Cortical Lifelogging: the posterior parietal cortex as sensory history buffer

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Abstract

To compare information and reach decisions effectively, our brain uses multiple heuristics which can however induce biases in behaviour. An elegant study by Akrami et al finds evidence for one such heuristic in a sensory-based comparison task, and identifies its location to the posterior parietal cortex.

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We base our decisions on sampling a sensory environment full of raw information. Although our sensors are capable of transducing a great deal of this information into neural signals, no nervous system has the sheer capacity to process and store all of it. But the natural world is heavily structured, with regularities and correlations that make some of the raw “information” redundant: sensory pathways rely on this to filter out signals, make predictions, and accentuate novel or surprising events valuable to our survival. This balances an economical use of resources against keeping as much information as necessary. Similarly, when making decisions on a course of action, the brain does not construct a perfect record of continuously updated information, which would quickly saturate our capacity for storing and evaluating evidence. Instead, we keep an imperfect running buffer of relevant ongoing evidence, in which newly acquired – perhaps noisy – information is used to update existing – perhaps incomplete – beliefs about our situation. It is by comparing new sensory inputs to our memories and expectations that those inputs become meaningful – a process mediated by the cerebral cortex. Sometimes explicitly, sometimes implicitly, we compare and blend current inputs with recent sensory history to reduce noise and establish a stable benchmark for sensation. The brain uses a number of heuristics to combine and sift through information in this way, and these balance the need for accurate estimation in a noisy world against
speed and resource use. How this is achieved is a central question in systems and behavioural neuroscience.

One example of an everyday decision-making task that relies on such a running estimate and comparison of sensory evidence is familiar to those of us who keep losing our cell phone. We often locate the phone by calling the number and listening for rings: we then track changes in ring volume as we move around from room to room. In general, by estimating variations in the loudness of a sound, we can tell whether we are approaching its source or moving away from it. We do this (hopefully) reasonably reliably, by comparing each sound to a running memory of the perceived intensity of recent sounds over several seconds. As part of the heuristics underlying this sort of computation, our comparative judgment of the current stimulus is affected by the history of previous stimuli. This phenomenon comes in multiple forms, referred to by terms such as “time-order effect”, “assimilation to context”, etc. In one prominent version known as “contraction bias”, first discovered over one hundred years ago by Hollingworth, our record of a stimulus held in working memory is shifted towards the mean magnitude of recent stimuli – thus blending current inputs with earlier history. In real life, when successive sensory samples typically come from a related source, each sample might be noisy, and our ability to determine and remember the source might be compromised, contraction bias can help improve sensory estimation, providing a useful best-guess heuristic.

A new study (Akrami et al., 2018) uses an elegant experimental paradigm applicable to rats and humans – similar in some ways to the lost phone situation, and to scenarios relevant to foraging (Figure 1) – to reveal and modify contraction bias. The authors optogenetically manipulated neural activity during the task and were able to determine the effects on contraction bias, thus illuminating posterior parietal cortex (PPC) as a brain region underpinning the buffer for sensory history and evidence heuristics.
Figure 1. A game show task for rats inspired by Akrami et al. Participants move from room to room in a noisy corridor; within each room, the rat must listen in succession to the noise behind two doors, and must choose the door hiding the loudest swarm of crickets for a tasty reward.

Rats were trained on a two-alternative forced choice paradigm in an operant conditioning chamber with three nose-poke ports. This experimental setup facilitated high-throughput psychophysics analysis. Animals could initiate each trial by poking their nose into the centre port upon a cue; there were also reward ports on both sides of the central one. On every trial, rats were presented with two sounds separated by a varying delay of a few seconds; animals judged whether the magnitude (loudness) of the first sound – kept in memory during the delay period – was greater than that of the second sound. Rats were rewarded with water from the side ports for correctly reporting which of the two stimuli was louder. If the first sound was louder than the second rats had to nose poke into the left-hand port to get a reward, whereas if the second sound was louder rats were rewarded for nose poking into the right-side port. Similar setups using both auditory and tactile stimulation were used to assess and compare human performance, which was comparable to rats’. Various sets of stimulus pairs were used across trials in every session, to manipulate task difficulty: the smaller the difference in sound volume, the harder the task. Stimulus pair values were designed so that the task could not be done by sensing the loudness of just one of the sounds. Difficulty affected the behaviour of rat and human participants similarly. Consistent with previously observed patterns of contraction bias in delayed comparison tasks, Akrami et al found that the estimation of the first stimulus in a trial was shifted towards the mean volume of previous trials. So when the mean loudness of previously presented stimuli was greater (smaller) than the first stimulus in the trial, then this stimulus was overestimated (underestimated).
Depending on the relative values of both sounds, this bias could be helpful, but in the majority of cases it led to suboptimal performance. The authors next determined that this bias depended specifically on the sensory history of previous trials, by using a logistic regression model that fit behaviour to a linear combination of the magnitudes of the first and second sounds in a trial, together with factors that accounted separately for earlier stimuli, choices, and rewards (which may also bias decisions).

