



Research report

Suppression of EEG mu rhythm during action observation corresponds with subsequent changes in behavior



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ABSTRACT

Movement is intrinsically linked to perception such that observing an action induces in the observer behavioral changes during execution of similar actions. Electroencephalogram (EEG) studies have revealed that at the group level, action observation suppresses oscillatory power in mu (8–12 Hz) and beta (15–25 Hz) bands over the sensorimotor cortex – a phenomenon associated with increased excitability of cortical neurons. However, it is unclear whether differences in suppression level across individuals is linked with individual differences in subsequent behavioral changes. Here 32 subjects performed self-paced finger tapping with their right hand before and after observation of a video displaying finger-tapping at either 2 or 4 Hz. Behaviorally, subjects' rate of self-pace tapping increased following observation, with higher increases following 4 Hz observation. The level of EEG power suppression in the low frequency range (low mu; 8–10 Hz) during observation corresponded to subsequent behavioral changes in tapping rate across individuals. Our results demonstrate that observing actions implicitly shifts subsequent execution rates, and that individual differences in the level of this implicit shift can be explained by activity in the sensorimotor cortex during observation.

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1. Introduction

Observing actions performed by others influences subsequent actions performed by the observer. Such influences can take various forms, including changes in reaction time and explicit imitation (Sturmer et al., 2000; Brass et al., 2001; Craighero et al., 2002), facilitation, or interference with executed movement (Kilner et al., 2003; Boutin et al., 2010). In the context of learning, action observation can even result in significant performance gains – despite the absence of physical practice (Mattar and Gribble, 2005; Cross et al., 2009; Ossmy and Mukamel, 2016a,b).

Studies focusing on the implicit aspects of action observation have demonstrated that observing others induces a higher tendency to adopt the gestures and mannerisms of interacting partners (Chartrand and Bargh, 1999; Ferguson and Bargh, 2004), or implicitly primes subsequent actions (Edwards et al., 2003). Similarly, it has been demonstrated that observing an action performed

at a certain rate can implicitly influence the endogenous rate of subsequent execution by the observer (Bove et al., 2009; Avanzino et al., 2015; Aridan and Mukamel, 2016). Understanding the neural substrates of these implicit changes can provide a useful account of how we acquire new behaviors (Iacoboni et al., 1999; Heyes, 2001). Such implicit changes in tapping rate across individuals are related to fMRI activity in primary motor cortex contralateral to the observed hand (Aridan and Mukamel, 2016). In the current study we used electroencephalography (EEG) to further examine this issue.

There are good reasons to believe that shared neural representations during action perception and action execution underlie implicit changes in behavior. Many electroencephalography (EEG) and magnetoencephalography (MEG) studies show that event-related desynchronization (ERD) is associated with increased excitability of cortical motor regions during self-initiated movements (Altschuler et al., 1998; Babiloni et al., 1999; Pfurtscheller and Neuper, 2001; Muthukumaraswamy and Johnson, 2004; Pineda, 2005; Hari, 2006). The recorded ERD is most prominent in the mu (8–13 Hz) and beta (~15–25 Hz) frequency ranges (Neuper et al., 1999) over the sensorimotor regions and is believed to reflect increased excitability of cortical motor regions

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(Altschuler et al., 1998; Babiloni et al., 1999; Pfurtscheller and Da Silva, 1999). Over the last two decades, similar decreases in oscillatory power have been reported while subjects imagine or passively observe actions (or videos depicting actions) performed by others (Hari et al., 1998; Neuper et al., 1999; Pineda, 2005). Within the mu rhythm, the low frequency band (8–10 Hz) has been reported to be more sensitive to action observation while the higher frequency band (10–13 Hz) to be more sensitive to action execution (Frenkel-Toledo et al., 2013). Given the spatial overlap in ERD's during execution and observation of actions in sensorimotor regions, they are commonly used as an EEG index of mirror-like activity (Pineda, 2005; Perry and Bentin, 2009; Perry et al., 2011). Simultaneous fMRI and EEG studies further validated the anatomical distribution of Mu and beta suppression as indicators of activity in cortical regions with mirror properties. Co-variation of EEG ERD and fMRI BOLD signal during action observation was found in the inferior parietal lobe (IPL), premotor, and inferior frontal gyrus (IFG; (Goldman et al., 2002; Laufs et al., 2003; Arnstein et al., 2011; Braadbaart et al., 2013). However, while mirror-like activity is implicated in imitation and learning, the link between the magnitude of EEG ERD during observation and subsequent behavioral changes has been much less explored – both at the group and individual subject level. To examine this issue, we recorded EEG activity and behavioral changes in spontaneous tapping rate of healthy subjects before and after observing a video of someone else performing the same task.

