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**The mu-rhythm can mirror: Insights from experimental design, and looking past
the controversy**

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4 **1. Overview**
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7 Hobson & Bishop (2016) present a compelling investigation of whether mu suppression
8 is a useful index of a human mirror neuron system, and parallel the focus of our own
9 recent meta-analysis “Assessing Human Mirror Activity with EEG Mu Rhythm: A Meta-
10 Analysis” (Fox et al., 2015). In their pre-registered study, Hobson and Bishop collected
11 the largest sample yet studied in this area of research and include thoughtful controls and
12 analyses, constituting an admirable and important contribution to the field. Based on this
13 important investigation, Hobson and Bishop conclude that “mu suppression can be used
14 to index the human mirror neuron system, but the effect is weak and unreliable and easily
15 confounded with alpha”. In their abstract, they state that their conclusions are in contrast
16 to those of our own meta-analysis; however, we disagree with this statement and show
17 here that their findings converge with our meta-analytic results.
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28 Indeed, contrary to the authors’ impressions, we believe our findings and arguments
29 complement those of Hobson & Bishop (2016). Both papers report mu suppression
30 during action-execution and -observation conditions, and conclude these results are not
31 inconsistent with ‘neural mirroring’. Further, both papers recommend methodological
32 improvements to more reliably isolate mu suppression that is functionally linked to
33 action. Hobson and Bishop echo our call for caution in interpreting claims about ‘mirror
34 system activity’ from experiments that (a) do not establish a basic mirroring property by
35 including both action-execution and -observation conditions, (b) do not report EEG
36 activity from multiple electrode sites, and (c) do not evaluate potential domain-general
37 visual and attentional confounds. In spite of these shared concerns, we remain optimistic
38 regarding the utility of mu suppression as an index of mirroring. It is this optimistic view
39 that appears to contrast with Hobson and Bishop. In this response, we defend our original
40 position that, under careful and controlled experimental conditions, mu rhythm is
41 suppressed during both action-execution and -observation, making it a useful index for
42 neural mirroring.
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57 **2. Isolating action-specific processes in the mu rhythm: The limits of scalp**
58 **topography and simple comparisons to controls**
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6 To exhibit mirroring properties, the mu signal associated with action observation must be
7 demonstrably similar to the signal associated with the actual execution of action. The
8 point of contention between our meta-analysis and the report by Hobson and Bishop
9 (2016) appears to be over the extent to which mu suppression during action observation is
10 a reliable and valid index of neural activity specific to motor/action processes, beyond
11 any domain-general visual attentional processes that may be associated with observing
12 actions more generally.
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21 To accept a reliable separation between action-specific processes and domain-general
22 attentional processes, Hobson and Bishop (2016) set the premise that (a) mu suppression
23 must demonstrate strongest activation at central electrode sites (which overlay the
24 sensorimotor cortex) versus occipital sites (which should predominantly capture domain
25 general processes reflected in the occipital alpha rhythm), and (b) that central suppression
26 must be stronger for action conditions compared to a non-action control condition. While
27 on the surface this premise seems reasonable, a heavy reliance on scalp topography to
28 reveal functional specificity seems inappropriate given EEG's extremely poor spatial
29 resolution. Measurement from a given electrode reflects activity from several populations
30 of underlying neurons whose signals are blurred through volume conduction to the scalp
31 surface (Holsheimer & Feenstra, 1977). Though Hobson and Bishop's use of current
32 source density (CSD) reduces the issue of volume conduction, it by no means eliminates
33 it, and as Tenke and Kayser (2005, pg. 2840) note, "despite the empirical and theoretical
34 elegance of CSD methodology, [it] is restricted to the spatial domain in which the EEG is
35 recorded: the scalp." Thus, though mu suppression may not be specific to or even greatest
36 at central electrode sites, such topographical patterns do not preclude the possibility that
37 activity measured at a scalp electrode could, in part, originate from sensorimotor cortex.
