



The role of neural oscillations in visuo-motor communication at the time of saccades

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ABSTRACT

Saccadic eye-movements are fundamental for active vision, allowing observers to purposefully scan the environment with the high-resolution fovea. In this brief perspective we outline a series of experiments from our laboratories investigating the role of eye-movements and their consequences to active perception. We show that saccades lead to suppression of visual sensitivity at saccadic onset, and that this suppression is accompanied by endogenous neural oscillations in the delta range. Similar oscillations are initiated by purposeful hand movements, which lead to measurable changes in responsivity in area V1, and in the connectivity with motor area M1. Saccades also lead to clear distortions in apparent position, but only for verbal reports, not when participants respond with rapid pointing, consistent with the action of two separate visual systems in neurotypical adults. At the time of saccades, *serial dependence*, the positive influence on perception of previous stimulus attributes (such as orientation) is particularly strong. Again, these processes are accompanied by neural oscillations, in the alpha and low beta range. In general, oscillations seem to be tightly linked to serial dependence in perception, both in auditory judgments (around 10 Hz), and for visual judgements of face gender (14 Hz for female, 17 Hz for male). Taken together, the studies show that neural oscillations play a fundamental role in dynamic, active vision.

1. Introduction

Mel Goodale changed the way we study vision, probably more than any other neuroscientist of recent years. Traditionally, vision has been studied under highly controlled conditions with body, head and eyes immobilized. Mel was amongst the first to realize, that as a principal function of vision is to guide action, visual processing must be intrinsically linked to action and movement control. This insight led not only to the famous dissociation of vision for perception from vision for action (Goodale and Milner, 1992), but also initiated a paradigm shift in vision research towards more natural conditions, especially in the context of action. This soon led to many examples showing how action impacts greatly on perception and on the organization of neuronal visual processing (Anobile et al., 2021; Goodale, 2011, 2014; Harman et al., 1999; Tomassini et al., 2018).

Saccadic eye-movements, the fast, ballistic eye-movements that serve to purposefully explore the environment, provide a natural bridge between vision and action. These exploratory movements are fundamental for *active* vision, allowing us to purposefully sample the environment with our small, high-resolution fovea. But they also create major challenges: the system must distinguish external from self-generated motion to understand the external world (sometimes

referred to as the *credit assignment problem*). Incorrect assignment of the cause of retinal motion and displacement could lead to several adverse consequences: one is the retinal image *motion* generated by the eye-movement, confusable with real, wide-field motion; the other the *displacement* of the image on the retina with each movement, jumbling the spatial relationships necessary to map the retinal image onto a veridical representation of the external world. Both are serious challenges for a system attempting to make sense of the structure of the world from sensors mounted on highly unstable platforms (Burr and Morrone, 2011, 2012, 2022; Ross et al., 2001).

This perspective reviews work from our laboratories addressing these general, related issues, focusing on the role of endogenous oscillations. We first show that saccadic suppression, the decrease in sensitivity at the onset of saccades, is strongly linked to oscillations in sensitivity in the delta range. Purposeful hand-movements are also linked to oscillations, which affect sensitivity to V1 and connectivity with M1, revealed by fMRI studies. Visual mislocalization at the time of saccades (occurring only for “perception” not “action”) is also associated with oscillations, in the alpha-beta range. These effects are strongly linked to the concept of “serial dependence” and “predictive coding”, efficient strategies for using past information to predict the present, and to aid perceptual continuity at the time of saccades.

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2. Saccadic suppression and behavioural oscillations

One reason we are not disturbed by the image motion generated by saccades is that it is actively – but selectively – suppressed (but see Castet and Masson, 2000, for an alternate point of view). Thresholds for stimuli briefly presented peri-saccadically (at the time of a saccade) are higher than when presented to the fixating eye, by up to an order of magnitude. The suppression is selective, maximal for stimuli that would be most effective in invoking a sensation of movement: luminance-modulated, low spatial frequency stimuli. As Fig. 1A shows, the characteristic tightly tuned suppression occurs only when the eyes move during a saccade (filled squares), not when the image is slid across the retina with similar dynamics to a saccade (open circles).

