saygin et al., 2004; Puce & Perrett, 2003). However, we found that BM perception and memorization share similar processing mechanisms.

This study also adds several new aspects to the understanding of BM. For one, we provide the first neuroimaging evidence confirming that only a limited set of BM stimuli can be held in WM (i.e., three to four BM stimuli at most; for behavioral results, see Shen et al., in press; Wood, 2007, 2011; Smyth & Pendleton, 1989, 1990; Smyth et al., 1988).

All previous studies have addressed the storage capacity of BM via behavioral methods; hence, the results may be affected by other factors such as task difficulty in the comparison phase of a WM task³ (e.g., Awh, Barton, & Vogel, 2007). By investigating mu suppression, we were able to examine the maintenance phase of WM directly. Second, we reveal that BM perception as well as holding BM in WM modulates mu suppression, suggesting that the MNS is involved in internally simulating the BM regardless of processing stage. Third, the current study demonstrates for the first time that the mu suppression evoked by BM is significantly correlated with the behavioral performance of participants on a cognitive task. This finding is consistent with a recent study suggesting that BM processing has two distinct components: social cognition and motor imagery (Miller & Saygin, 2013). Another study, from a social cognition perspective, has shown that mu suppression is significantly correlated with empathy scores (Perry, Troje, et al., 2010). Our study adds further evidence from a motor imagery perspective, suggesting that the memorized BM stimuli are internally simulated via the MNS.

Beyond the contribution to BM processing, our study extends the current knowledge of the mu rhythm. For instance, we have shown for the first time that mu suppression can be observed during the maintenance phase of a WM task. Since the seminal discovery of mirror neurons in monkeys (e.g., Rizzolatti et al., 1996; di Pellegrino et al., 1992), the search for an analogous MNS in humans has become an important topic in both motor cognition and social cognition (e.g., Oosterhof, Tipper, & Downing, 2013; Molenberghs, Cunnington, & Mattingley, 2009; Rizzolatti & Craighero, 2004; see Iacoboni & Mazziotta, 2007, for a review). To explore this topic, it is important to take advantage of various neuroimaging techniques, including EEG. On the basis of the elegant and careful investigations of the recent decade, researchers now consider mu suppression to be a manifestation of the MNS (e.g., Perry & Bentin, 2009; Oberman et al., 2007; Ulloa & Pineda, 2007; Pineda, 2005). In previous studies, the participants perceived, executed, or imagined actions, for instance, watching or performing a glass-grasping action; however, no study has examined whether mu suppression could be evoked in a higher-level task such as memory. The current study provides clear evidence that mu suppression and modulation can be observed during a WM task. Therefore, we suggest that mu suppression can be used as a sensitive and useful index for exploring the memorization of BM information in future studies.

Additionally, the current study provides further evidence that the functions of central mu and occipital alpha rhythms are dissociable (e.g., Perry et al., 2011; Pineda, 2005; Pfurtscheller, Stancak, & Neuper, 1996). This is in contrast to many previous studies showing similar degrees or trends of suppression between the two rhythms (e.g., Perry, Bentin, Bartal, et al., 2010; Perry, Bentin, Shalev, et al., 2010; Perry, Troje, et al., 2010). Here, we found a larger degree of suppression for mu compared

with alpha (see Figures 3B and 7B). More importantly, only the mu rhythm was modulated by the BM memory load. These results strongly suggest that the mu rhythm indeed reflects motor activities. On the other hand, the occipital alpha in the current study showed limited suppression and was even enhanced in Experiment 1. This can be explained by the task difficulty of Experiment 1, because the behavioral performance for BM was significantly better than that for rectangle animations (control motion). Consequently, under the same memory load, processing the control motion required more attentional resources (and hence had a lower alpha rhythm power). This unbalanced task difficulty also slightly affected the result profile of mu rhythms, as mu had somewhat weaker suppression in Experiment 1 than in Experiment 3. Corroborating this explanation, we found that, once the task difficulty was balanced between BM and non-BM (Experiment 3), the alpha enhancement vanished, and the alpha suppression ($\log [\text{BM power}/\text{control power}]$) was close to zero. Furthermore, the mu suppression in Experiment 3 was stronger than that in Experiment 1. These results were in line with previous suggestions that occipital alpha is affected by increased attentional demands (Klimesch, 1999, 2012). It is worth noting that, although previous studies have suggested that alpha rhythms are closely related to maintaining information in WM or function to inhibit task-irrelevant brain areas in a WM task (see Roux & Uhlhaas, 2014 for a review), the alpha suppression/enhancement we observed has a different meaning from that found in previous studies. This is because we calculated the alpha suppression/enhancement of BM stimuli by adopting the power of non-BM as the baseline, which was used to avoid any non-BM-related contamination. In contrast, previous studies exploring alpha rhythms computed the amplitude/power directly (e.g., Sauseng et al., 2009) or adopted a resting period (e.g., pre-stimulus interval) as the baseline (e.g., Jensen, Gelfand, Kounios, & Lisman, 2002). Therefore, the current study did not observe any modulation by set size on the occipital alpha, because it is not involved in rehearsing BM information.

