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How neuronal oscillations code for temporal statistics

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Link to publication

Download date: 20 Sep. 2021

CHAPTER 9

SUMMARY AND DISCUSSION

The work in this thesis focuses on the influence of temporal associations between audio-visual stimulus pairs on perception. In the first part of the thesis the perceptual benefit of temporal associations acquired during one experimental session either through rhythmicity or temporal cueing is explored. In the second part the temporal association between the onset of mouth movements and onset of speech sounds and the consequences for behavior and syllable coding are central.

Part I: Short term temporal statistics

Temporal regularities in the environment have been shown to have behavioral benefits both decreasing reaction times through temporal preparation (Correa, Lupiáñez, Milliken, & Tudela, 2004; Coull & Nobre, 1998; Los & Van der Burg, 2013; Niemi & Näätänen, 1981) as well as improving perception in discrimination (Ellis & Jones, 2010; Jones, Moynihan, MacKenzie, & Puente, 2002; Mathewson, Fabiani, Gratton, Beck, & Lleras, 2010) and detection tasks (Cravo, Rohenkohl, Wyart, & Nobre, 2013; Rohenkohl, Cravo, Wyart, & Nobre, 2012). In chapter 2 we show that this detection improvement is also acquired even when the temporal regularity itself is not yet perceived. Moreover, adding multiple types of temporal information (rhythmicity as well as temporal cueing) improves detection even more, even though one type of temporal information would already have been sufficient to estimate the temporal arrival exactly. This last effect is likely mediated by the fact that temporal estimates are never fully accurate (Eisler, 1976) and adding multiple types of not fully accurate estimates collectively improve perception. This finding relates to cue integration and Bayesian models of perception which state that the brain combines multiple perceptual cues to optimize perception (Ernst & Bülthoff, 2004; Fetsch, DeAngelis, & Angelaki, 2013; Knill & Pouget, 2004). Each sensory cue is typically weighted by its own reliability, improving perception in an optimal fashion. Conclusively, the benefit of combining multiple types of temporal information seems to be similar compared to other types of sensory cues (also see Elliott, Wing, & Welchman, 2014).

The optimized percept in Bayesian models is not only influenced by directly preceding information. Instead, information from multiple time scales is integration and updated online to arise to an optimal

percept (Kim, Basso, 2010; Montagnini, Mamassian, Perrinet, Castet, Masson, 2007; Ernst & Bülthoff, 2004). In chapter 4, there are two types of temporal information on two different time scales. Firstly, the rhythmic structure of the entrainment stimuli aids participants to attend to moments in time that they expect a stimulus to occur in the rhythm. Secondly, there are different lengths of the entrainment train, thus participants have an expectation of the entrainment train continuing. We show that temporal estimations of stimulus occurrence are influenced by expectations whether a rhythmically presented stream of stimuli will continue and thereby shows that the estimates do not just respond to the immediately preceding stimuli, but instead estimates are updated continuously to improve perception (Friston, 2011; Siegel, Buschman, & Miller, 2015; Schroeder, Wilson, Radman, Scharfman, & Lakatos, 2010).

Rhythmicity of stimuli is picked up by the brain by resonating the neuronal responses to the presented rhythmic stimuli (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2008). We also find this resonance effect both in chapter 3 and 4. Chapter 3 shows that these resonating properties can even be present when 1) the participant is unaware of the stimulus stream and 2) the stimuli do not induce any direct measurable evoked response. This chapter shows that it is the alignment of oscillatory phase and not the change in amplitude of an oscillation that drives the entrainment effect (Makeig et al., 2002). This alignment could be a mechanism to attend to specific moments in time, thereby increasing the sensitivity of detection at that time point (Schroeder & Lakatos, 2009). This has a benefit as there is one specific most excitable phase on an oscillation, where neurons are more likely to fire with less input (Buzsáki & Draguhn, 2004; Lakatos et al., 2005). The entrainment is also highly influenced by context. Stefanics et al. (2010) have shown stronger entrainment effects for more probable events. In chapter 4 we further elaborate on this finding, showing that expectancy of entrainment continuation also influences the strength of the entrainment. These results highlights that the brain's response is not a direct reflection of the environmental input, but instead entrainment to environmental stimuli is mediated by mechanisms that predict whether the rhythmic input will continue.

