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The ubiquitousness and functional roles of evidence accumulation

Article reviewed:

Morito, Y., & Murata, T. (2022). Accumulation System: Distributed Neural Substrates of Perceptual Decision Making Revealed by fMRI Deconvolution. *The Journal of Neuroscience*, 42(24), 4891-4912.

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Abbreviated title: Ubiquitous evidence accumulation

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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, terminates at a stereotypical level (equal to the bound) at the time of the decision (Shadlen & Kiani, 2013).

At least two lines of research have focused on identifying accumulators in the brain. On the one hand, seminal work in non-human 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 & 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 blood oxygen level-dependent (BOLD) response. Later studies showed that some accumulators were content-specific (i.e., selectively accumulating evidence for a certain category of stimuli) while others were content-general (i.e., irrespective of stimulus category; Tremel & 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 Ploran and colleagues' (2007), but were able to categorize accumulators more finely based on the dynamical properties of the BOLD response, uncovered by means of deconvolution. Regions-of-interest 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 standard deviation 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

(Figure 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 anatomical 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 & 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.

Morito and Murata's 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 sub-processes, 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 centro-parietal 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 centro-parietal areas, are affected by an urgency signal (Kelly et al., 2020). 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 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 and others. Deconvolved BOLD signal was classified as evidence accumulation more leniently in Morito and Murata's study compared to 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 non-human 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 & Gold, 2010). Noteworthy, their activity peaked before rather than after the decision, suggesting they are different from unbounded accumulators in Morito and Murata's study. Relaxing the constraints on the state of accumulators at the time of decision, Morito and Murata's results 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 if this mechanism is implemented along neuronal population-response manifolds (Okazawa et al., 2021).

The view that evidence accumulation represents an 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 & Shadlen, 2009), or is there a separate accumulator for confidence (Balsdon et al., 2020)? *Unbounded* accumulators in Morito and Murata's 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 if 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 sum, Morito and Murata's study 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.

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