The most striking aspect of Fig. 1A is the narrow tuning of the suppression, peaking at saccadic onset. Given that the suppression is specific to active saccades, it is likely generated by an internal signal accompanying the saccade, a *corollary discharge* (Sperry, 1950; von Holst and Mittelstaedt, 1950), rather than by the image motion itself. But how does this signal synchronize so perfectly with the saccadic movement, given all the lengthy and variable transmission times involved in both perception and motor preparation? One possibility is that a common brain rhythm keeps the two in synchrony. Recent human and non-human primate studies suggest that cross-modal influence in sensory cortex is mediated by ongoing endogenous rhythms that become synchronized in each modality cortex (for review see Bauer et al., 2020). The phase of the endogenous oscillation modulates many aspects of perception, including TMS-evoked phosphene perception/MEPs (Dugué et al., 2011; Romei et al., 2012), visual discrimination, visual attention and time perception (Bauer et al., 2020; Fries, 2015; Schroeder et al., 2010; Senkowski et al., 2008). It is therefore reasonable to suggest that endogenous neural oscillations may facilitate the temporal alignment of sensory signals and of pre-motor signals during saccades.

When visual sensitivity around saccades is measured with higher precision, averaging over thousands of trials, it becomes clear that the sharp dip in sensitivity at saccadic onset is not the only change in

sensitivity, but is accompanied by clear oscillations of delta frequencies (Benedetto and Morrone, 2017; Hogendoorn, 2016). Fig. 1B: show that sensitivity (measured as accuracy in target identification) oscillates at the time of a saccade, at 3 Hz before, then more slowly, at 2 Hz, after. Interestingly, the usual signature of visual suppression, the large dip at saccadic onset, is embedded within the periodic oscillation, together with the post-saccadic enhancement. They are both part of the phasic modulation, opening the possibility that the ongoing oscillation determines the time of the transient saccadic phenomena. There are also oscillations in criteria judgements (Benedetto and Morrone, 2019), but these occur at higher frequencies, around 12 Hz, discussed in the following section.

There are two logical possibilities of how the oscillations become synchronized so precisely to saccades. One is that the intention to make a saccade initiates the oscillations, which in turn regulate sensitivity, with a minimum coinciding with saccadic onset. Although possible, this seems unlikely, as the oscillations are observed up to 600 ms before saccadic onset (Hogendoorn, 2016), probably preceding the onset of saccadic preparation. A fascinating alternative is that the causality is in the other direction: that ongoing, endogenous neural oscillations govern both the sensitivity, and the time when a saccade can be initiated, and hence the start of both the motor programming phase of the saccade and the corollary discharge signal. Many exploratory behaviours in animals, such as sniffing and whisking, have a rhythmic component. Similarly, small saccadic eye movements (micro-saccades) occur naturally at a rate of 2–3 Hz (Rucci et al., 2018). The analogy between the overt rhythmicity of motor behaviour and the covert rhythmicity of attentional sampling is appealing, and the two may rely on similar neuronal mechanisms (Helfrich, 2018; Schroeder et al., 2010). The crucial questions of how the synchronization of endogenous oscillation is governed, and whether a master clock mechanism exists, are still open to further investigation.

Phase-locked oscillations in visual sensitivity are linked not only to eye-movements, which form an integral part of the visual system, but can also be synchronized to voluntary hand movements. Tomassini et al.