Acknowledgments

This article is dedicated to the memory of Prof. Shomo Bentin. This research was supported by NSFC (nos. 31271089, 31170974, and 31170975), RFDE (no. Y201224811), RFD (no. 20120101120085), and SRF for ROCS, SEM.

Reprint requests should be sent to Zaifeng Gao or Mowei Shen, Department of Psychology and Behavioral Sciences, Xixi Campus, Zhejiang University, Hang Zhou, P.R. China 310007, or via e-mail: zaifengg@zju.edu.cn, mwshen@zju.edu.cn.

Notes

1. Wood (2007) estimated the WM capacity of BM by averaging K values when participants had to remember four and five stimuli. However, because K often decreased in conditions where the set size exceeded an individual's WM capacity, to in-

crease the accuracy of our capacity estimate compared with that by Wood (2007), we used the maximum K (K -max) among the four load conditions as an individual's WM capacity (e.g., Curby & Gauthier, 2007).

2. To ensure the participants had enough encoding time, the exposure time of the memory array increased as the number of to-be-remembered stimuli increased (see the Methods section for details). This setting led certain information to be stored in WM during the encoding phase, particularly during conditions with larger set sizes. However, because we focused on the rehearsal mechanism after all information was encoded into WM and the different exposure times may have affected the potential mu/alpha suppression in the encoding phase, we did not conduct further analysis on the encoding phase.

3. Related, although we found that the WM capacity was lower for rectangle animations than for BM stimuli in Experiments 1 and 2, we could not conclude that fewer rectangle animations were remembered relative to BM stimuli. Instead, we argue that similar to the BM stimuli, three to four rectangle animation stimuli were also encoded into WM. The underestimated capacity for non-BM stimuli was largely because the rectangle animations were meaningless and novel to the participants (e.g., Awh et al., 2007), leading to a higher comparison difficulty relative to the BM condition.

REFERENCES

- Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological Science*, *18*, 622–628.
- Blake, R., & Shiffrar, M. (2007). Perception of human motion. *Annual Review of Psychology*, *58*, 47–73.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Curby, K. M., & Gauthier, I. (2007). A visual short-term memory advantage for faces. *Psychonomic Bulletin & Review*, *14*, 620–628.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*, 9–21.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.
- Drew, T., & Vogel, E. K. (2008). Neural measures of individual differences in selecting and tracking multiple moving objects. *Journal of Neuroscience*, *28*, 4183–4191.
- Ester, E. F., Serences, J. T., & Awh, E. (2009). Spatially global representations in human primary visual cortex during working memory maintenance. *Journal of Neuroscience*, *29*, 15258–15265.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Gao, T., Gao, Z., Li, J., Sun, Z., & Shen, M. (2011). The perceptual root of object-based storage: An interactive model of perception and visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 1803–1823.
- Gao, Z., Li, J., Liang, J., Chen, H., Yin, J., & Shen, M. (2009). Storing fine detailed information in visual working memory—evidence from event-related potentials. *Journal of Vision*, *9*, 1–12.
- Gao, Z., Li, J., Yin, J., & Shen, M. (2010). Dissociated mechanisms of extracting perceptual information into visual working memory. *PLoS ONE*, *5*, e14273.