2. Results

Thirty-two subjects performed a repeated serial button-pressing task using their right index-finger while wearing an EEG cap. In an initial execution stage, subjects sequentially pressed four color-marked keys back and forth at their own pace for 5 s followed by 5 s of resting period (see Fig. 1 and Experimental Procedure). After performing 10 such blocks, subjects passively observed a video of someone else performing the task at a rate of either 2 Hz ('2Hz-OBS' group; 16 subjects) or 4 Hz ('4Hz-OBS' group; 16 subjects, Movie 1). Finally, subjects performed another 10 execution blocks (See Fig. 1 and Experimental Procedure).

Subjects' execution rate during the first execution session ranged between 2.14 and 4.17 Hz, and the majority (29 out of 32) had a spontaneous rate lower than 4 Hz (See Table 1). Initial tapping rates were not significantly different between the two groups ($p = 0.26$; two-tailed equal variance t -test).

At the group level, performance rate of subjects from the '4Hz-OBS' group increased from an average of 2.92 Hz to 3.76 Hz following the observation session (mean \pm SD difference = 0.84 ± 0.6 ,

$t_{(15)} = 4.8$, $p = 2.2 \cdot 10^{-5}$, $CI = [0.33 \ 1.08]$, two-tailed paired t -test; left panel in Fig. 2A). Subjects from the '2Hz-OBS' group also exhibited an increase in tapping rate (averaged rate before = 3.19 Hz, after = 3.48 Hz; mean \pm SD difference = 0.29 ± 0.32 ; $t_{(15)} = 3.48$, $p = 3.2 \cdot 10^{-3}$, $CI = [0.03 \ 0.13]$, two-tailed paired t -test; left panel in Fig. 2B). A mixed model ANOVA revealed an interaction effect between session (pre- and post-observation sessions) and group ($F_{(2,31)} = 7.99$; $p = 8 \cdot 10^{-3}$), indicating the increase in 4 Hz-OBS group was significantly higher than the increase in the 2 Hz-OBS group. These increases in tapping rate resulted in a lower Relative Distance (RD; See Experimental Procedure) index following observation in the 4 Hz group (mean \pm SD $RD_{pre} = 1.09 \pm 0.66$, $RD_{post} = 0.49 \pm 0.43$ averaged across subjects; see right panel in Fig. 2A and Experimental Procedure), and a higher RD index following observation in the 2 Hz group (mean \pm SD: $RD_{pre} = 1.19 \pm 0.6$, $RD_{post} = 1.48 \pm 0.71$ averaged across subjects; right panel in Fig. 2B). Taken together, these findings indicate that in both groups, spontaneous rate of finger tapping increased following observation of a video depicting someone else performing the task, with higher increases in the 4 Hz-OBS group.

At the neural level, we examined the averaged event-related spectral perturbation (ERSP) in all subjects and electrodes during execution and observation (for multi subject map from the 4 Hz-OBS and 2 Hz-OBS groups see Figs. 3A and 4A respectively). A data-driven approach using nonparametric cluster analysis revealed wide range significant suppression in frequency (from 8 Hz to 25 Hz) and time (1 s–4 s after trial onset) – see Supplement material and Fig. S1 for further details. We therefore focused on 3 predetermined frequency bands – low mu (8–10 Hz), high mu (11–12 Hz) and beta (15–25 Hz) which have been reported in previous studies (Frenkel-Toledo et al., 2013; Fox et al., 2016). We focused on the left sensorimotor sites (electrodes FC1, FC3, FC5, C1, C3, C5, CP1, CP3, CP5; contralateral to the executing hand) and bilateral occipital sites (O1 and O2). During the two execution sessions, oscillation power in both the sensorimotor and the occipital sites was significantly suppressed relative to baseline in all frequency bands we examined (see Figs. 3A and 4A for the 4 Hz-OBS and 2 Hz-OBS groups respectively, and also Table 2). Table 3 provides a statistical comparison of the suppression level in the two execution sessions, and Table 4 a statistical comparison of suppression levels across the two observation groups. We did not find significant differences in suppression levels between groups in the sensorimotor or occipital sites during the execution tasks.

During the observation session, suppression was significant in the low mu frequency band in both sensorimotor and occipital sites but not in the other frequency ranges (Figs. 3A and 4A). Similar to the execution sessions, we did not find a significant difference in suppression levels between groups in the observation



Fig. 1. Experiment design. Subjects performed 10 consecutive blocks of a repeated serial button-pressing task at their own pace. Each 5 s execution block was preceded by 5 s of observation of a video clip depicting flowing water. The execution blocks were followed by 10 consecutive observation blocks of a video depicting someone else performing the button-pressing task at a rate of either 2 or 4 Hz (16 subjects in each group). Finally, subjects performed the execution task again.