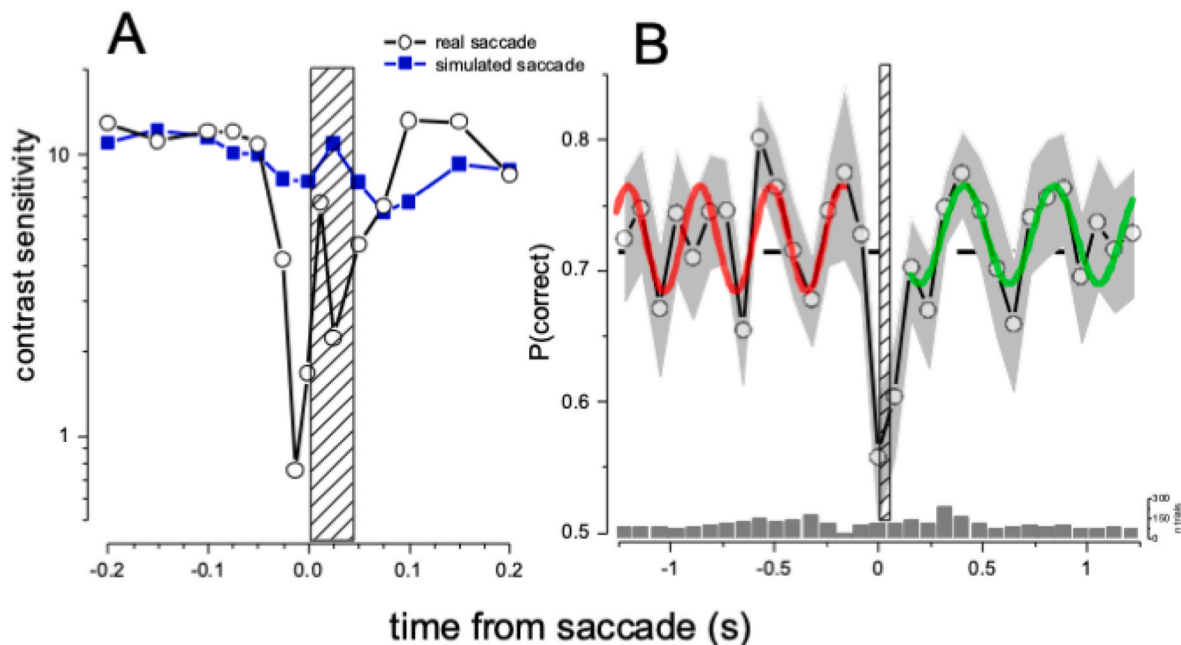


Fig. 1. Saccadic suppression and oscillations at the time of saccades. The saccade is illustrated by the hatched regions in both graphs. **A)** Contrast sensitivity for detecting a grating briefly flashed at various times relative to a large (12°) horizontal saccade (open circles) or a simulated saccade of match duration and dynamics (blue squares). During real saccades there was a large, 1 log-unit decrease in sensitivity, narrowly tuned around saccadic onset. The simulated saccade had little effect. Reproduced with permission from the data of Diamond et al. (2000), with finer sampling bins. **B)** Percent correct detection of a briefly presented grating patch, as a function of time relative to saccadic onset. Measuring accuracy over a longer period reveals that the suppression of Fig. A is embedded within an ongoing oscillation, 3 Hz before saccadic onset, 2 Hz after. Reproduced with permission from Benedetto and Morrone (2017).

(2015) had observers initiate trials with a purposeful hand-movement, and found that sensitivity fluctuated over time. The fluctuation was faster than for saccades, in the low beta range. As with saccades, the action-locked oscillation in performance emerged long before initiation of the movement. This result has been replicated several times, also with

EEG evidence for the oscillations, revealing again that the phase of pre-frontal motor activity can predict future rhythmic fluctuations of sensitivity (for review: [Benedetto et al., 2020](#); [Tomassini et al., 2020](#)). Fig. 2A shows a recent replication, where participants discriminated target spatial frequency or contrast after button-press. Accuracy

