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1 **Movement Variability is Processed Bilaterally by Inferior Parietal Lobule**

2 Target Article: Haar S, Donchin O, Dinstein I (2017b) Individual Movement Variability
3 Magnitudes Are Explained by Cortical Neural Variability. J Neurosci 37:9076–9085
4

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36 Robots with artificial intelligence have made enormous progress in solving complex
37 cognitive tasks, but when it comes to learning and executing coordinated, smooth, and
38 complex movements, humans and animals still excel. To ensure consistent skilled
39 movements, the motor system needs to learn how to control and exploit movement
40 variability.

41

42 While some movement variability is “noise” that results from stochastic neural and
43 muscle activity and can reduce task success (Faisal et al., 2008), other movement
44 variability does not harm performance. For instance, when one is playing tennis,
45 multiple combinations of movement of the shoulder, elbow, and wrist joint can result in a
46 successful hit. This abundance of possible movements constitutes “task-irrelevant”
47 motor variability, so-called because it does not affect successful task completion; the
48 motor system can, however, exploit task-irrelevant variability to optimize motor
49 performance (Sternad et al., 2011; Wolpert et al., 2011). Moreover, it can learn through
50 such variability that certain body positions minimize the impact of unexpected
51 perturbations and how to flexibly switch to a different movement to compensate for
52 muscle fatigue or injuries (Latash, 2012). Understanding the neural control of both forms
53 of movement variability is hence central for the study of human movement control in
54 health and disease.

55

56 Non-invasive brain stimulation can probe neural sources of motor variability, but current
57 techniques are limited by relatively poor control over perturbation site and intensity
58 (Siebner et al., 2009; Horvath et al., 2014). Invasive recordings from implanted
59 electrodes allow researchers to correlate movement kinematics with neural activity in
60 small populations of neurons (Churchland et al., 2006; Kaufman et al., 2014), but these
61 methods are too invasive for use in healthy humans and they do not allow measurement
62 of simultaneous neural activity from many sites in the brain. In contrast, non-invasive
63 neuroimaging with fMRI can record the neural correlates of motor variability across the
64 brain. The blood-oxygen-level dependent (BOLD) signal captured by fMRI reflects the
65 ratio of oxygenated to deoxygenated blood, which largely depends on energy
66 consumption by local neural populations and resulting increases in local blood flow due

67 to neurovascular coupling, but it is also affected by other, non-neural factors. Potential
68 methodological concerns for fMRI include the slowness of vascular responses to neural
69 activity and the presence of non-neural variability (e.g., heart-beat, breathing, and head
70 motion) that can confound measurements. However, by modelling the delay and
71 correcting for non-neural noise, fMRI signals can reveal brain activity during fast-
72 evolving behavior like arm reaches.

73

74 In a recent study, Haar et al. (2017b) report intriguing correlations between inter-trial
75 neural variability (measured with fMRI) and inter-trial movement variability during arm
76 reaches. They instructed 32 healthy adults to perform out-and-back reaching
77 movements to near and far target locations using a pen stylus on a digital drawing tablet
78 while fMRI was recorded. No visual feedback about the endpoint position or trajectory
79 was provided during or after movements to minimize neural variability stemming from
80 visual feedback. Hence, subjects did not know whether their reaches were accurate.

81

82 The authors quantified the trial-by-trial neural variability (fMRI variability around
83 individual mean response) and variability in reach extent, direction, and velocity for each
84 subject, and they tested whether subjects exhibited consistent magnitudes of neural
85 variability in multiple cortical motor regions of interest (ROIs) during reaches to different
86 targets and during reaches with each arm. Neural variability in several motor and pre-
87 motor ROIs in each hemisphere were correlated across reaches to different targets by
88 the right arm (Fig 5A) and by the left arm (Fig 5B). In addition, variability in the premotor
89 cortex, superior parietal lobule, and supplementary motor area in each hemisphere was
90 correlated for right and left arm reaches (Fig. 5C). Taken together, these results indicate
91 that subjects exhibited consistent magnitudes of neural variability regardless of the arm
92 used to perform the movements or the target to which they reached.

93

94 To study the neural control of movement variability, Haar et al. tested whether neural
95 variability was correlated with any of their three measures of movement variability:
96 reach extent, direction, or velocity. A link between neural variability and movement
97 variability was found bilaterally in the inferior parietal lobule (IPL), which explained about

98 24% of between-subject differences of variability in movement extent (Fig 6). This
99 finding was corroborated by an exploratory searchlight analysis of the cortical surface.
100 The searchlight identified additional clusters in a medial area of the superior parietal
101 lobule (SPL), the precuneus (Fig 7). These results extend previous reports of effector-
102 invariant encoding of movement directions (Haar et al., 2017a) to effector-invariant
103 encoding of movement variability in the IPL and SPL.