Table 1

Subjects' performance rate. Individual subjects' tapping rate during pre- and post- observation sessions, and corresponding behavioral modulation index (RM; see Experimental Procedure).

Subject	4 Hz-OBS			2 Hz-OBS		
	Frequency before (Hz)	Frequency after (Hz)	RM index	Frequency before (Hz)	Frequency after (Hz)	RM index
1	2.37	4.69	0.94	2.77	2.77	0.01
2	3.64	3.88	0.24	3.90	4.62	-0.72
3	4.17	4.82	-0.65	2.27	2.23	0.04
4	2.17	2.83	0.66	4.16	4.46	-0.29
5	2.23	2.26	0.03	3.57	4.16	-0.59
6	3.57	4.03	0.4	2.77	3.2	-0.42
7	2.49	3.80	1.31	3.125	3.47	-0.34
8	2.87	3.81	0.94	4.16	4.46	-0.29
9	3.98	4.17	-0.15	3.78	3.12	0.66
10	3.90	3.37	-0.53	2.60	2.77	-0.17
11	2.20	3.71	1.51	2.97	3.67	-0.7
12	2.98	3.83	0.85	2.45	2.65	-0.2
13	2.14	3.54	1.40	2.71	3.12	-0.4
14	2.86	3.50	0.64	2.77	3.04	-0.27
15	2.99	4.38	0.63	3.28	3.84	-0.55
16	2.18	3.56	1.38	3.78	4.16	-0.37