To better understand the computations underlying this working memory-mediated sensory task, the authors next sought to manipulate performance by interfering with neural activity. They chose to do so in the posterior parietal cortex (PPC), a region key to on-the-fly sensory-guided decision making – sensorimotor transformations – in both primates and rodents. In rodents, PPC receives visual, auditory and somatosensory input and, based on related experimental designs, has been implicated in retaining and integrating sensory information over time, holding working memory, and representing choice-selective activity (Harvey et al., 2012; Raposo et al., 2014; Morcos and Harvey, 2016). If PPC underpins working memory by enabling comparison of the two sounds in a trial, storing the magnitude of the first sound until the second can be perceived, then interfering with PPC during the trial should impair performance on the task. To test this, the investigators optogenetically inactivated CaMKII-expressing neurons on a randomly chosen 20% of the trials. Surprisingly, rather than impairing performance outright, optogenetic interference significantly improved the rats' performance on average. The experiments were consistent with this improvement operating through the suppression of contraction bias. Thus during a trial, inhibiting activity eliminated the influence of contraction bias on how the first sound was stored in working memory, leading to more accurate comparison of the two sounds presented. This improvement was present both when activity was suppressed throughout the trial and when suppression was constrained to the delay period when the first sound was being held in memory. For trials involving certain specific pairs of sound magnitudes, contraction bias should lead to an increase in the apparent separation between the loudnesses, improving “discriminability”: satisfyingly, on these trials optogenetically suppressing contraction bias did decrease performance. A further interesting check would have involved determining performance on trials where the loudness of the first sound matched the mean previous loudness. In these cases, one imagines that the averaging inherent to contraction bias might have improved estimation of the first sound and had a positive effect as well: thus, here one might predict decreased performance from optogenetic interference. In conclusion, that optogenetic manipulation specifically affected contraction bias suggests a role for PPC as a site where information on sensory history is buffered or accumulated and combined with present information, at least in the context of this task.
Akrami et al provide further support for this idea from recordings of neuronal activity in a separate set of sessions. These measurements revealed a (limited) subset of PPC neurons that carries significant information about sensory history (i.e. about sound magnitudes in earlier trials). After a trial ended and during the intertrial period, neurons in this subset remained informative about stimulus values in the just-finished trial; further, some neurons also remained informative during the next trial, when the delayed comparison between sounds was being carried out. This is consistent with the finding that optogenetic manipulation interfered with contraction bias when delivered specifically during the delay period. In light of these recordings, it would have been interesting to also suppress activity optogenetically during intertrial periods, to check whether suppression of local PPC activity eliminated any trace of earlier trials or, on the contrary, PPC activity during a trial reflects a mnemonic sensory trace originating elsewhere. Even more intriguing is the identity (and connectivity) of the subset of neurons informative about sensory history; this will need to be resolved by future work.

If PPC provides an evidence buffer enabling accumulation of sensory information relevant to a task, one might expect its responses and behavioural role to depend on the details of the task. Research has indeed revealed an apparent multiplicity of roles for rodent PPC, as well as for the analogous region in primates. These results, although fascinating, have sometimes seemed difficult to reconcile. For example, several studies have appeared to suggest that PPC is necessary for tasks involving accumulation of evidence based on vision but – judging from optogenetic manipulation – not on hearing or touch (Harvey et al., 2012; Guo et al., 2014; Raposo et al., 2014; Goard et al., 2016; Licata et al., 2017). Yet the study by Akrami et al demonstrates an effect of optogenetic PPC manipulation in a hearing-based task. However, for some of the experimental designs cited, little or no integration of sensory history is actually necessary to perform the task: the decision as to how to respond can be made upon stimulus presentation, regardless of any information held in memory, perhaps helping to explain the lack of necessity for PPC. Rather, PPC seems most relevant when information about a stimulus needs to be held in memory while accumulating evidence over time, perhaps for later comparison (Akrami et al., 2018), e.g., in the context of navigation or foraging (Harvey et al., 2012).

