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The Ubiquitousness and Functional Roles of Evidence Accumulation

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Review of Morito and Murata

Perceptual decision-making, the process of using information from our senses to guide behavior, is successfully described by evidence accumulation, where noisy sensory evidence is accumulated over time up to a threshold. Neural activity that represents evidence accumulation is typically found shortly after stimulus onset, when firing rates ramp up to a bound, whence the decision process terminates in a choice. This ramping activity shows a steeper slope for earlier decisions and terminates at a stereotypical level (equal to the bound) at the time of the decision (Shadlen and Kiani, 2013).

At least two lines of research have focused on identifying accumulators in the brain. On the one hand, seminal work in nonhuman primates indicates that some neurons in motor planning regions, such as the lateral intraparietal area, frontal eye field, or superior colliculus, represent the integral of sensory evidence encoded by upstream sensory regions. It is unclear, however, how this integration occurs and whether it does so in those regions or

elsewhere (Shadlen and Kiani, 2013). On the other hand, neuroimaging studies in humans have uncovered a much wider range of putative accumulators in occipital, inferior temporal, parietal, and inferior frontal regions (Ploran et al., 2007). These findings were obtained by slowly and gradually revealing stimuli in object categorization tasks to compensate for the sluggishness of the BOLD response. Later studies showed that some accumulators were content-specific (i.e., selectively accumulating evidence for a certain category of stimuli), whereas others were content-general (i.e., regardless of stimulus category) (Tremel and Wheeler, 2015). Nonetheless, the functional relationship between these widespread accumulators remains unknown.

In a recent article, Morito and Murata (2022) used an experimental paradigm similar to that of Ploran et al. (2007), but were able to categorize accumulators more finely based on the dynamical properties of the BOLD response, uncovered by means of deconvolution. ROIs were identified based on task-related activations, then segregated into content-specific regions when BOLD activation was specific to one category of stimulus (face, body, scene, or tool) and content-general regions otherwise. According to a bounded account of evidence accumulation, ramping activity should peak at consistent times when time-locked to the response times, but at inconsistent times when time-locked to the stimulus onset. Using these two metrics, quantified by the SD of peak times of

the deconvoluted BOLD signal, a clustering algorithm could identify content-general accumulators in previously identified brain regions (Ploran et al., 2007). When the authors added two more metrics, the slope of the ramping activity and the average peak time, their algorithm distinguished between two types of accumulators: Bounded accumulators (aAccum in the article's nomenclature) that peaked at the response time and had a steep slope, and unbounded accumulators (bAccum) that peaked less consistently after the response and showed a more gradual slope. Bounded accumulators thus appeared to stop accumulating after the decision (indexed by the response time), consistent with bounded evidence accumulation. They were interpreted to be directly involved in the decision process. Interestingly, unbounded accumulators peaked after the decision, especially for short response times. Although they did not fulfill the criteria for bounded accumulation, the slope of these accumulators was still inversely proportional to response times (Morito and Murata, 2022, their Fig. 9B), suggesting a role in the decisional process. The authors also attempted to classify content-selective regions. The results appeared inconsistent across regions and failed to map convincingly onto either bounded or unbounded accumulator classes. This pushed the authors to introduce a third type of accumulator: content-specific accumulators (cAccum), involved in accumulating evidence for the choice of one stimulus, in competition with others.

The three types of accumulators broadly followed an anatomic hierarchy: content-specific accumulators were all located in inferior occipito-temporal regions, while unbounded accumulators were mainly found in the parietal and temporal cortices and bounded accumulators principally in the frontal cortex. This hierarchy is reminiscent of serial processing accounts suggesting that perceptual decisions gradually build up throughout the cortex at the cellular level (de Lafuente and Romo, 2006). The authors proposed that each accumulator type takes part in a hierarchical implementation of evidence accumulation that subserves the decision process: Content-specific accumulators provide specific information to content-general unbounded accumulators, which in turn flexibly extract information for bounded accumulators directly involved in the decision.