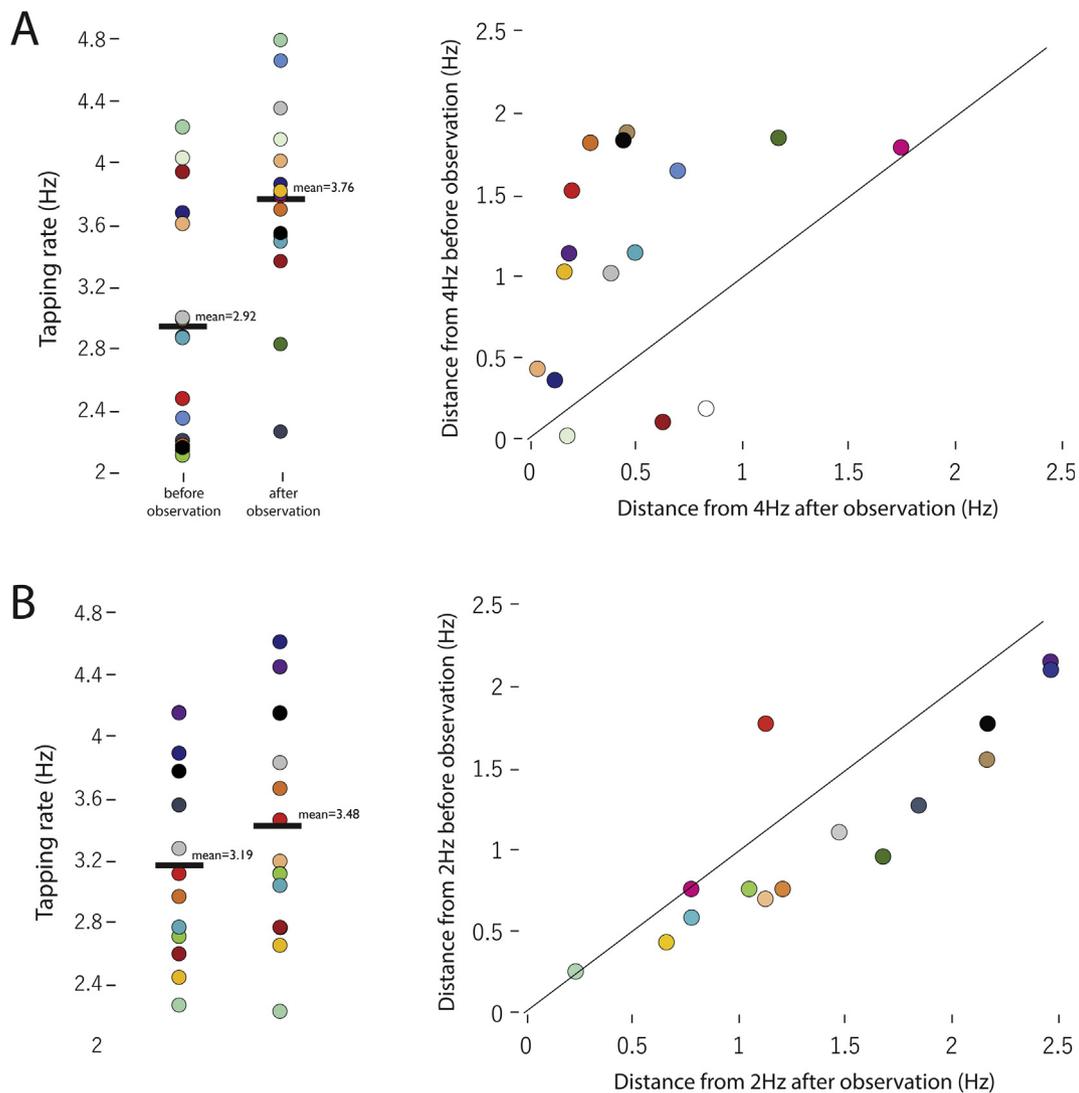


Fig. 2. Behavioral results. (A) Rate changes in 4 Hz-OBS group. Left panel – For each subject, we compared self-paced tapping performance in Hz before and after observing a video of finger tapping in 4 Hz. Each dot represents a single subject and the dark lines represent the group mean. Individual subjects are color coded. Right panel – Scatter plot of the difference between individual subjects' self-pace tapping before observation relative to 4 Hz (RD_{pre} ; y-axis; See Experimental Procedure) and the same difference after observation (RD_{post} ; x-axis). The diagonal line represents no change. Note that most subjects are above the diagonal – corresponding to a shift in performance rate towards 4 Hz following video observation. (B) Rate changes in 2 Hz-OBS group. Similar to (a) for subjects that observed 2 Hz. Left panel shows tapping rates before and after 2 Hz finger tapping observation. Right panel depicts a scatter plot of the difference between individual subjects' self-pace and 2 Hz. Most subjects are below the identity line indicating an increased difference in tapping rate from 2 Hz following video observation.

Table 2

Suppression levels relative to baseline in sensorimotor and occipital sites. The numbers represent suppression level averaged across all sensorimotor/occipital electrodes and subjects from both groups. We determined significance by using unequal variance *t*-test relative to zero, corrected for 3 frequency bands. CI are 95% confidence interval for the true mean of X. Asterisks denote significant suppression relative to baseline (Bonferroni corrected for 3 frequency bands).

Sites	Frequency	Execution session 1			Observation session			Execution session 2					
		Mean ± SD	t(31)	p	CI	Mean ± SD	t(31)	p	CI	Mean ± SD	t(31)	p	CI
Sensorimotor	Low mu	-0.92 ± 0.06 dB	2.5	0.01*	[-0.14-0.009]	-1.21 ± 0.06 dB	4.62	6.2·10⁻⁵*	[-1.69-0.65]	-1.01 ± 0.06 dB	4.3	1.5·10⁻⁴*	[-1.88-0.67]
	High mu	-0.97 ± 0.06 dB	2.22	0.03	[-4.2-0.07]	-0.28 ± 0.14 dB	1.8	0.08	[-0.29 0.01]	-1.14 ± 0.07 dB	3.66	9·10⁻³*	[-1.76-0.5]
	Beta	-0.42 ± 0.03 dB	1.91	0.05	[-2.23-0.08]	-0.12 ± 0.1 dB	1.75	0.09	[-0.14 0.007]	-0.69 ± 0.03 dB	2.8	7.9·10⁻³*	[-0.5-0.08]
Occipital	Low mu	-1.09 ± 0.11 dB	3.2	3·10⁻³*	[-1.96-0.43]	-1.27 ± 0.05 dB	4.43	1.5·10⁻⁴*	[-1.33-0.44]	-1.29 ± 0.06 dB	3.4	1.7·10⁻³*	[-2.58-0.64]
	High mu	-0.7 ± 0.04 dB	2.56	0.01*	[-0.88-0.09]	-0.31 ± 0.19 dB	1.79	0.08	[-0.35-0.26]	-0.87 ± 0.04 dB	3.15	3.6·10⁻³*	[-1.25-0.26]
	Beta	-0.49 ± 0.02 dB	3.06	4.5·10⁻³*	[-0.4-0.07]	-0.18 ± 0.09 dB	1.55	0.12	[-0.19 0.009]	-0.61 ± 0.02 dB	3.78	6.6·10⁻⁴*	[-0.57-0.17]

Bold values represent statistically significant effects.

