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Dynamics of Active Sensing and perceptual selection

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Sensory processing is often regarded as a passive process in which biological receptors like photoreceptors and mechanoreceptors transduce physical energy into a neural code. Recent findings, however, suggest that: first, most sensory processing is active, and largely determined by motor/attentional sampling routines; second, owing to rhythmicity in the motor routine, as well as to its entrainment of ambient rhythms in sensory regions, sensory inflow tends to be rhythmic; third, attentional manipulation of rhythms in sensory pathways is instrumental to perceptual selection. These observations outline the essentials of an Active Sensing paradigm, and argue for increased emphasis on the study of sensory processes as specific to the dynamic motor/attentional context in which inputs are acquired.

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Current Opinion in Neurobiology 2010, 20:172–176

This review comes from a themed issue on
Cognitive neuroscience
Edited by Earl Miller and Liz Phelps

Available online 20th March 2010

0959-4388/\$ – see front matter

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DOI 10.1016/j.conb.2010.02.010

Introduction

‘Active Sensing,’ as a term in robotics, refers to use of a sensor or detector device that requires input energy from a source other than that which is being sensed. Classic examples of Active Sensing in biological systems include echolocation in bats and marine mammals [1] and electrollocation in fish [2]. In contrast, biological sensors like

the eyes and finger tips traditionally have been thought of as passive sensors that transduce the energy of the input into a neuronal code. However, closer examination of the manner in which humans and other animals gather data from the environment suggests that overall, it is more of an Active Sensing process. Natural somatosensory exploration, for example, typically involves use of the fingers to feel textures and manipulate objects. Only rarely do we leave the hand still and wait for something to touch it. Similarly in natural viewing, we do not just stare at a spot and wait for things to happen around it, but rather, we actively sample the scene with a systematic pattern of eye movements and fixations [3,4]. In short, much of the sensory input that enters the brain does so because we actively locate and acquire it using a motor sampling routine. As elaborated in the next section, motor control of sensory inflow has strong implications for the way we must think about sensory processing.

Attention is the neural process by which the brain enhances the representation of task relevant input at the expense of irrelevant input, and it is the essential component of Active Sensing. Attention and motor sampling routines can be dissociated, in that attention can either operate in the absence of any overt motor activity, or can be directed to a location other than that upon which the sensors are aligned, as in covert spatial attention [5]. However, attention in isolation from any motor routine is relatively uncommon in natural Active Sensing.

This paper will explore the concept of Active Sensing as a collaboration of motor and sensory rhythms that is advantageous for information processing. We will review and consider: first, the role of motor activity in Active Sensing, using olfaction and vision as examples; second, the mechanisms by which the rhythms inherent in motor sampling routines may engage corresponding rhythms in olfactory and visual systems, and role of attention in this process; third, the extent to which these concepts generalize to somatosensation and audition. Throughout, we will attempt to make clear the uncertainties and open questions in our perspective.

Rhythm in motor routines used in Active Sensing

Motor output is modulated by motor cortical oscillatory rhythms in the delta (1–3 Hz), theta (5–7 Hz), mu (8–12 Hz), and beta (13–30 Hz) bands [6–11], and in our view, the motor system’s imposition of these rhythms on sensory inflow is a critical factor in Active Sensing.

However, the senses vary in the degree to which they explicitly depend on motor routines, and thus also, in their apparent sensitivity to rhythmic motor influences. Olfaction, owing to its utter dependence on the motor routine of respiration, is at one extreme.

Olfactory processing

Mammalian, olfactory sensory neurons are located in a specialized olfactory epithelium deep within the nose. Thus, odor stimulation requires airflow to draw volatile molecules into the nose, and into contact with odor receptors on the membranes of olfactory sensory neurons. Of course, this airflow is generated by pressure differential due to movement of the diaphragm. Although respiration is an automatic, rhythmic motor output (i.e. you can breathe while asleep), it is also under the control of higher order circuits [12], and can come under voluntary control. An example is the shift from a homeostatic driven respiratory mechanism to an olfactory sampling, or 'sniffing' mechanism. Both human [2] and nonhuman [3,4] mammals demonstrate rapid shifts in respiratory patterns in response to odor detection or changes in arousal, and the change in respiratory motor rhythms from homeostatic respiration to active sniffing produces a variety of changes in both peripheral and central odor processing.