During temporal cueing the brain also seems to optimize perception at the time at which a stimulus is expected by using oscillatory

mechanisms. In chapter 5 we show low frequency oscillatory responses when temporal information is predicted over a longer time window. This effect occurs as there is an optimal detection window on the oscillation period when stimuli are closer to threshold (Buzsáki & Draguhn, 2004; Lakatos et al., 2005). By resetting lower frequencies this window is broadened, effectively increasing the window at which stimuli are optimally processed, which is beneficial when stimuli are predicted to occur for a longer time period (also see Wilsch, Henry, Herrmann, Maess, & Obleser, 2015). This is further verified since the phase of low frequency oscillations also determines whether a target will be detected or not. These findings fit closely to mechanisms proposed for temporal attention during rhythms (Schroeder & Lakatos, 2009; Peele & Davis, 2012) as they indicate that the phase of oscillations is reset to optimally improve detection also during temporal cues. Additionally, they indicate that the frequency of the phase reset seems to depend on the temporal statistics in the environment.

Part I of this thesis shows that stimulus detection is pro-actively optimized by using the temporal regularities in the environment both afforded via rhythmicity and temporal cueing. It is shown that oscillatory brain responses change both their phase and frequency to align the most excitable phase of the oscillation to the time point that stimuli are expected. These results highlight that attention can be directed in time (Coull, Frith, Büchel, & Nobre, 2000) and that these mechanisms are mediated via oscillatory properties in the brain (Schroeder & Lakatos, 2009; Zion Golumbic, Poeppel, & Schroeder, 2012).

Part II: Long term temporal statistics during audio-visual speech
Some temporal associations between audio-visual stimuli can be quite consistent. Especially in speech there are many temporal consistencies that have behavioral relevance to optimize speech perception both in audio only (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Poeppel, 2003; Rosen, 1992) and audiovisual speech (Myers, 1971; Schroeder, Lakatos, Kajikawa, Partan, & Puce, 2008; Zion Golumbic et al., 2012). In chapter 6 we show that there is a consistent relationship between the onset of mouth movements and the onset of a speech sound. This relationship is unique to specific syllables [see also (Chandrasekaran,

Trubanova, Stillittano, Caplier, & Ghazanfar, 2009)] and is used to perceive syllable identity. These results indicate that audio-visual temporal cues do not only indicate when auditory information will occur, but also aid the identification and categorization of syllables (the what). These results go beyond the function of temporal information to drive attention in time (Nobre, Correa, & Coull, 2007), but show that temporal information itself is a cue for categorizing stimuli.

The neuronal coding of these consistent temporal relationships has not been investigated thoroughly. The unique feature of varying temporal visual-to-auditory delays for different syllables provides an exclusive starting point to investigate whether temporal information in audiovisual settings can influence the neuronal coding of syllables. In chapter 7 we show that syllable identification of an ambiguous syllable (either perceived as /da/ or /ga/) is biased when the syllable is presented at a specific phase. The phase difference between whether the ambiguous syllable will be identified as /da/ or /ga/ exactly matches the audio-visual delay difference between these two syllables and indicates that the temporal information afforded by audiovisual presentation is transferred to the coding of the auditory information. This is further supported in chapter 8 where we show that temporal cortex can decode syllable identity better when the syllables are presented at their preferred phase. These results show that phase information is integral part of the representations of these syllables.

The idea of a temporal code that codes different representations on oscillatory phase is not new (see Bernstein, 1967 for one of the first accounts). For example, O'Keefe and Recce (1993) found that specific neuronal populations coding for locations in the environment fire at specific phases of the ongoing theta oscillation in the hippocampus. Neuronal populations coding for different locations thus have one specific preferred phase of firing. More recently, the role of phase for content representation in the cortex is being uncovered (Kayser, Montemurro, Logothetis, & Panzeri, 2009; Lopour, Tavassoli, Fried, & Ringach, 2013; Panzeri, Petersen, Schultz, Lebedev, & Diamond, 2001; Watrous, Fell, Ekstrom, & Axmacher, 2015). It seems evident from these data that indeed different representations fire synchronously at one specific phase. On the one hand, this coding scheme binds the different features that the neurons are coding for (Crick & Koch, 1998; Engel & Singer, 2001; Fries,

2005; Singer & Gray, 1995). On the other hand, it provides a clear separation between different representations and this separation should improve the memory for these representations (Fell & Axmacher, 2011; Lisman, 2005; O'Keefe and Recce, 1993; Singer, 1999; Watrous et al., 2015).