session (See Table 4). Next, we examined whether changes in oscillation power during observation can explain individual differences in subsequent behavioral modulations of tapping rate. Since significant suppression during observation was only found in the low mu frequency band at the group level, we used this frequency band to examine correlation with behavior across subjects. The magnitude of suppression in low mu oscillation power during the observation session in each electrode (suppression index) was examined with respect to the change in execution rate as measured by the self-pace RM index (See Experimental Procedure). The left panel in Fig. 3B displays the level of correlation across subjects from the 4 Hz-OBS group for all 64 electrodes. Although oscillation power in low mu frequency was suppressed in all 64 electrodes during observation (Fig. 3A), we found that only in C3 (sensorimotor cortex contralateral to the observed hand) suppression magnitude across subjects correlated with behavioral modulation rate (Fig. 3B right panel; electrode C3, $r = -0.78$ Spearman correlation, $p = 2.86 \cdot 10^{-4}$, $CI = [-0.91-0.46]$, Bonferroni corrected for number of electrodes). In other electrodes within the sensorimotor cluster, correlation did not survive correction: C5, $r = -0.7$, $p = 2.4 \cdot 10^{-3}$, $CI = [-0.88 0.31]$; C1, $r = -0.54$, $p = 0.02$, $CI = [-0.81-0.06]$; FC5, $r = -0.72$, $p = 1.5 \cdot 10^{-3}$, $CI = [-0.895-0.349]$; FC3, $r = -0.59$, $p = 1.5 \cdot 10^{-2}$, $CI = [-0.84-0.13]$; CP5, $r = -0.62$, $p = 9 \cdot 10^{-3}$, $CI = [-0.85-0.18]$; CP3, $r = -0.53$, $p = 0.03$, $CI = [-0.81-0.04]$. Similarly, we did not find significant correlation between the behavioral change and low mu oscillation power over the sensorimotor cortex ipsilateral to the observed hand (electrode C4; $r = -0.46$; $p = 0.06$, $CI = [-0.77 0.04]$ uncorrected Spearman correlation). In occipital sites, the correlation was much lower (O1 and O2; $r = -0.23$, $p = 0.37$, $CI = [-0.65 0.3]$ and $r = -0.17$, $p = 0.51$, $CI = [-0.61 0.35]$ respectively). Thus, although action observation at the group level evokes significant mu suppression in most of the visuomotor regions, only suppression level in the sensorimotor cortex contralateral to the identity of the observed hand corresponded to subsequent behavioral changes in action performance. In the 2 Hz-OBS group, correlation between suppression of low mu oscillation power in contralateral sensorimotor electrodes and behavioral modulation rate failed to reach significance (range r -values = [0.05 0.47]; maximal r -value in electrode C5 = -0.47 , $p = 0.06$; Spearman correlation not corrected; See Fig. 4B). Correlation values in visual sites were also not significant (maximal r value = -0.42 , $p = 0.1$; Spearman correlation).

3. Discussion

In the current study, we examined shifts in spontaneous tapping rate of healthy subjects before and after observation of a video depicting the task performed by someone else. Importantly, during the observation session subjects were instructed to watch the movie without explicit instructions or cues to attend a particular feature of the video. Therefore, the shifts reflect implicit changes in spontaneous tapping rate. Previous studies reported implicit changes in execution rate using similar observation tasks (Bove et al., 2009; Avanzino et al., 2015). While some of these studies report both increases and decreases in spontaneous tapping rate that depend on the observed rate, Aridan and Mukamel have recently reported only increases in spontaneous tapping rate following observation of videos depicting higher tapping rates than those of the observers (Aridan and Mukamel, 2016). In the same study, subjects who did not observe a video at all also showed a non-significant increase in spontaneous tapping rate suggesting that task repetition by itself (even in the absence of intervening visual stimulus) might be sufficient to induce an increase in performance rate. In the current study, task repetition induced a significant increase in performance rate in both the 2 Hz and 4 Hz