- Gilaie-Dotan, S., Bentin, S., Harel, M., Rees, G., & Saygin, A. P. (2011). Normal form from biological motion despite impaired ventral stream function. *Neuropsychologia*, *49*, 1033–1043.
- Gilaie-Dotan, S., Kanai, R., Bahrami, B., Rees, G., & Saygin, A. P. (2013). Neuroanatomical correlates of biological motion detection. *Neuropsychologia*, *51*, 457–463.
- Grezes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*, 1–19.
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*, 632–635.
- Hommel, B., Musseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*, 849–878; discussion 878–937.
- Iacoboni, M., & Mazziotta, J. C. (2007). Mirror neuron system: Basic findings and clinical applications. *Annals of Neurology*, *62*, 213–218.
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage*, *14*, S103–S109.
- Jensen, O., Gelfand, J., Kounios, J., & Lisman, J. E. (2002). Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex*, *12*, 877–882.
- Johansson, G. (1973). Visual-perception of biological motion and a model for its analysis. *Perception & Psychophysics*, *14*, 201–211.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research. Brain Research Reviews*, *29*, 169–195.
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Science*, *16*, 606–617.
- Kuhlman, W. N. (1978). Functional topography of the human mu rhythm. *Electroencephalography and Clinical Neurophysiology*, *44*, 83–93.
- Miller, L. E., & Saygin, A. P. (2013). Individual differences in the perception of biological motion: Links to social cognition and motor imagery. *Cognition*, *128*, 140–148.
- Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2009). Is the mirror neuron system involved in imitation? A short review and meta-analysis. *Neuroscience and Biobehavioral Reviews*, *33*, 975–980.
- Neuper, C., Scherer, R., Wriessnegger, S., & Pfurtscheller, G. (2009). Motor imagery and action observation: Modulation of sensorimotor brain rhythms during mental control of a brain-computer interface. *Clinical Neurophysiology*, *120*, 239–247.
- Oberman, L. M., Pineda, J. A., & Ramachandran, V. S. (2007). The human mirror neuron system: A link between action observation and social skills. *Social Cognitive and Affective Neuroscience*, *2*, 62–66.
- Oberman, L. M., & Ramachandran, V. S. (2007). The simulating social mind: The role of the mirror neuron system and simulation in the social and communicative deficits of autism spectrum disorders. *Psychological Bulletin*, *133*, 310–327.
- Oberman, L. M., Ramachandran, V. S., & Pineda, J. A. (2008). Modulation of mu suppression in children with autism spectrum disorders in response to familiar or unfamiliar stimuli: The mirror neuron hypothesis. *Neuropsychologia*, *46*, 1558–1565.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, 156869.
- Oosterhof, N. N., Tipper, S. P., & Downing, P. E. (2013). Crossmodal and action-specific: Neuroimaging the human mirror neuron system. *Trends in Cognitive Science*, *17*, 311–318.
- Pavlova, M. (2012). Biological motion processing as a hallmark of social cognition. *Cerebral Cortex*, *22*, 981–995.
- Pavlova, M., Lutzenberger, W., Sokolov, A., & Birbaumer, N. (2004). Dissociable cortical processing of recognizable and non-recognizable biological movement: Analysing gamma MEG activity. *Cerebral Cortex*, *14*, 181–188.
- Perry, A., & Bentin, S. (2009). Mirror activity in the human brain while observing hand movements: A comparison between EEG desynchronization in the mu-range and previous fMRI results. *Brain Research*, *1282*, 126–132.
- Perry, A., Bentin, S., Bartal, I. B., Lamm, C., & Decety, J. (2010). “Feeling” the pain of those who are different from us: Modulation of EEG in the mu/alpha range. *Cognitive Affective & Behavioral Neuroscience*, *10*, 493–504.
- Perry, A., Bentin, S., Shalev, I., Israel, S., Uzevovsky, F., Bar-On, D., et al. (2010). Intranasal oxytocin modulates EEG mu/alpha and beta rhythms during perception of biological motion. *Psychoneuroendocrinology*, *35*, 1446–1453.
- Perry, A., Stein, L., & Bentin, S. (2011). Motor and attentional mechanisms involved in social interaction-evidence from mu and alpha EEG suppression. *Neuroimage*, *58*, 895–904.
- Perry, A., Troje, N. F., & Bentin, S. (2010). Exploring motor system contributions to the perception of social information: Evidence from EEG activity in the mu/alpha frequency range. *Social Neuroscience*, *5*, 272–284.
- Pfurtscheller, G., Brunner, C., Schlogl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *Neuroimage*, *31*, 153–159.
- Pfurtscheller, G., Stancak, A., Jr., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—An electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology*, *24*, 39–46.
- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into “doing.” *Brain Research Reviews*, *50*, 57–68.
- Pineda, J. A., Allison, B. Z., & Vankov, A. (2000). The effects of self-movement, observation, and imagination on mu rhythms and readiness potentials (RP’s): Toward a brain-computer interface (BCI). *IEEE Transactions on Rehabilitation Engineering*, *8*, 219–222.
- Pineda, J. O., & Oberman, L. M. (2006). What goads cigarette smokers to smoke? Neural adaptation and the mirror neuron system. *Brain Research*, *1121*, 128–135.
- Poom, L. (2012). Memory of gender and gait direction from biological motion: Gender fades away but directions stay. *Journal of Experimental Psychology: Human Perception and Performance*, *38*, 1091–1097.
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, *9*, 129–154.
- Puce, A., & Perrett, D. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *358*, 435–445.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research, Cognitive Brain Research*, *3*, 131–141.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661–670.