Consistent with a role for PPC as a sensory buffer that combines multiple sources of information is the presence of multisensory responses. Intriguingly, neurons in rat PPC can display optimal multisensory integration (Nikbakht et al., 2018; visual and tactile inputs). This was observed in a design where rats were trained to solve a task based on available
multimodal information – visual inputs, tactile inputs or a combination of both. In this specific setting, visual and tactile inputs were similarly reflected in neural responses, which then effectively communicated task-relevant information in a modality-free manner. This contrasts with the notion that PPC necessarily privileges one modality over another; again, resolving the contradiction seems to require that the degree of multisensory weighting depend flexibly on task and context.

In considering how PPC receives and combines signals from different sensory modalities, it is important to note that PPC in rodents corresponds to a narrow strip between the somatosensory and visual cortices, coterminous with areas identified by retinotopic mapping as being higher-order visual in nature. Beyond this overlap and possible terminological issue, PPC includes different subareas with varying connectivities, with most of the differences in connectivity occurring along a medial-lateral gradient rather than a rostral-caudal one (Wilber et al., 2014). However, the apparent disagreements among studies cannot be resolved by connectivity gradients alone: studies obtaining different results as to the visual or multisensory character of PPC have used identical coordinates. The multisensory character of a PPC neuron’s responses is likely to depend partly on layer- and cell-type specific connectivity (Olcese et al., 2013). Furthermore, different PPC neurons likely belong to diverse intermingled pathways with distinct connectivities and responses (Hwang et al., 2017). Further progress on connectivity will be crucial to understanding how PPC carries out its roles, and in what way it is particularly suited for them. In addition to properties of intra- and inter-regional connectivity, functionally relevant distinguishing features of PPC could include rules for plasticity and the pattern of neuromodulation. For now, the evidence is consistent with the notion that PPC neurons have highly plastic response properties, sculpted in a task-dependent manner, so that e.g. extensive experience of tasks and settings where combining multisensory information is important will lead to an increase in the proportion of neurons with multimodal responses.

Does PPC behave similarly across species? The analogous region in humans and other primates appears to be anatomically and functionally homologous, and has also been reported to play myriad roles: PPC involvement spans attentional modulation of multisensory integration and stimulus binding; spatial processing and navigation, including encoding of position, speed and heading direction; sensorimotor co-registration and planning, e.g. in the estimation of relationships between object and body location during locomotion; and working memory in the context of decision making. In our reading, these functions are broadly similar across species. Primate studies have been more successful in identifying functional specificity (i.e. function localised to specific subareas): e.g., sensorimotor association area
LIP is specific to saccade planning, and the parietal reach region (PRR) for hand reaching. Given that the role of PPC in any given learned task may depend heavily on adjustments in its connectivity to other areas, differences in mesoscale connectivity patterns between rodents and primates could ultimately affect the degree of specificity of PPC function; however, existing results do not seem to have identified hard differences in this regard.

We conclude by returning to perceptual and cognitive biases in decision making. Recent sensory and behavioural history causes biases both in perception and in post-perceptual decision steps, not just for visual sensing of simple features but for numerosity or recognition of complex stimuli such as faces. For instance, both humans and other animals bias future choices according to their recent choice history (beyond the history of rewards). PPC responses also reflect choice history and history-dependent decision biases (Morcos and Harvey, 2016; Hwang et al., 2017). These results, taken together with the observations of Akrami et al and unpublished recent findings from the Brody lab (Constantinople et al, Cosyne abstract 2018), which suggest that PPC may represent reference points for economic decisions based on utility variables, raise the exciting prospect that circuit-level investigation of PPC will illuminate the workings of high-level cognitive phenomena.

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References