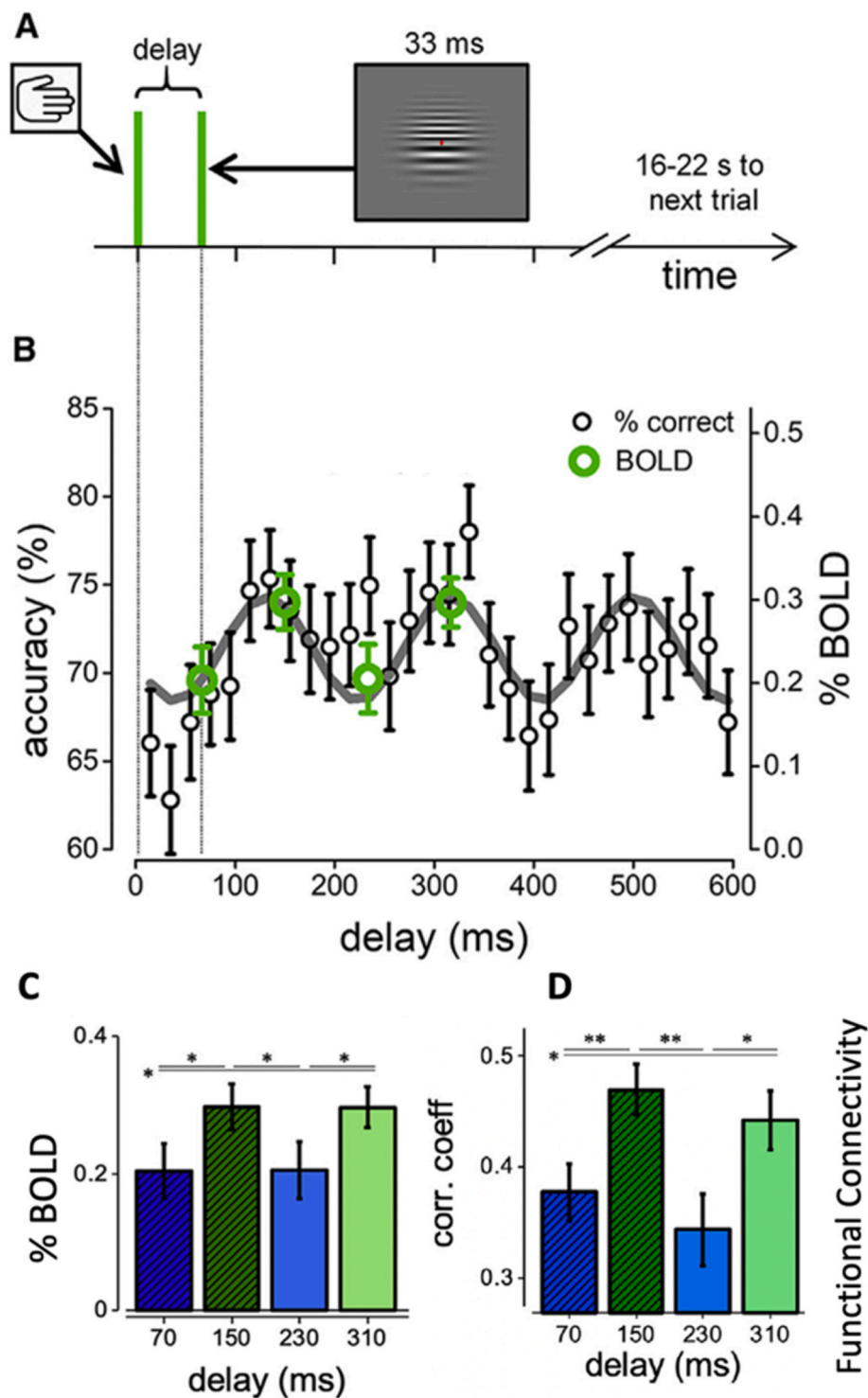


Fig. 2. Neural substrate of oscillations. A) Participants initiated each trial with a voluntary button-push, causing a grating to appear briefly after a random interval. They identified whether the grating was above or below screen centre. B) Accuracy as a function of the delay from button-push. Sensitivity is clearly modulated at 5 Hz, with peaks and troughs alternating every 50 ms. C) V1 BOLD amplitude to stimuli presented at post button-press latencies corresponding to the psychophysically measured troughs (green) and peaks (blue) in sensitivity: response was significantly higher for the peaks. D) Correlation coefficients between activity in V1 and M1, measured from the residuals of the responses to stimuli presented at latencies corresponding to troughs (green) or peaks (blue) of sensitivity. The correlations were significantly higher at the peaks. Reproduced with permission from [Benedetto et al. \(2021\)](#).

oscillated rhythmically at a theta frequency of about 5 Hz (Benedetto et al., 2016).

Benedetto et al. (2021) went on to investigate the neural locus of the oscillations, measuring BOLD responses. Having established by psychophysics the periodicity of the oscillation in sensitivity, they measured BOLD responses with fixed delays from button-press, sampling the first two peaks and troughs of the distribution (green circles of Fig. 2B). The BOLD response in V1 followed the psychophysical changes in sensitivity, significantly higher at the peaks in accuracy than at the troughs (Fig. 2C). Importantly the oscillations were present at all eccentricities, also far from the visual target, demonstrating a resting ongoing oscillation. This shows that the action-linked modulations in sensitivity have their origins in primary visual cortex, suggesting that cortical excitability is modulated rhythmically by theta-frequency oscillations.

Interestingly the delays between stimuli and action onset are too small to be reliably discriminated (Nijhawan, 2002). Nevertheless, the visual cortex can encode these small delays. But why does the primary visual cortex need to do so? A fascinating hypothesis is that the encoding of the delay of stimulus from action may solve the fundamental problem of the motor-sensory loop, and may account for the often unpredictable delays between neuronal activity related to sensory analysis, and activity related to action temporal dynamics (Andersen, 2011; Lennie, 1981; Ross and Hogben, 1975). To examine further the visuo-motor link, the authors measured functional connectivity between V1 and M1 by correlating residuals of the general linear model fit at the different delays after button-press. The correlations, like the BOLD response in V1, were strongly modulated over time, higher for the peaks in psychophysical performance and lower at the troughs (Fig. 2D). This strongly implicates a mechanism of “communication through coherence” (Fries, 2015) between motor and sensory cortices, to achieve precise temporal coordination and to encode sensory-motor timing.