- Rouder, J. N., Morey, R. D., Morey, C. C., & Cowan, N. (2011). How to measure working memory capacity in the change detection paradigm. *Psychonomic Bulletin & Review*, *18*, 324–330.
- Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha-gamma versus theta-gamma codes for distinct WM information?. *Trends in Cognitive Sciences*, *18*, 16–25.
- Sauseng, P., Klimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., et al. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology*, *19*, 1846–1852.
- Saygin, A. P. (2007). Superior temporal and premotor brain areas necessary for biological motion perception. *Brain*, *130*, 2452–2461.
- Saygin, A. P., Wilson, S. M., Hagler, D. J., Jr., Bates, E., & Sereno, M. I. (2004). Point-light biological motion perception activates human premotor cortex. *Journal of Neuroscience*, *24*, 6181–6188.
- Semlitsch, H. V., Anderer, P., Schuster, P., & Presslich, O. (1986). A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. *Psychophysiology*, *23*, 695–703.
- Shen, M., Gao, Z., Ding, X., Zhou, B., & Huang, X. (in press). Holding biological motion information in working memory. *Journal of Experimental Psychology: Human Perception and Performance*.
- Singh, F., Pineda, J., & Cadenhead, K. S. (2011). Association of impaired EEG mu wave suppression, negative symptoms and social functioning in biological motion processing in first episode of psychosis. *Schizophrenia Research*, *130*, 182–186.
- Smyth, M. M., Pearson, N. A., & Pendleton, L. R. (1988). Movement and working memory: Patterns and positions in space. *The Quarterly Journal of Experimental Psychology*, *40*, 497–514.
- Smyth, M. M., & Pendleton, L. R. (1989). Working memory for movements. *The Quarterly Journal of Experimental Psychology*, *41*, 235–250.
- Smyth, M. M., & Pendleton, L. R. (1990). Space and movement in working memory. *The Quarterly Journal of Experimental Psychology*, *42*, 291–304.
- Thompson, J., & Parasuraman, R. (2012). Attention, biological motion, and action recognition. *Neuroimage*, *59*, 4–13.
- Troje, N. F. (2013). What is biological motion?: Definition, stimuli and paradigms. In M. D. Rutherford & V. A. Kuhlmeier (Eds.), *Social perception: Detection and interpretation of animacy, agency, and intention* (pp. 13–36). Cambridge, MA: MIT Press.
- Ulloa, E. R., & Pineda, J. A. (2007). Recognition of point-light biological motion: Mu rhythms and mirror neuron activity. *Behavioural Brain Research*, *183*, 188–194.
- van Kemenade, B. M., Muggleton, N., Walsh, V., & Saygin, A. P. (2012). Effects of TMS over premotor and superior temporal cortices on biological motion perception. *Journal of Cognitive Neuroscience*, *24*, 896–904.
- Vanrie, J., & Verfaillie, K. (2004). Perception of biological motion: A stimulus set of human point-light actions. *Behavior Research Methods, Instruments, & Computers*, *36*, 625–629.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751.
- Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature*, *438*, 500–503.
- Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 92–114.
- Wood, J. N. (2007). Visual working memory for observed actions. *Journal of Experimental Psychology: General*, *136*, 639–652.
- Wood, J. N. (2008). Visual memory for agents and their actions. *Cognition*, *108*, 522–532.
- Wood, J. N. (2010). Visual working memory retains movement information within an allocentric reference frame. *Visual Cognition*, *18*, 1464–1485.
- Wood, J. N. (2011). A core knowledge architecture of visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 357–381.
- Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, *440*, 91–95.