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53 To be clear, an examination of EEG across multiple scalp locations is critical for mu
54 rhythm investigations, as we argue in our original meta-analysis (Fox et al., 2015) and as
55 Hobson & Bishop (2016) also suggest. A comparison of EEG activity across central and
56 occipital electrode sites can shed light on the strength of mu rhythm activity associated
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4 with action-specific processes relative to a confounding occipital alpha rhythm associated
5 with domain-general, attentional processes. Mu suppression in Hobson and Bishop's
6 action-execution condition is clearly greater in central versus occipital electrode sites—a
7 finding that replicates our meta-analysis. Our argument here is that, given the low spatial
8 resolution of EEG, a lack of topographic specificity is not, in and of itself, sufficient to
9 rule out the possibility that EEG scalp signals during action observation reflect, in part,
10 action-specific processes. For example, in some experimental situations, domain-general
11 attentional processes captured in occipital alpha may dwarf mu suppression that is
12 specific to motor/action processes; yet the motor/action processes captured in mu
13 suppression may nonetheless be real and measurable. Indeed, in such situations, for an
14 action-observation condition, we would expect to see some suppression in both central
15 and occipital sites (reflecting both action-specific and domain-general attentional
16 processes). However, the occipital suppression for an action-observation condition should
17 likely still be less than the occipital suppression for a control condition designed to
18 minimally reflect motor/action processes and maximally reflect domain-general visual
19 attention (e.g., Hobson and Bishop's kaleidoscope condition). Hobson and Bishop's
20 findings demonstrate this pattern: across all analyses, suppression in occipital electrodes
21 was smaller in both of the action-observation conditions when compared to the occipital
22 suppression in the non-action kaleidoscope control.
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41 If the action-specific portion of mu suppression in central electrodes is small during
42 action observation and potentially dwarfed by a larger domain-general attentional signal,
43 the key question is how best to isolate those action-specific processes of the mu rhythm.
44 This question was a central focus of Hobson & Bishop's (2016) study as well. Some
45 researchers have used repetition suppression designs to reveal specificity of mu rhythm
46 function (e.g., Coll et al., 2015). As an alternative approach, Hobson and Bishop
47 compared EEG activity during action-observation and -execution conditions to activity in
48 a control condition. We argue that, beyond simple comparison to a control condition
49 designed to capture domain-general attentional processes, data from such a condition
50 could be subtracted from data in the condition of interest in order to help isolate the
51 portion of the neural signal most specific to motor/action processes. Subtraction
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4 procedures across two or more conditions are routinely employed in fMRI analyses (Faro
5 & Mohamed, 2010). Although there are certainly limitations to this approach, it may be
6 useful in disentangling the action-specific aspects of the mu rhythm from the domain-
7 general attentional processes that are also captured in the EEG.
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13 Though Hobson and Bishop (2016) did not subtract the control condition activity from
14 the action-observation condition activity, aspects of their third analysis using static
15 baseline images provide support for the subtraction approach in isolating mu rhythm's
16 action-specific processes. Recall that the calculation of mu suppression is already a
17 subtraction procedure wherein the EEG signal in a 'baseline' period is subtracted from a
18 condition of interest. Hobson and Bishop's first two analyses used baselines that did not
19 closely match the visual scene or attentional demand of the action-observation condition
20 of interest. However, their third analysis used static images of the scene that, when in
21 motion, constituted the action-observation condition of interest. These static image
22 baselines therefore captured the most similar visual and attentional qualities of the event
23 of interest, and thus they were likely able to best isolate the portion of the neural signal
24 most specific to motor/action processes, revealing mu rhythm's mirroring properties.
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26 Indeed, with this third, more fine-grained analysis, Hobson and Bishop (2016; pg. 302)
27 agree that mu suppression "did give a pattern of results that was consistent with mirror
28 neuron activity".
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42 Note that subtraction conditions need not be specific to dynamic stimuli. For example,
43 mu suppression could be calculated when viewing static images of a hand performing an
44 action (e.g., a hand grasping a silver handle), as well as when viewing a control condition
45 of static images matched for domain-general visual/attentional content but critically
46 devoid of implied human action (e.g., a silver circle next to a skin colored triangle). Mu-
47 suppression in the control condition could then be subtracted from that in the hand
48 condition to reveal the neural processes specific to the implied object-directed action,
49 beyond the domain-general attentional processes present in both conditions. Designing a
50 control condition that is equal in attentional demands to the experimental condition but
51 devoid of action execution or observation can be difficult, as Hobson & Bishop (2016)
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4 note. Researchers may turn to fMRI studies in which this subtraction procedure has been
5 commonly employed for inspiration and approaches to match attentional demands across
6 conditions.
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11 The notion that a phenomenon is best revealed under a more specific set of parameters
12 and with specific methodological approaches does not necessarily reduce its significance.
13 Researchers must determine what those specific parameters and optimal approaches are.
14 It is clear that to reveal action-specific processes reflected in the mu rhythm and evaluate
15 its mirroring properties, domain-general attentional processes must be controlled. Hobson
16 and Bishop's (2016) findings support this point: in their first two analyses, the action-
17 specific processes associated with observing action were arguably less well isolated, and
18 in these first two analyses central mu suppression in the action-observation conditions
19 was weak and potentially overshadowed by the domain-general attentional signal
20 reflected in occipital alpha. Thus their findings raise a note of caution for interpreting mu
21 rhythm studies that lack necessary domain-general controls.