104

105 These results raise a question: why does the motor system involve both hemispheres in
106 processing movement variability of either arm? One possible reason is that the motor
107 system integrates knowledge of movement variability across arms to maximize error
108 reduction and thereby facilitate motor learning. Movement extent variability is critical for
109 task success and provides a crucial learning signal that has been extensively studied in
110 perturbation experiments (Wolpert et al., 2011). Encoding movement variability across
111 both arms may come at a higher computational cost for the motor system, but it allows
112 both hemispheres to learn from errors made by either limb. Transfer of learning
113 between hands and limbs has been described in simple and complex motor tasks (Lee
114 et al., 2010; Dickins et al., 2015), and the IPL and precuneus may facilitate this process.
115 Furthermore, effector-invariant encoding of reaching directions has been shown in an
116 identical task for several ipsi- and contralateral cortical motor areas, but barely for the
117 IPL (Haar et al., 2017a). Together, these findings suggest that the IPL might mainly
118 encode movement variability during reaching when no task feedback is provided.
119 However, the function of the IPL (and precuneus) in this task setting remains an open
120 and intriguing question.

121

122 Another interpretation for the observed bilateral IPL and precuneus activity relates to
123 processes that were emphasized in the present experiment because of the lack of
124 visual task feedback. While the interpretation above relies on the role of the IPL in motor
125 planning and preparation (Cohen and Andersen, 2002), these processes typically
126 require knowledge of task success from previous motor actions. Without visual
127 feedback about task success, however, motor planning in the present experiment was
128 limited. As a result, two other processes likely interacted to guide the reaches subjects

129 performed in the experiment: 1) shifting attention towards the action space (informed by
130 reappearing target locations), and 2) monitoring joint configurations (informed by
131 proprioception). Haar et al's findings are in line with the expected neural bases of these
132 processes: the IPL is critically involved in processing and attending to peripersonal
133 space (Fogassi and Luppino, 2005), i.e., the action space that immediately surrounds
134 the body, and the IPL's role in spatial attention has previously been demonstrated
135 (Mattingley et al., 1998). Similarly, the precuneus – which receives input from premotor
136 regions and the IPL (Margulies et al., 2009) – is also involved in shifting spatial attention
137 between different target locations in the absence of visual feedback (Wenderoth et al.,
138 2005) and updating postural representations of the upper limb during reaching (Pellijeff
139 et al., 2006). The specific experimental design used in the present study likely recruited
140 these IPL and precuneus functions; therefore, it remains to be tested whether these
141 regions also process movement variability when visual feedback is provided.

142
143 Another open question is which brain regions process task-irrelevant variability. The
144 stylus pen recorded movement data only from the tip and thus only quantified task-
145 relevant variability, but the whole movement required complex coordination in multiple
146 joints of the arm. Therefore, the same position of the stylus tip may have been executed
147 using many different joint configurations across trials, leading to task-irrelevant
148 variability. While task-irrelevant joint variability tends to be larger than task-relevant
149 endpoint variability for healthy subjects (Wolpert et al., 2011), high task-relevant
150 endpoint variability dominates when joint control is impaired, e.g. due to stroke (Cirstea
151 and Levin, 2000). Neural correlates of joint-based control over reaching directions for an
152 identical task included activity in the IPL and SPL (Haar et al., 2017a). Extending this
153 work to task-irrelevant variability could yield valuable insights into the neural
154 mechanisms contributing to both the benefits (Sternad et al., 2011; Wolpert et al., 2011;
155 Latash, 2012), and challenges (Cirstea et al., 2003) that arise from movement variability
156 in movement control.

157
158 Haar et al. demonstrate that humans show consistent magnitudes of neural variability
159 across hemispheres regardless of the movements performed. Additionally, they report

160 that bilateral IPL, a key region in motor planning, processes movement extent variability
161 irrespective of arm use. This suggests that both hemispheres cooperate in controlling
162 movement extent variability, a metric critical for task success and motor learning.
163 However, the function of IPL, and the generalizability of findings to tasks that involve
164 visual feedback and quantify task-irrelevant variability remains to be tested.

165

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