Temporal expectancies driven by self- and externally generated rhythms

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ABSTRACT

The dynamic attending theory proposes that rhythms entrain periodic fluctuations of attention which modulate the gain of sensory input. However, temporal expectancies can also be driven by the mere passage of time (foreperiod effect). It is currently unknown how these two types of temporal expectancy relate to each other, i.e. whether they work in parallel and have distinguishable neural signatures. The current research addresses this issue. Participants either tapped a 1 Hz rhythm (active task) or were passively presented with the same rhythm using tactile stimulators (passive task). Based on this rhythm an auditory target was then presented early, in synchrony, or late. Behavioural results were in line with the dynamic attending theory as RTs were faster for in-compared to out-of-synchrony targets. Electrophysiological results suggested self-generated and externally induced rhythms to entrain neural oscillations in the delta frequency band. Auditory ERPs showed evidence of two distinct temporal expectancy processes. Both tasks demonstrated a pattern which followed a linear foreperiod effect. In the active task, however, we also observed an ERP effect consistent with the dynamic attending theory. This study shows that temporal expectancies generated by a rhythm and expectancy generated by the mere passage of time can work in parallel and sheds light on how these mechanisms are implemented in the brain.

Introduction

Making temporal predictions is central to our everyday life. To hit a tennis ball we need to accurately predict when the ball will arrive. Otherwise the action will result in a swing and a miss. Two sources of information that humans can use to generate temporal expectancies are the sense of elapse of time and, if available, rhythm. There is evidence that humans and animals are capable of using both these sources (see Nobre and Rohenkohl (2014) for review). Although it is evident that the two types of temporal expectancy generation are not mutually exclusive, it is currently unknown how they relate to each other, i.e., whether or not they work in parallel and have distinguishable neural signatures. The current research addresses this issue.

The sense of elapsed time has been shown to be involved in generating expectancies about upcoming events, the control of actions, and the inference of causality (Gallistel and Gibbon, 2000; Janssen and Shadlen, 2005). One way to create temporal expectancies is using a warning signal indicating that an event is about to occur. The time interval between the warning signal and the impending stimulus is also known as the foreperiod. Varying this time interval has shown to affect behaviour, such as increasing the foreperiod leads to faster response times (Niemi and Näätänen, 1981). The foreperiod effect is typically explained by the fact that the likelihood of the occurrence of a conditional event that has not yet occurred increases with time. This probability of increased expectancy is driven by the Hazard function (Janssen and Shadlen, 2005; Luce, 1986). For example, the likelihood that the traffic light will turn green increases the longer you wait.

On the other hand, rhythms, if available, provide additional information compared to the mere lapse of time when generating temporal expectancies. Many events in our environment follow a rhythmic pattern. Evidence of how rhythms form temporal expectations comes mainly from rhythmic cueing experiments (and, thus, concerns external rhythms). For example, Jones et al. (2002) presented participants with a standard tone at the start of a trial and a comparison target tone at the end of the trial. The participants' task was to judge if the two tones had the same pitch. Sandwiched between these two tones was a task irrelevant rhythm. Importantly, the comparison tone could be presented in synchrony, or slightly too early or too late compared to the rhythm. The accuracy of judging the pitch was best when the comparison tone was in synchrony with the rhythm and tailing off either side in an inverted U-shaped pattern.

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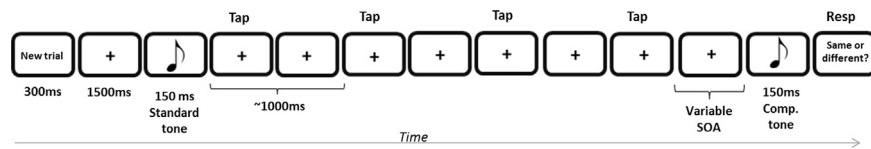 *E-mail address:* a.j.jones@mdx.ac.uk (A. Jones).

Fig. 1. Schematic representation of events in an Active and Passive task trial. The order of events in a trial was the same in both tasks. However, the *Tap* refers to the keypress in the active task. In the passive task, the *Tap* refers to a tactile tap presented to the participant using a tactile stimulator. The variable SOA was based on the average interval in that trial and refers to either early, in synchrony, or late condition. After the comparison tone the fixation cross stayed on screen until the participant had responded. If they were incorrect they received an Error message on the screen for 1000 ms.

The dynamic attending theory was suggested to explain these results (Jones, 1976, 2010).