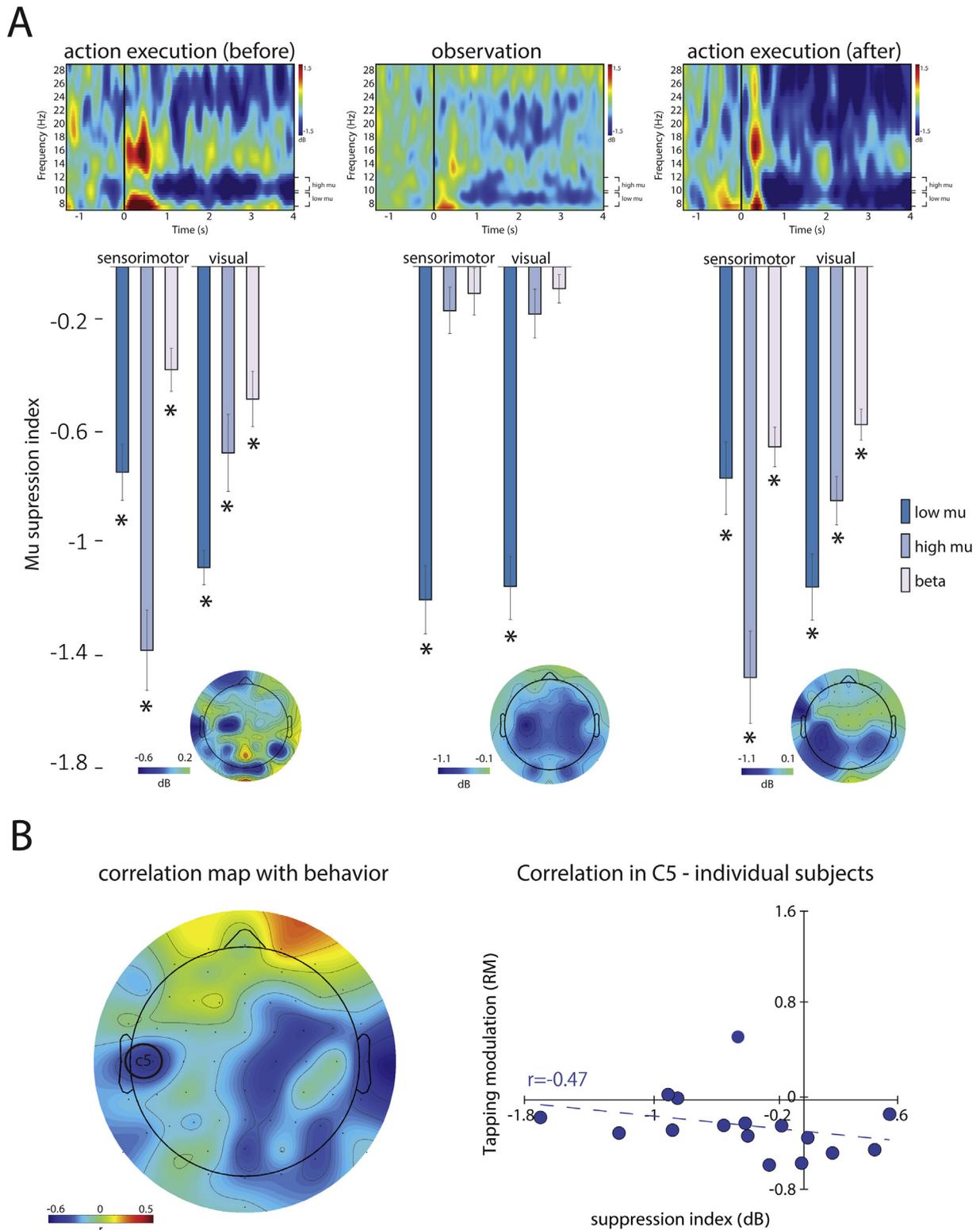


Fig. 4. 2 Hz-OBS: neural results. (A) Top panel: Similar to Fig. 3. Event-Related Spectral Perturbation map representing changes in averaged oscillation power across sensorimotor electrodes of all subjects; bottom panel: ERD values and the mean scalp ERSP map across subjects in 2 Hz-OBS group (See Experimental Procedure and Fig. 3A). Error bars represent SEM; asterisks denote significant suppression relative to zero ($p < 0.05$). (B) Correlation with behavior. Similar to Fig. 3B, scalp map for the 2 Hz-OBS group representing correlation between neural activity and behavioral modulation ($N = 16$). The maximal correlation was obtained in C5 ($r = 0.47$, $p = 0.06$; Spearman correlation; not corrected for multiple comparisons). Right panel shows low mu suppression level of individual subjects in C5 during action observation plotted against subsequent behavioral modulation rate (RM; see Experimental Procedure). Negative RM values correspond to a behavioral shift away from the observed tapping rate (2 Hz).

observation groups. Importantly, the induced increase was significantly higher following observation of higher tapping rates (4 Hz vs. 2 Hz), pointing to the importance of observed tapping rate

above and beyond simple task repetition. An open question is why subjects do not slow down following observation of lower tapping rates. Future research can address this by examining

Table 3

Differences in Suppression levels between first and second execution sessions. Differences in oscillation power in the sensorimotor and occipital sites between the first and the second execution session in each one of the groups. Significance was evaluated using paired *t*-test, corrected for 3 frequency bands. Asterisks denote significant difference in suppression (Bonferroni corrected for 3 frequency bands).

Sites	Frequency	2 Hz-OBS Group			4 Hz-OBS Group		
		t(15)	p	CI	t(15)	p	CI
Sensorimotor	Low mu	1.19	0.25	[−0.004 0.01]	2.33	0.03	[0.01 0.38]
	High mu	1.41	0.17	[−0.016 0.081]	1.99	0.05	[−0.001 0.36]
	Beta	1.9	0.07	[−0.008 0.16]	2.73	0.01*	[0.03 0.27]
Occipital	Low mu	0.61	0.55	[−0.01 0.02]	2.03	0.06	[−0.002 0.15]
	High mu	2.52	0.02	[0.03 0.48]	1.87	0.08	[−0.003 0.06]
	Beta	2.09	0.05	[−9.10 ^{−5} 1.8.10 ^{−5}]	2.75	0.01*	[0.003 0.03]

Bold values represent statistically significant effects.