The Morito and Murata (2022) proposal is consistent with electrophysiological studies that have started to unravel how high-level computational descriptions of evidence accumulation can be dissociated into a hierarchy of accumulation subprocesses, such as decision formation and motor preparation. For example, neurons in the parietal and frontal cortices all show firing rate patterns consistent with evidence accumulation, but parietal neurons encode a graded value of the accumulating evidence while frontal neurons simultaneously encode a categorical value that is more consistent with the provisional decision (Hanks et al., 2015). Furthermore, different accumulators are differentially affected by some experimental manipulations. When human participants make decisions without yet knowing which effector to use to respond, electroencephalographic correlates of evidence accumulation can be observed over centroparietal areas but no longer over sensorimotor areas (Twomey et al., 2016). Also, under time pressure, evidence accumulation correlates observed over sensorimotor areas, but not over centroparietal areas, are affected by an urgency signal (Kelly et al., 2021). These findings suggest that ramping activity in sensorimotor areas is directly involved in motor preparation, whereas accumulation earlier in the processing hierarchy is linked to decision formation. Together, they urge us to consider that decisions might not be formed locally but along a broad cortical hierarchy, each node of which incorporates additional factors, such as urgency. Future fMRI studies can test how the three classes of accumulators introduced by Morito and Murata (2022) are affected under such experimental manipulations.

Still, to confirm the neural architecture of evidence accumulation, the field needs cellular recordings in the regions found by Morito and Murata (2022) and others. Deconvolved BOLD signal was classified as evidence accumulation more leniently in the Morito and Murata (2022) study compared with electrophysiological studies. Some accumulators did not show the typical inverse relationship between the slope of the ramping activity and response times (e.g., the middle cingulate gyrus or the palladium). Other hallmarks of bounded evidence accumulation, like increased trial-by-trial variability over time (Churchland et al., 2011) or accumulators coalescing at a stereotyped level, could not be tested. These methodological aspects raise questions about which conditions are sufficient to conclude that neural activity instantiates evidence accumulation. Information accumulation in the brain surely exists beyond the archetypal accumulation-to-bound account of neurons in the lateral intraparietal area of nonhuman primates. Are there other unbounded accumulation processes that exhibit only a subset of the hallmarks of bounded evidence accumulation? Neurons in the caudate nucleus were found to represent a cellular equivalent to unbounded accumulators (Ding and Gold, 2010). Noteworthily, their activity peaked before rather than after the decision, suggesting they are different from unbounded accumulators in Morito and Murata (2022). Relaxing the constraints on the state of accumulators at the time of decision, the results of Morito and Murata (2022) and others suggest that evidence accumulation could be a much more ubiquitous process, possibly driven by the different timescales at which neurons are thought to operate along the decisional processing hierarchy (Chaudhuri et al., 2015). While electrophysiological recordings might not uncover neurons that accumulate evidence, it will be important to also assess whether this mechanism is implemented along neuronal population-response manifolds (Okazawa et al., 2021).

The view that evidence accumulation represents a ubiquitous brain mechanism could imply a functional role beyond decision-making. Growing evidence supports a role of evidence accumulation in the subjective perception of time (Toso et al., 2021), and the subjective confidence associated with a perceptual decision (Desender et al., 2021). Are accumulators for confidence the same as accumulators for motor responses (Kiani and Shadlen, 2009), or is there a separate accumulator for confidence (Balsdon et al., 2020)? Unbounded accumulators in the Morito and Murata (2022) study could account for post-decisional revisions of confidence, as they seem to continue accumulating evidence after the decision is taken (van den Berg et al., 2016). More intriguingly, another role of unbounded accumulators might be to stabilize noisy sensory evidence into a conscious experience of the stimulus (Pereira et al., 2022), which does not necessarily end when committing to a decision. Some theoretical accounts of consciousness posit that conscious experience occurs after accumulators reach a threshold (Dehaene et al., 2014). To test this prediction, it is necessary to design experiments that can disentangle perceptual processes from decision-making. One way forward is to observe whether neurons or populations that accumulate evidence in a typical report task show similar evidence accumulation patterns after stimuli in no-report paradigms (Tsuchiya et al., 2015), where participants passively view stimuli without being required to report a decision. Results from a recent study suggest that single neurons accumulating evidence in the parietal cortex of a human participant are also responsive in the absence of task demands (Pereira et al., 2021), unlike what is observed at the scalp level (Twomey et al., 2016). Such research can help distinguish between accumulators solely involved in decisional processes and those that could accumulate evidence beyond decisions, thereby giving rise to conscious experience and the associated sense of confidence.