3. Visual mislocalization during saccades

As mentioned in the introduction, spurious retinal image motion is not the only problem created by saccades. Perhaps the main challenge for perception is the fact that each eye movement displaces the retinal image to a new focus of interest, centring it on the high-resolution fovea which receives a magnified cortical projection. Much research has been dedicated to uncovering the mechanisms behind this process, often termed “remapping” (see for example Hall and Colby, 2011). One of the consequences of remapping during saccades is the mislocalization of stimuli briefly presented at saccadic onset, resulting in a compression of visual space. The red symbols of Fig. 3 show a typical result (Burr et al., 2001; Morrone et al., 1997; Ross et al., 1997). Vertical lines were flashed briefly to observers, just before they started to make a large (15°) rightward saccade. The bars are not seen in their veridical positions, but systematically mislocalized towards the saccadic target. The localization errors can be large, over 10° of visual angle.

The effect has been robustly replicated over the years (eg Cicchini et al., 2013; Kaiser and Lappe, 2004; Lappe et al., 2000; Michels and Lappe, 2004; Xie et al., 2023; Zimmermann, 2015; Zimmermann et al., 2014). However, if instead of reporting verbally the apparent position of the flashed bar, observers point rapidly at its perceived location (without visual feedback), the average responses are more or less veridical (Burr et al., 2001; Morrone et al., 2005). The results are reproduced by the blue symbols of Fig. 3, falling close to the identity line. This is a very clear confirmation of Mel’s signature idea of separate neural processes for perception and action, that he also demonstrated in saccades and in reaching arm movements (Desmurget et al., 1998; Goodale et al., 1986). Although observers were unable to report the correct position of the bar without large, systematic distortions, their motor systems could localize it accurately.

Why should briefly flashed objects be perceptually mislocalized during saccades? Saccades represent a moment of maximum uncertainty

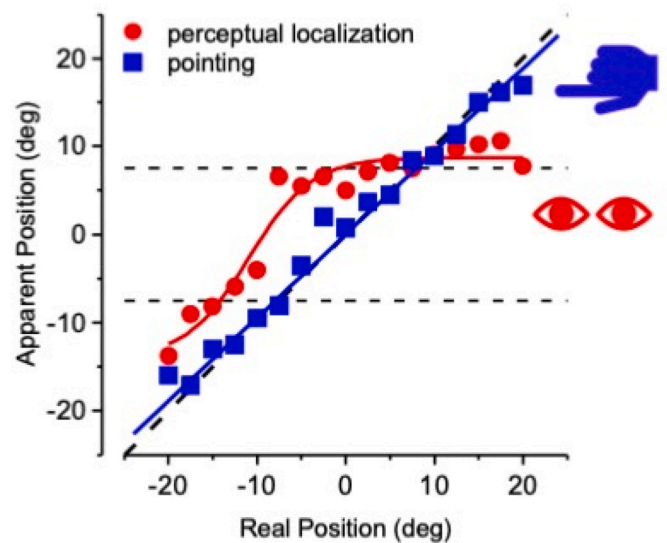


Fig. 3. Mislocalization of brief targets at the time of saccades. Green bars were briefly presented on a red background at various times relative to saccadic onset. Participants either reported verbally their position on the screen relative to a visible ruler (red circles) or rapidly pointed at the perceived position (with hand and other visual references obscured from view). The verbal reports revealed strong mislocalizations – up to 10° – towards the saccadic landing point, while the rapid pointing was almost veridical. Reproduced with permission from Burr et al. (2001).

for the visual system, when coordinate systems need to be rapidly updated to account for the effect of the eye movement, as the system attempts to blend the pre-saccadic with the post-saccadic views. Many physiological changes occur, including the temporary shift in receptive fields to anticipate the motion (Duhamel et al., 1992; Hall and Colby, 2011). When stable stimuli of similar form are presented before or after the saccade, peri-saccadic stimuli are drawn towards them (Binda et al., 2007; Cicchini et al., 2013). All these results support a Bayesian-like explanation of mislocalization (Niemeier et al., 2003), where the system attempts to accommodate uncertain signals within a model of a stable world. This could easily lead to compression of information towards the centre of post-saccadic gaze, as observed. The information about a stable world may be transmitted with memory signals, usually called *priors*. The dissociation between perceptual and action localization, even in neurotypical observers, could imply that action is less subject to prior information associated with saccadic landing point. That is not to say that action is not influenced by priors and expectations: on the contrary, action needs to be highly predictive to function effectively (Wolpert and Flanagan, 2001), given all the neural delays in transmission and processing. But the priors that drive those predictive processes may be quite different from those leading to perceptual experience.