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33 However, when optimal parameters and approaches are employed, mu rhythm may be a
34 reliable index of neural mirroring. Hobson and Bishop's (2016) findings provide support
35 for this notion as well, and offer an important extension to the results of our meta-
36 analysis. Mu suppression during both action execution and observation was detected in
37 our meta analysis (Fox et al., 2015) across studies with disparate methods and in some
38 cases without optimal controls, demonstrating a degree of robustness to mu rhythm's
39 "mirroring" property. However, we also found that while mu suppression during action
40 execution showed topographic specificity, mu suppression during action observation did
41 not. Hobson and Bishop's large-scale empirical investigation replicated each of these
42 patterns of results, and critically further demonstrated that when attentional and other
43 domain-general processes were better controlled (as in the case of their third analysis
44 with static, within-trial, baseline images), mu suppression during action observation did
45 show topographic specificity, similar to mu suppression during action execution.
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4 Thus, Hobson and Bishop's (2016) approach underscores the importance of rigorous
5 methodological controls to elicit mu rhythm activity reflective of the action-specific
6 processes of interest. Taken together, our meta-analytic findings and the empirical
7 findings from Hobson and Bishop strengthen and complement each other, evincing a
8 detectable mirroring property in the mu rhythm, and laying a foundation for future
9 research to use mu rhythm as a reliable and valid index of neural activity associated with
10 action-specific processes.
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19 Lastly, to address Hobson and Bishop's concern that even under their most optimal
20 condition parameters 16-21% of individual participants did not exhibit significant mu
21 suppression at central electrode sites, we note that it is not uncommon for a particular
22 neural signature to fall short of full statistically significant expression in some
23 individuals in a given study. Drawing from the fMRI literature, when region of interest
24 (ROI) analyses are conducted, not all participants meet criteria for ROI selection. For
25 example, a meta-analysis of fMRI data found that the medial prefrontal cortex (MPFC)
26 and temporoparietal junction (TPJ) are the two regions most consistently involved in
27 mental-state reasoning across studies (Schurz et al., 2014); however, considering one
28 individual study (e.g., Saxe et al., 2009), 15-30% of participants did not exhibit
29 significantly different activation in mental-state-reasoning versus a non-mental control
30 conditions in either the MPFC or TPJ. The lack of significant activation in the mental
31 versus control condition in these regions for some individuals does not discount the
32 regions' involvement in mental-state reasoning more generally, as evinced by the meta-
33 analytic data. This type of individual variation in strength of neural response is not
34 specific to the one example we present; it occurs across fMRI, EEG, and ERP studies
35 alike (e.g., Taylor-Colls & Pasco Fearon, 2015).
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52 Extending this argument to mu rhythm research, even though not every individual may
53 meet criteria for significant mu suppression during action observation and execution, mu
54 suppression may still be considered a reliable and valid index of neural mirroring as a
55 whole. Moreover, such individual differences in presence and strength of mu suppression
56 could be a valuable source of meaningful variation across participants. Recent
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4 developmental literature has capitalized on the relation between individual differences in
5 mu suppression and additional behavioral/cognitive characteristics related to observing
6 and executing actions. For example, individual differences in 9- and 12-month-olds'
7 central mu suppression during action observation was positively related to individual
8 differences in the infants' ability to competently reach for and grasp objects (Cannon et
9 al., 2016). This correlation was specific to mu suppression at central sites, and did not
10 exist for mu suppression at frontal, parietal, or occipital sites (satisfying Hobson &
11 Bishop's, 2016 criteria for topographic specificity). For 3- to 5-year-old children,
12 stronger mu suppression during action execution in central-parietal (but not frontal or
13 occipital) electrode sites was positively associated with advances in behavioral measures
14 of children's motor skill and action-representation (Bowman et al., 2016). Moreover,
15 central mu suppression was not related to domain-general behavioral measures of
16 executive functioning or language skills.
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30 The developmental literature is newly emerging, and the same cautions for interpreting
31 existing mu rhythm research in adults should also be applied to developmental research
32 when methodological controls are absent. Indeed, the issue of confounding domain-
33 general attention could perhaps be particularly pertinent in developmental studies in
34 which young participants may be especially attentive to actions that they are just learning.
35 Nonetheless, when appropriate procedures and corrections are applied, developmental
36 data illustrate the potential importance of individual differences in mu-suppression during
37 action observation and execution, and underscore the utility of using behavioral measures
38 of motor/action performance, as well as behavioral domain general control measures, to
39 help isolate action-specific neural processes reflected in the mu rhythm.