In conclusion, the study by Morito and Murata (2022) raises awareness that evidence accumulation might be a widespread hierarchical mechanism. This adds to a growing body of work attempting to unveil the neural implementation of evidence accumulation across the brain. It opens exciting perspectives for cross-disciplinary investigations of the role of each hierarchical level of accumulation for perceptual decisions and possibly beyond.

References

Balsdon T, Wyart V, Mamassian P (2020) Confidence controls perceptual evidence accumulation. Nat Commun 11:1753.

Chaudhuri R, Knoblauch K, Gariel MA, Kennedy H, Wang XJ (2015) A large-scale circuit mechanism for hierarchical dynamical processing in the primate cortex. Neuron 88:419–431.

Churchland AK, Kiani R, Chaudhuri R, Wang XJ, Pouget A, Shadlen MN (2011) Variance as a signature of neural computations during decision making. Neuron 69:818–831.

de Lafuente V, Romo R (2006) Neural correlate of subjective sensory experience gradually builds up across cortical areas. Proc Natl Acad Sci USA 103:14266–14271.

Dehaene S, Charles L, King JR, Marti S (2014) Toward a computational theory of conscious processing. Curr Opin Neurobiol 25:76–84.

Desender K, Ridderinkhof KR, Murphy PR (2021) Understanding neural signals of post-decisional performance monitoring: an integrative review. Elife 10:e67556.

Ding L, Gold JI (2010) Caudate encodes multiple computations for perceptual decisions. J Neurosci 30:15747–15759.

Hanks TD, Kopec CD, Brunton BW, Duan CA, Erlich JC, Brody CD (2015) Distinct relationships of parietal and prefrontal cortices to evidence accumulation. Nature 520:220–223.

Kelly SP, Corbett EA, O'Connell RG (2021) Neurocomputational mechanisms of prior-informed perceptual decision-making in humans. Nat Hum Behav 5:467–481.

Kiani R, Shadlen MN (2009) Representation of confidence associated with a decision by neurons in the parietal cortex. Science 324:759–764.

Morito Y, Murata T (2022) Accumulation system: distributed neural substrates of perceptual decision making revealed by fMRI deconvolution. J Neurosci 42:4891–4912.

Okazawa G, Hatch CE, Mancoo A, Machens CK, Kiani R (2021) Representational geometry of perceptual decisions in the monkey parietal cortex. Cell 184:3748–3761.e18.

Pereira M, Megevand P, Tan MX, Chang W, Wang S, Rezai A, Seeck M, Corniola M, Momjian S, Bernasconi F, Blanke O, Faivre N (2021) Evidence accumulation relates to perceptual consciousness and monitoring. Nat Commun 12:3261.

Pereira M, Perrin D, Faivre N (2022) A leaky evidence accumulation process for perceptual experience. Trends Cogn Sci 26:451–461.

Ploran EJ, Nelson SM, Velanova K, Donaldson DI, Petersen SE, Wheeler ME (2007) Evidence accumulation and the moment of recognition: dissociating perceptual recognition processes using fMRI. J Neurosci 27:11912–11924.

Shadlen MN, Kiani R (2013) Decision making as a window on cognition. Neuron 80:791–806.

Toso A, Fassihi A, Paz L, Pulecchi F, Diamond ME (2021) A sensory integration account for time perception. PLoS Comput Biol 17:e1008668.

Tremel JJ, Wheeler ME (2015) Content-specific evidence accumulation in inferior temporal cortex during perceptual decision-making. Neuroimage 109:35–49.

Tsuchiya N, Wilke M, Frässle S, Lamme VA (2015) No-report paradigms: extracting the true neural correlates of consciousness. Trends Cogn Sci 19:757–770.

Twomey DM, Kelly SP, O'Connell RG (2016) Abstract and effector-selective decision signals exhibit qualitatively distinct dynamics before delayed perceptual reports. J Neurosci 36:7346–7352.

van Den Berg R, Anandalingam K, Zylberberg A, Kiani R, Shadlen MN, Wolpert DM (2016) A common mechanism underlies changes of mind about decisions and confidence. Elife 5:e12192.