4. Perceptual continuity across saccades: Serial dependence and oscillations

We further tested the Bayesian approach during saccades by measuring not only perceived position, but also perceived orientation for peri-saccadic stimuli, after observers have viewed a *prior* stimulus oriented $\pm 15^\circ$ away from the test (Xie et al., 2023). Fig. 4A shows that judgements of the flashed stimulus were systematically biased towards the previously viewed prior. Importantly the largest effects occurred when the test was presented peri-saccadically. This is consistent with a phenomenon recently termed *serial dependence*, where judgments of many stimulus characteristics tend to be biased towards previously viewed stimuli (Cicchini et al., 2023; 2014; Fischer and Whitney, 2014).

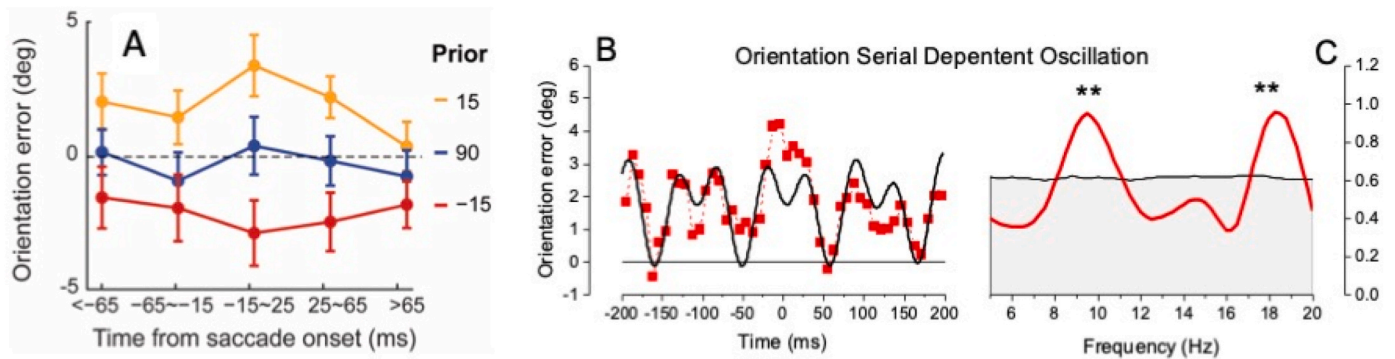


Fig. 4. Serial dependence at the time of saccades. A) Orientation error as a function of time relative to saccade onset. Errors are towards the prior, positive for priors of $+15^\circ$ (yellow symbols), negative for priors of -15° (red symbols), and little effect for orthogonal priors (blue symbols). The attraction towards priors was strongest near saccadic onset. B) Error towards the direction of the prior (subtracting the data for priors of -15° from those of $+15^\circ$), sampled at a finer timescale relative to saccadic onset. The attractive effect of the prior oscillates (red symbols), following a complex waveform comprising 9.5 and 19 Hz (black waveform). C) Fourier transform of Fig. B, showing the clear and significant peaks at 9.5 and 19 Hz. Figures produced from data collected by Xei et al. (2023).

Serial dependence is usually taken as evidence for perception being active, and to some extent generative, meaning that the system has clear predictions and expectations about a stimulus (based on previous perceptual history), and then verifies those predictions against current evidence (Cicchini et al., 2023). The influence of perceptual history should be greatest when the current stimulus itself is ambiguous or uncertain, as would be expected during saccades. Indeed, saccades

provide an excellent testbed to study concepts like serial dependence and active vision in general, as it is the moment when retinal images change, and vision has to rely more firmly on predictions.

The previous section showed how saccades and movements in general are accompanied by oscillations. It therefore seems reasonable to ask if motor-synched perceptual oscillations are also involved in encoding prediction and serial dependence? Does bias, as well as