In passively respiring rodents, stimulation by odors (as well as other factors) can induce a rapid shift in respiration rate from 1–3 Hz basal rates to 5–12 Hz during active sniffing [13]. This increase in sampling rate has at least four consequences for odor processing, and thus constitutes an active behavioral regulation of odor sensing. First, changes in airflow affect odor sorption at the olfactory epithelial mucus, and thus differential stimulus access to odor receptors based on physicochemical properties of the odor molecules [14]. Second, sniffing-induced changes in olfactory sensory neuron temporal activation appears to act as an active filter, reducing input to second order olfactory bulb neurons to stable background odors, while maintaining responses to odors against this background [15]. Third, changes in temporal patterns of input to olfactory bulb local circuits modify levels of lateral and feedback inhibition, perhaps affecting contrast enhancement [16]. Fourth, olfactory system oscillations in both the beta and gamma bands are generally time-locked to the respiratory cycle. In both the olfactory bulb and olfactory cortex, changes in sampling rate are associated with changes in these high frequency local circuit oscillations in neural activity that are involved in coding of odor identity and significance. Thus, sniffing can be thought of as an active behavioral mechanism to sample and modulate sensory input, affecting acuity and discrimination, and its rhythms are essential dynamics of olfactory processing.

Visual processing

In natural vision, information is almost always available to the photoreceptor arrays in the eyes, but nonetheless

appears to be actively acquired by pointing the eyes towards items of interest [17]. Some animals may rely more on head gaze [18], however, humans and other primates typically use variations in eye gaze, scanning a visual scene with a rhythmic pattern of brief fixations (about 3 Hz), separated by rapid 'saccadic' eye movements [19,20]. At each fixation, a volley of retinal outputs courses into the system [21–24]. With a few exceptions, such as pursuit eye movements [25,26], rhythmic fixation patterns are the major means of sampling the visual environment. Recognizing the potential importance of these dynamics, investigations have increasingly turned to study the influence of eye movement and fixation patterns on visual processing and perception [27–30], and in particular, the way that these rhythmic events organize and amplify visual input. 'Perisaccadic' modulation of neuronal excitability, generally suppression during the saccade, and then enhancement at the onset of fixation, has been observed throughout the visual pathways from lateral geniculate nucleus (LGN) to prefrontal cortex (reviewed by [31]). Importantly, perisaccadic modulation is observed in total darkness, and thus, has a nonvisually mediated component [30,32–37]. We have proposed [30] that fixation-related excitability increase in (V1) and elsewhere is accomplished by phase modulation of ongoing neuronal oscillations, and that this effect is likely orchestrated across the visual system by an 'efference copy' mechanism. As discussed below, the phenomenon of phase modulation is of specific interest, as it allows ongoing neuronal oscillations, actually dynamic fluctuations in network excitability, to be utilized as instruments of input amplification and suppression. On a more fundamental level, these findings, like those reviewed for olfactory processing, support the idea that the brain's sensory and motor systems operate in coordination. In this view, fixation-related modulation reflects the ability of the brain's gaze control systems to 'predictively prepare' the visual system for a temporal pattern of visual input that results directly and simply from the way that the eyes are used in actively sensing/sampling [30,38]. As in olfaction, the motor rhythms become essential dynamics of sensory processing.

Instrumental functions of sensory rhythms and their subordination by attention and motor rhythms

Neuroelectric oscillations

Neuroelectric oscillations, ubiquitous in the brain of an awake subject at rest [39], reflect a synchronization of cyclical fluctuations in neuronal excitability across populations of neurons, that may be critical to normal sensory processing (reviewed by [40]). Of particular relevance here, we have shown that lower frequency oscillatory rhythms in the range of those observed in sniffing and free viewing can function as instruments of cross modal amplification and attentional selection in primary visual and auditory cortices [41,41–43]. We have also proposed

that there is a crucial distinction between ‘rhythmic’ and ‘continuous’ modes of attentional operation [40]. The essence of this distinction is that when behaviorally relevant stimuli occur in rhythmic and thus, predictable streams, attention operates in a *rhythmic mode*, enforcing the entrainment of low frequency neuronal oscillations to the events in the stream. Essentially, this aligns the oscillation’s high excitability phase with the events in that stream, which amplifies their neural representation. At the same time, the oscillation acts as a temporal filter, as stimuli out of phase with the relevant stream elicit responses during the oscillation’s low excitability phase and are thus suppressed. When, in contrast, behaviorally relevant stimuli are random and unpredictable, attention operates in a *continuous mode*, maximizing the sensitivity of the system by suppressing lower frequency oscillations and exploiting the advantages of extended continuous gamma band oscillations [44]. The dynamics of the brain during either olfactory or visual exploration would clearly be those of rhythmic mode processing since, as we described above key sensory events (inhalation and fixation) occur rhythmically. In this broadly representative case, where attention and motor sampling are yoked together, we would predict that top-down attentional influences would enforce entrainment of sensory oscillatory rhythms to efference copy signals stemming from motor areas, and/or to motor event-related variations in sensory signals, resulting in enhancement of the neural representation of the task-relevant information. We suggest that in vision, as in olfaction, rhythmic is by far the most common mode of operation. Even when the system should be in an extreme continuous mode operation, such as under the conditions of the classic vigilance paradigm, it appears that low frequency neuronal oscillations can still inject rhythm into sensory processing. For example, when a subject’s eyes are fixated on a point in a static scene, microsaccades (occurring at ~ 3 Hz) impose a strong rhythm on visual processing [45].