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50 **3. On Existing and Future Studies: Cautions and Approaches to Move Ahead**

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53 Our meta-analysis (Fox et al., 2015) and the Hobson and Bishop (2016) empirical
54 investigation have each called for implementation of more rigorous methodological
55 approaches to isolate action-specific processes of the mu rhythm, as well as for caution in
56 interpreting existing mu rhythm studies should such controls be absent. We reiterate each
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4 of these points in the present paper. Caution is particularly warranted in studies that
5 attempt to investigate neural mirroring in other complex cognitive processes or
6 conditions (e.g., language, theory of mind, autism) if it is not first demonstrated that the
7 mu rhythm signal is sufficiently similar across both action-execution and -observation
8 conditions to constitute ‘mirroring’, and further that the signal being modulated in these
9 more complex processes is indeed specific to action-processes.
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17 We have touched on several possible approaches to help isolate action-specific processes
18 of the mu rhythm in section 2 above and refer readers to Hobson and Bishop (2016) and
19 Fox et al. (2015) for a more in depth discussion of these approaches. Briefly, in future
20 investigations of mu rhythm and neural mirroring, researchers should: 1) examine and
21 report mu rhythm activity from multiple electrodes across the scalp, 2) be mindful of
22 baseline effects on calculation of mu suppression and ensure baselines are at very least
23 the same for all conditions, and 3) include controls for confounding domain-general
24 attentional processes to isolate the action-specific processes mirrored in mu suppression.
25 These action-specific processes could be isolated with repetition suppression designs,
26 subtraction of non-action control conditions from action conditions of interest,
27 associations with behavioral measures of action, and statistical control of behavioral
28 measures of domain-general skills. Lastly, for studies in which interpretation is
29 contingent on mu rhythm having accurately indexed a neural mirroring network, both
30 action-observation and -execution conditions should be included in the same experiment
31 and examined across all participants to demonstrate specific mirroring properties of the
32 mu signal that are then further modulated in other constructs of interest.
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48 **4. On Monkeys and Humans: Looking Past the Controversy**

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52 A final discussion that is separate but related to the current topic centers on the extent to
53 which patterns in the mu rhythm are comparable to those observed from single cell
54 recordings in the rhesus macaque (di Pellegrino, et al., 1992). The discovery of these
55 classic ‘mirror neurons’ fueled rising interest in the potential ‘mirroring properties’ found
56 with the mu rhythm. There are many researchers who use mu rhythm to investigate a
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4 'human mirror neuron system', or who assume mu rhythm activity reflects such a system
5 and wish to examine its role in other constructs. We have noted issues associated with
6 these approaches in section 3 above. More generally, the function and nature of a mirror
7 neuron system in humans and monkeys is controversial (e.g., Heyes, 2010, Hickok, 2014;
8 Glenberg, 2015). How we conceptualize 'mirroring' in the human brain may be
9 necessarily more complex, and involve multiple neural systems that are separate but
10 functionally related. As we (Bowman et al., 2016) and others (e.g., Pineda, 2005) have
11 argued, the fluctuations in mu rhythm measured at the scalp surface may reflect activity
12 from multiple functionally related neural systems networked together. While activation of
13 this type of integrated network could still exhibit mirroring (e.g., if activated during
14 observation and execution of action), this more complex conceptualization of mu rhythm
15 may be disparate from the classic mirror neuron system identified with single cell
16 recordings in monkeys. On the other hand, such an integrated neural network in the
17 human brain could be consistent with new views on an extended mirror neuron network
18 in monkeys, in which recent neuroanatomical and neurophysiological research implicates
19 a broad system of cortical regions with reciprocal connections that extend beyond classic
20 mirror neurons in inferior parietal lobule and premotor cortex (Bonini, 2016).
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37 Regardless of where one might fall on the position of a mirror neuron system in humans
38 or monkeys, we urge researchers not to let such controversy overshadow investigations of
39 mu rhythm as an index of sensorimotor function, and of the potential importance and
40 utility of mu rhythm's 'mirroring properties'. We encourage the field to continue the use
41 of mu-rhythm, but to do so in the context of acknowledging and understanding the
42 boundaries of both studying and interpreting mu rhythm. We believe that mu rhythm may
43 indeed be a useful tool to shed light on how humans develop complex actions, and how
44 humans make sense of the complex actions and interactions of others. We argue that with
45 careful and controlled designs—like those demonstrated in Hobson & Bishop's (2016)
46 third analysis—mu rhythm can illuminate mechanisms that support these important
47 functions, and that mu rhythm thus has important implications for research in basic
48 neuroscience, cognition, and development.
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