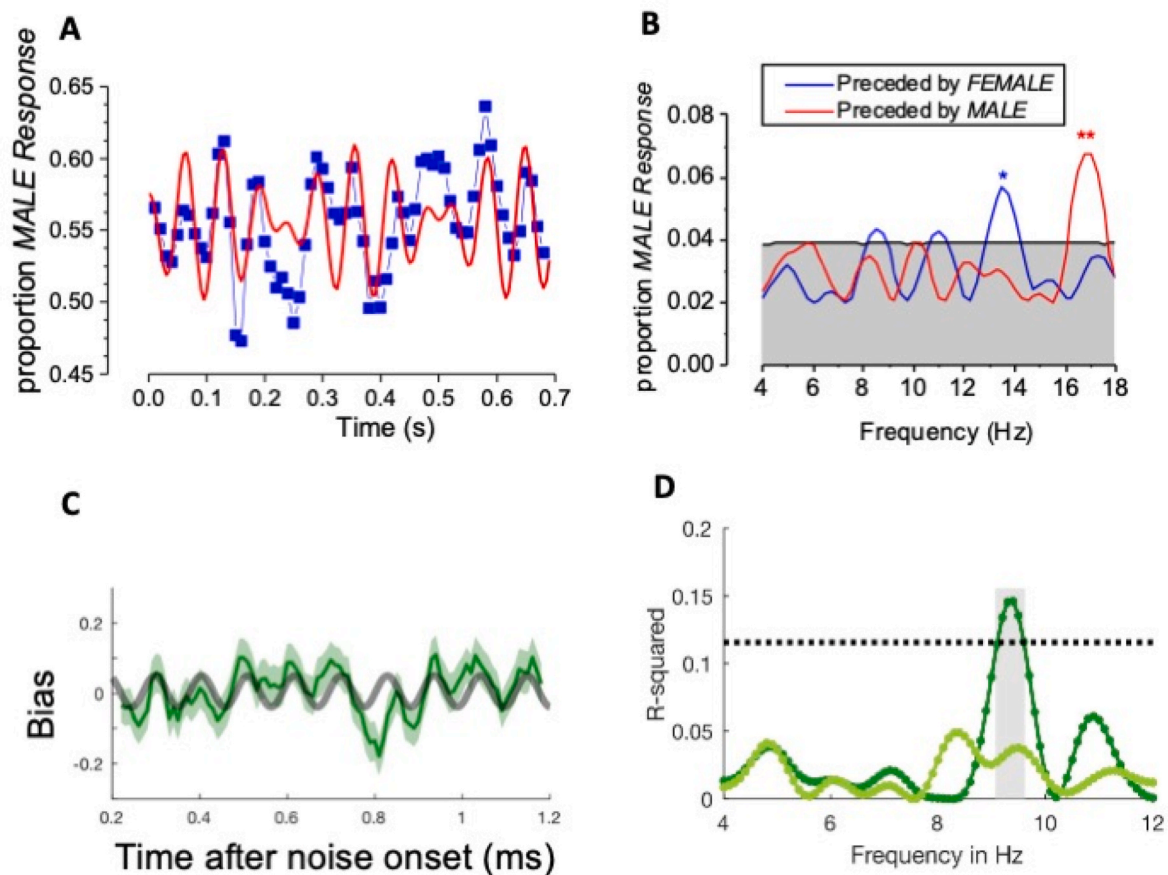


Fig. 5. Behavioural oscillations in bias for judgments of face gender and ear of origin. A) Proportion of trials where androgynous faces are judged male, as a function of time after button-press (blue symbols). The bias oscillates in the low-beta range, following a complex waveform comprising 14 and 17 Hz (red curve). B) Fourier transform of the data of Fig. A, separately for trials preceded by male (blue symbols) or female (red symbols) faces: there are two distinct peaks, at 14 and 17 Hz for female and male respectively. C) Bias in identifying the ear of origin of a weak tone presented in noise, as a function of latency from noise onset (green curve, within 95% confidence intervals). The bias oscillates at 9.5 Hz (grey curve). D) Fourier transform of the data of Fig. C, separately for trials following a presentation to the same ear (dark green) and those to the other ear (light green). Only congruent trials (following a presentation to that ear) show the alpha-frequency oscillation.

sensitivity, oscillate in synchrony with time of stimulus presentation? Benedetto and Morrone (2019) showed that response bias during saccades oscillated in synchrony with saccadic onset at a frequency around 12 Hz. But are those oscillations related to the *prior* signals? Fig. 4B shows how attraction towards the prior orientation is not constant over time, but oscillates between zero and around 4°. The oscillation pattern was best fitted by a composite waveform, comprising 9.5 and 19 Hz, possibly harmonics of the same driving frequency. Why the effect of the prior should be modulated at these two frequencies, phase-locked to saccadic onset, is not yet determined, but it is clear that the oscillations play an important role in mediating the action of the prior. One possibility is that the prior may be available only when gated by the endogenous beta band activity, phase-locked to saccadic onset. This is consistent with work with intracranial and magnetoencephalography recordings showing that saccades are locked to the phase of visual alpha oscillations, whose magnitude is related to successful mnemonic encoding of visual scenes (Staudigl et al., 2017).