Table 4

Differences in Suppression levels between groups. Differences in oscillation power in the sensorimotor and occipital sites between 4 Hz and 2 Hz group. These are averaged across all sensorimotor/occipital electrodes and subjects from each group. We determined significance by using an equal variance *t*-test. CI are 95% confidence interval for the true mean of X-Y for a paired test. No significant differences were found.

Sites	Frequency	Execution session 1			Observation session			Execution session 2		
		t(15)	p	CI	t(15)	p	CI	t(15)	p	CI
Sensorimotor	Low mu	0.48	0.63	[−0.52 0.33]	1.05	0.3	[−0.02 0.007]	0.87	0.39	[−1.02 0.42]
	High mu	0.61	0.54	[−1.12 0.62]	0.46	0.64	[−0.39 0.25]	0.31	0.75	[−1.05 0.79]
	Beta	1.62	0.12	[−0.09 0.01]	1.39	0.18	[−0.15 0.033]	0.91	0.37	[−0.08 0.03]
Occipital	Low mu	0.09	0.91	[−0.09 0.1]	0.65	0.52	[−0.004 0.002]	0.35	0.72	[−0.35 0.5]
	High mu	0.09	0.92	[−0.05 0.06]	0.66	0.54	[−9.10 ^{−4} 3.5.10 ^{−4}]	0.09	0.91	[−0.06 0.06]
	Beta	0.09	0.9	[−0.02 0.02]	0.71	0.48	[−6.5.10 ^{−4} 3.10 ^{−4}]	0.23	0.81	[−0.04 0.05]

whether repetition effects are stronger than implicit learning effects.

Mu and beta suppression during action observation have been previously reported (Hari et al., 1998; Pineda, 2005) and suggested to be specific to sensorimotor sites (Neuper et al., 1999; Muthukumaraswamy and Johnson, 2004). Our results support these findings by demonstrating that power in mu and beta rhythms is suppressed when subjects observed a hand engaged in a tapping task. However, although at the group level suppression during observation was stronger in a cluster of electrodes located around the standard sensorimotor sites (C3 and C4 positions), we found it to hold significance in other scalp regions as well. Further research is required to determine regional specificity of such power suppression to sensorimotor regions during visual presentation of actions.

At the individual subject level, we examined behavioral variation in spontaneous tapping rate with respect to neural activity during the action observation task, as measured using EEG. We report a link between the magnitude of low mu suppression during action observation and behavioral changes in performance across subjects. In the 4 Hz-OBS group, we found a significant correlation between the magnitude of mu suppression and the behavioral measure, indicating that subjects with stronger mu suppression during observation exhibited stronger shifts in their subsequent spontaneous tapping rate towards the observed rate (positive RM values). Conversely, in the 2 Hz-OBS group, we found that subjects exhibiting stronger mu suppression during observation tended to have weaker increases in their spontaneous tapping rate (i.e. tended to have RM values closer to zero corresponding to tapping rates that remain closer to the observed rate). However this correlation in the 2 Hz group failed to reach significance level. Taken together, these results suggest that subjects who are more sensitive to the observed stimulus (at the physiological level as indexed by the level of mu suppression), also exhibit a stronger behavioral shift towards the observed rate of the stimulus.

In terms of anatomical laterality, in the current study we only used videos depicting a right hand performing the task and

obtained correlations with behavior in left (contralateral) sensorimotor electrodes. This is in agreement with our previous report, in which fMRI cortical activity in the left (contralateral) motor cortex was found to covary with changes in tapping rate following right hand observation (Aridan and Mukamel, 2016). Additionally, using an explicit learning-by-observation task, we reported correlation of fMRI activity in superior parietal lobule contralateral to the observed hand (right/left) with subsequent behavioral changes in right/left hand rate of finger sequence performance across subjects (Ossmy and Mukamel, 2016a,b). In similar lines, it has been recently demonstrated that observation of a specific tapping rate altered the excitability of contralateral M1 such that it resonates better with the observed tapping rate (Lagravinese et al., 2016). Although not the focus of our current study, these findings suggest a specific and important role for activity in contralateral motor pathways during action observation in the induction of subsequent changes in behavior. Nonetheless, since we did not have left-hand observation videos in the current study, it remains an open question whether in an implicit observation task, such as the one we used here, symmetrical laterality effects would be obtained when comparing videos depicting a right or left hand.

Although most studies examining the effect of action observation on implicit behavior did not focus on the variation in individual subjects, our results demonstrate that such differences correspond to individual variations in oscillation power in the low mu frequency during action observation. These results may have implications for understanding individual differences in the susceptibility to perceptual input of actions performed by others.

4. Experimental Procedure

4.1. Subjects

Thirty-two right-handed healthy volunteers participated in the EEG study (22 females, mean age 24.04 years, range 20–35 years).