The separation of representations by phase is very attractive. However, up to date it is not clear how specific neuronal populations start preferring one specific phase over another. Most accounts state that the changing excitability during an oscillatory period is the driving force for any phase influence on perception or cognition (Buzsáki & Draguhn, 2004; Giraud & Poeppel, 2012; Jensen, Gips, Bergmann, & Bonnefond, 2014; Lisman & Jensen, 2013; Schroeder & Lakatos, 2009). For example, it has been proposed that attention mechanisms reset the phase of the oscillation to be most excitable at the time point that stimuli are expected (Schroeder & Lakatos, 2009); as is supported by part I of this thesis. However, coding information is very different from this type of temporal attention. To incorporate excitability in the coding of information, Jensen et al. (2014) proposed that more salient input is processed earlier on the duty cycle of the oscillation as they can still reach an action potential even though the potential is further from threshold. This mechanism provides an intuitive manner by which different representations are ordered on the oscillatory period. This mechanism can also explain how sequential locations are ordered: the first upcoming location will be at the least excitable point as it is the most salient representation. However, it would predict that dependent on the saliency of the external stimuli, the associated phase would change. Consequently, the coding of specific representations on specific phases is not possible in this type of coding scheme.

Excitability might be an intuitive way to code information, but the reported effects of preferred oscillatory phase for different syllables seems in contrast with this notion (chapter 7 and 8). There is no reason to believe that one syllable should be preferentially processed at the more excitable part of the cycle compared to another syllable. Moreover, we did not find a clear consistency in the phases coding the individual syllables over participants, suggesting that there is not one specific phase that codes for one syllable. This effect might be partly driven by variances in brain anatomy of the participants: different anatomies could shift the

phase as measured with EEG compared to the phase measured at the source of the oscillation. Nevertheless, it is striking that the phase difference between /da/ and /ga/ matches the exact temporal difference in visual-to-auditory delays found in natural speech between these syllables. The presence of a clear difference implies that at least one syllable representation is not preferentially processed at the most excitable phase of the oscillation. Our results instead suggest another way in which specific representations start preferring a specific phase: it is a consequence of the temporal associations that are present in the environment. As visual mouth movements are presented oscillatory patterns in auditory regions reset (Perrodin, Kayser, Logothetis, & Petkov, 2015). Dependent on the specific temporal delay to the auditory speech sound that is unique for each syllable, syllables are presented at a specific phase. This consistent sequence of events leads to the association of specific syllables to specific phases. In this scheme the phase of syllable coding is a consequence of the temporal association between stimulus pairs and becomes an integral part of the representation. This would suggest that it is not excitability, but temporal relationships in the environment that guide at which phase neurons start preferentially firing (also see Kösem, Gramfort, & van Wassenhove, 2014).

There is an increasing amount of data showing that there might be a temporal phase code by which representations are stored (Fell & Axmacher, 2011; Lisman & Jensen, 2013). Part II of this thesis suggests that this phase code might consist of the wiring of temporal associations via statistical learning. This coding provides a unique and natural way to categorize information, thereby optimizing perceptual processes. In the future experiments directly testing the learning phase of temporal associations need to be conducted to investigate the evolvement of the coding of these associations. These experiments could account for part of the phase coding effects found in the literature (Kayser et al., 2009; Lopour et al., 2013; O'Keefe, & Recce, 1993; Watrous et al., 2015) and would explain how temporal information required for speech perception is stored (Giraud & Poeppel, 2012; Peelle & Davis, 2012).

Concluding remarks

Temporal information is omnipresent in our environment, but as we use this information implicitly it is hard to imagine the influence that this information has on our perception and thereby behavior. In the current thesis we show that the use of temporal information cannot be underestimated. Ultimately, perceiving the environment around us requires the attentiveness to the changes in our environment (James, 1886; Myers, 1971). Stationarity does not convey new information, but instead it is the temporal dynamics in the environment to which any living creature has to learn to adapt and usefully interact.

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