Like oscillations in sensitivity, the behavioural oscillations in bias of Fig. 4 generalize to other sensory-motor loops. Similar results have been reported for judgements synchronized to button-press, but at different frequencies: Bell et al. (2020) measured gender perception in faces morphed along a male/female continuum. Gender judgements of androgenous faces (neither male nor female) were strongly influenced by the gender of the previous face, as previously reported (Liberman et al., 2014; Taubert et al., 2016). However, like orientation judgements during saccades, biases in the gender judgements are not constant, but oscillate in the high-alpha, low-beta range (Fig. 5A). Again, the curve best-fitting the data was not a single sinewave, but a composite, comprising 14 and 17 Hz. On further analysis, it was clear that the two separate frequencies were linked to serial history: when the androgenous stimuli were preceded by a male face the biases oscillated at 17 Hz; preceded by a female they oscillated at 14 Hz. One interesting possibility is that perceptual history is communicated via a frequency code, in a form of “frequency tagging”, but at present there is no firm evidence for this idea.

Oscillations in bias also occur in audition. Ho et al. (2019) had participants identify the ear of origin of brief sound sources embedded within a burst of random noise. Plotting responses as a function of time after noise onset revealed clear alpha-frequency oscillations in response bias, at 9.5 Hz (Fig. 5C). Again, the oscillations were not always present, but only on trials when the previous stimulus had been presented to the same ear (congruent trials); when presented to the other ear (incongruent trials), there was no measurable oscillation (Fig. 5D). That the oscillation occurred only for coherent trials clearly shows that it is related to serial dependence. The results further point to a sensory site of action, as the previous stimulus generated oscillations only if presented to the same ear. If the oscillation were at the level of decision criterion, then it should occur in both ears, irrespective of where the previous stimulus had been presented. The fact that it depends on the ear of stimulus presentation strongly implicates sensory processes.

At this stage we can only speculate on the role oscillations play in serial dependence. One possibility is that they serve to facilitate communication and bind the previous with the current stimuli. The frequency of the oscillations may signal the type of prior (such as male or female, in the gender task). The phase of the oscillation may signal time passed from action onset, helping to bind the motor and sensory activity, compensating for the variable but inevitably delays of brain excitations. Another not mutually exclusive idea is that they derive from the recursive nature of the prediction/verification cycle inherent to predictive perception. In all predictive models, higher processing levels generate predictions, or *priors*, which are fed back to early levels to test against sensory input, which in turn transmit an error signal to correct the prior, in a recursive loop. Given that each stage will have a characteristic delay, the loop will tend to reverberate at a certain frequency. Modelling shows that physiologically plausible delays will lead to experimentally observed oscillations (Alamia and VanRullen, 2019;

Friston, 2019; Friston et al., 2015). The two visual systems – for action and for conscientious perception – may be affected differently by prior knowledge, and this could well be communicated through oscillations.

5. Concluding remarks

We have outlined a series of experiments from our laboratories focusing on understanding how action, particularly saccadic eye-movements, affects perception. Saccades are fundamental for active vision, allowing humans to scan the visual environment rapidly and efficiently with a highly non-homogeneous retina. But the strategy also poses important challenges for vision, such as ignoring the spurious wide-field retinal motion, and realigning the retinal image on each successive fixation. These challenges are met with a variety of responses, often associated with strong neural and behavioural oscillations, showing that oscillations play a fundamental role in dynamic, active vision. The studies reviewed here were all very much motivated by Mel's research, and by the framework he created. We hope they give some insight into the processes mediating active vision, especially the tight visuo-motor coupling required to link vision with saccadic eye-movements. However, although the work strongly implicates neural oscillations in keeping perception and action aligned during eye-movements, it remains unclear what exact role they play. Are the oscillations a consequence of the interaction, or do they control the interaction and alignment of the two, providing a master clock to keep vision and action in synchrony? Are they a by-product of reiterative feedback loops inherent to predictive perception, or are they the means of communicating perceptual memory and expectations to perceptual systems? These questions will drive much research over the next decade, which will hopefully lead to more insights of the interplay between action and perception, continuing to leverage on the seminal ideas advanced by Mel Goodale four decades ago.

Credit author statement

David C. Burr and Maria Concetta Morrone: Conceptualization; Project administration; Resources; Roles/Writing original draft; and Writing - review & editing.

Data availability

No data was used for the research described in the article.

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