All subjects had normal or corrected-to-normal vision and provided written informed consent to participate in the study. The study conformed to the guidelines approved by the ethics committee at Tel-Aviv University.

4.2. Task and stimuli

Subjects performed a serial button-pressing task in which they sequentially pressed four color-marked keys back and forth. They were asked to press at their own pace for 5 s using their right index finger. Each key produced a different 70 ms duration pure tone of 400, 500, 600 or 700 Hz (see Fig. 1 and Movie 1). Each execution block was preceded by a 5 s baseline in which the subjects passively observed a video clip depicting flowing water (baseline condition; See Fig. 1). Subjects performed 10 such baseline/execution blocks consecutively. These baseline/execution blocks were followed by a passive observation task (see Fig. 1) in which subjects observed a video of someone else performing the execution task with their right hand at a rate of either 2 Hz ('2Hz-OBS' group; 16 subjects) or 4 Hz ('4Hz-OBS' group; 16 subjects, Movie 1). The observation task included 10 repetitions of 5 s of action observation preceded by 5 s of a video of flowing water (similar to the baseline used for the execution blocks, Movie 2). The subjects were asked to attend the videos. Finally, all subjects performed the execution task again. The entire run lasted 5 min. The rates of observed tapping depicted in the videos were 2 Hz and 4 Hz based on our previous study using a similar task (Aridan and Mukamel, 2016) in which we found the spontaneous tapping rate across 50 subjects to range between 2 Hz and 5 Hz.

4.3. Behavioral analysis

The self-paced tapping rate in each execution block was calculated based on the median Inter-Press-Interval in milliseconds and converted to Hz. We quantified the level of relative distance (RD) to an observed rate using the following formula:

$$RD_{pre} = |OR - P_{pre\ observation}|$$

$$RD_{post} = |OR - P_{post\ observation}|$$

Where $P_{pre\ observation}$ and $P_{post\ observation}$ correspond to the subject's average execution rate in Hz during pre and post observation blocks respectively, and OR corresponds to the observed tapping rate depicted in the video (either 2 Hz or 4 Hz depending on the experimental group of the subject).

The level of relative modulation (RM) was calculated according to the following formula:

$$RM = RD_{pre} - RD_{post}$$

Thus, positive RM values correspond to a shift in post-observation tapping rate towards the observed tapping rate.

4.4. EEG data acquisition and preprocessing

The EEG analog signal was recorded continuously via 64 Ag-AgCl pin-type active electrodes mounted on an elastic cap according to the extended 10–20 method of electrode placing (BiosemiTM Active II system, <http://www.biosemi.com>, Amsterdam, Netherlands). Seven additional electrodes were used: two mastoid electrodes (right and left), one electrode on the tip of the nose and four EOG channels for eye movement monitoring (two placed at the outer canthus of each eye and two placed at the orbital ridge centered directly above and below the right eye). EEG was digitized at a sampling rate of 256 Hz. Data was analyzed offline using the EEGLAB tool for MATLAB (Delorme and Makeig, 2004). Raw EEG data was Band-pass filtered offline between 0.5 and 35 Hz (Butter-

worth filter, 24 dB), and re-referenced offline to the digital average of the two mastoids. The continuous data were segmented into epochs from –2000 ms to +5000 ms relative to trial onset – video onset in the observation task, and 'PLAY' signal (cueing execution) in the execution task. Eye movements and blinks were detected and removed using independent component analysis (ICA; Jung et al., 2000). Data was visually inspected for noise (such as movement artifacts) or trials in which the EEG signal exceeded $\pm 100 \mu V$ (similar to Simon and Mukamel 2016). No trials were rejected from the analysis based on these criteria.

4.5. Time-frequency analysis

Event-related spectral dynamics was computed using a continuous Morlet wavelet transform (each epoch was defined from 2000 ms pre onset to 5000 post-trial onset). For each trial in each subject, we computed the logarithm of the power (from 0 to 5000 ms post-trial onset) relative to power during baseline (from 2000 ms to 500 ms pre onset). The suppression indices in the various frequencies were then calculated for each subject by averaging single trial log ratio values. A negative log ratio indicates a suppression in the power of EEG oscillations relative to baseline, whereas positive log ratios indicate enhanced power.

4.6. Correlation with behavior

For each of the subjects, the mean ERD power was calculated for low- μ (8–10 Hz) in each electrode during the action observation blocks. As behavioral measure, we took the corresponding subjects' level of modulation (RM; see behavioral analysis). Using Spearman correlation, we examined the correlation between the vector of ERD levels and the corresponding vector of RM values across subjects separately in each observation group (2Hz-OBS and 4 Hz-OBS). Significance of correlation values were corrected for the number of electrodes (64).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.brainres.2018.04.013>.

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