Generality of the influence of motor rhythms in somatosensation and audition

Somatosensation

Given the above considerations and the extensive interconnectivity between primary motor and somatosensory cortices in primates [46], we would expect that motor control of Active Sensing as outlined above would also operate in the somatosensory cortical hand/arm representation. Although there have been studies examining oscillatory activity in the hand representation of primate Area 3b (e.g. [47]), as far as we can determine, this is an open question.

Active Sensing has been examined to some extent in the context of whisking in rats. Phase locking of field potentials to whisks in rat S1 may indicate a reference signal, modulated by goal-directed activity [48]. Intracellular recordings indicate that the coherence of whisking and

membrane potential could vary in sign, and this is hypothesized to increase sensitivity to whisker deflection during specific phases of the whisking cycle [49]. This study also suggested that the rhythmicity of sensory input during Active Sensing is critical to its effectiveness; the response to random, passively acquired air puff stimuli was depressed, and highly variable during active whisking, though actively acquired whisking contacts of an object elicited robust and stereotyped responses.

Audition

Echolocation is an obvious example of active auditory sensing [1]. In nonecholocating species, movements of the head/pinnae and adjustment of the sensitivity of outer hair cells provide active mechanisms of gain control [1,50], but otherwise, auditory processing appears to be remarkably divorced from the subject’s ongoing motor activity. For example, it is common for an intently listening observer to become very still, presumably to minimize self-produced sounds. On the other hand, much of our auditory experience takes place during periods when we are moving, and in these cases, neuronal oscillations modulated by motor events could play a critical role in suppressing sounds that are generated by one’s own movements (e.g. walking) or other rhythmic motor behavior like speech. There clearly is evidence that as part of a ‘mirror’ system, an observer’s auditory experience of biologically significant sounds, such as feeding noises and conspecific vocalizations does impact on motor cortex (reviewed by [51]). Similarly, rhythmic visual gestures accompanying human speech may entrain auditory cortical rhythms, thus amplifying the representation of speech sounds in auditory cortex [52]. One possibility, in line with the Motor Theory of Speech Perception, is that ‘covert’ oscillatory influences from motor cortex entrain rhythmic activity in auditory cortex; however, several observations, including the fact that motor cortical destruction produces minimal comprehension impairment [53], make this proposition less than compelling. At present, clear evidence of rhythmic motor facilitation of Active Sensing in audition seems to be lacking. It is possible that in contrast to the other senses, Active Sensing in audition is mainly attention-based, but resolving this question will require further experimentation.

Conclusions

Passive stimulation paradigms have been a mainstay of basic neuroscience research because they afford simplification and stabilization of complex dynamic phenomena, and they will likely continue to be productive. On the other hand, these paradigms ablate key components of natural experience, particularly the rhythms that are inherent to our motor sampling routines. These drive and/or entrain rhythms in sensory regions that are fundamental tools in normal sensory processing and perceptual selection. At this point, there are numerous open questions, including: first, the degree to which

somatosensory and auditory processes adheres to the scenario outlined for olfaction and vision and how many clear exceptions to Active Sensing can be found in any system; second, the distance to which rhythmic influences extend beyond the primary cortices, and in particular, which brain structures or systems are immune to them (e.g. those that monitor events outside the focus of attention); third, the overall importance of efference copy/corollary discharge signals in mediating motor influences over sensory processes [54], and the cellular mechanisms by which they operate. At this point, the accumulating evidence that Active Sensing plays a major role in perception and sensory processing encourages us to increase the emphasis on studying sensory processing in the context of ongoing motor behavior.

Acknowledgements

The authors' work is supported by The New York State Office of Mental Health, and by NIH Grants RO1MH061989, RO1MH060358, P50MH086385, R21DC010415, R01DC03906, RO1DC008982, T32MH067763, R21MH084215 and RO1NS037562.

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