The dynamic attending theory proposes that rhythms entrain periodic fluctuations of attention which modulate the gain of sensory input (Large and Jones, 1999). A large number of studies support this notion. First, similar to the results from Jones et al. (2002), presenting stimuli in synchrony with a rhythm has been shown to improve choice response times (Martin et al., 2005), detection thresholds (Herrmann et al., 2016; Lawrance et al., 2014), and perceptual discrimination (Rohenkohl et al., 2012). Second, more recently, evidence in line with dynamic attending also comes from research showing that intrinsic neural oscillations can entrain to external rhythms by aligning the firing pattern of neurons with rhythms in our environment (Lakatos et al., 2008; Arnal and Giraud, 2012; for reviews see Calderone et al., 2014; Henry and Herrmann, 2014). Finally, perception of near threshold visual (Busch et al., 2009) and auditory stimuli (Henry and Obleser, 2012) has been shown to be influenced depending on where in the phase of the neural oscillation the stimulus falls (see VanRullen, 2016 for a recent review). Synchronous vs. asynchronous presentation of stimuli has also been shown to influence various EEG components such as N1 (e.g., Escoffier et al., 2015), N2 (Doherty et al., 2005), and P3 (Breska and Deouell, 2014; Doherty et al., 2005; Correa and Nobre, 2008; Rohenkohl and Nobre, 2011). As with external events, many actions are also rhythmic (such as running, walking, or speech) and the regularities of these human activities are typically in the seconds time-scale below 4 Hz (Arnal et al., 2015; Keitel et al., 2017). There is evidence to suggest the motor system is imperative in generating temporal predictions which shape perception (Grahn and Rowe, 2012; Schubotz, 2007; Morillon et al., 2015). For example, there is a strong link between the auditory and motor systems, in particular in relation to rhythms (for recent reviews see Ross and Balasubramaniam (2014), Ross et al. (2016), Lima et al. (2016)). Movements, such as tapping have been shown to influence the perception of temporal information and improving temporal sensitivity (Iordanescu et al., 2013; Manning and Schutz, 2015). Morillon et al. (2014) showed a benefit of target processing when participants were tapping along to a beat compared to passive listening to the same beat. Further, Nozaradan et al. (2015) showed that tapping to music involves two distinct types of entrainment: neural entrainment to the auditory rhythm underlying beat processing, and a distinct neural entrainment to movement which underlies the production of synchronized movements. What is less well understood is whether self-generated rhythms in the absence of external auditory cues also entrain neural oscillations and how stimuli in and out of phase with this rhythm are processed.

The current study aims to investigate how rhythmic entrainment influences perceptual and behavioural processes by using both externally induced as well as internally generated rhythms within the seconds time-scale (here around 1 Hz), which is commonly observed in everyday rhythmic actions (Arnal et al., 2015; Rose et al., 1994; Buhusi and Meck, 2005). The aforementioned two types of temporal expectancy should yield dissociable result patterns. Contrary to the inverted U-shaped pattern observed in rhythmic cueing studies, the foreperiod effect typically results in shorter response times for longer foreperiods, suggesting a greater response preparation with increasing probability of occurrence of the stimulus (see Nobre et al. (2007), Niemi and Näätänen (1981) for reviews), as well as attenuated N1 at longer compared to shorter foreperiods (Correa and Nobre, 2008). The inverted U-shaped and the linearly increasing pattern of results are thus indicative of the two types of

temporal expectation, respectively. The present study adapted the paradigm used by Jones et al. (2002, described earlier). Participants performed a pitch judgement task but instead of being presented with a sequence of tones, they tapped a rhythm and a comparison target was then presented in synchrony, earlier, or later than the self-paced tapping (active task). In a second task, exactly the same rhythm was presented back to the participant using tactile stimulators (passive task). The first objective of the study was to investigate whether or not self-paced tapping and external tactile rhythms entrain slow wave delta oscillations. Second, we aimed at testing the effect of external and internal rhythmic entrainment on auditory stimulus processing as measured by means of reaction times/errors and ERPs. There were two possible outcomes, both of which might be observed but at different processing stages. A.) Any processing that is driven by the passage of time, should show a pattern of results corresponding to a foreperiod effect. For example, decreasing attenuated sensory components for late compared to in synchrony and also early stimuli. B.) Any processing that is driven by the rhythm should show a pattern in line with the dynamic attending theory, e.g., enhanced components in synchrony compared to early and late stimuli. To foreshadow the results, in the condition with internally generated rhythms we observed two separate ERP effects consistent with the foreperiod effect and dynamic attending theory, respectively.

Methods

Participants

Twenty-one paid participants took part in this study (2 were removed due to excessive artefacts and 1 due to excessive errors in the rhythm task, the experiment being prematurely aborted for this participant). There were 11 male and 7 female participants, all right handed, with a mean age of 26.4 years. Ethical approval for the study was granted by the Comité de Protection des Personnes (CPP) Ile de France II. All participants provided written informed consent.

Stimuli and apparatus

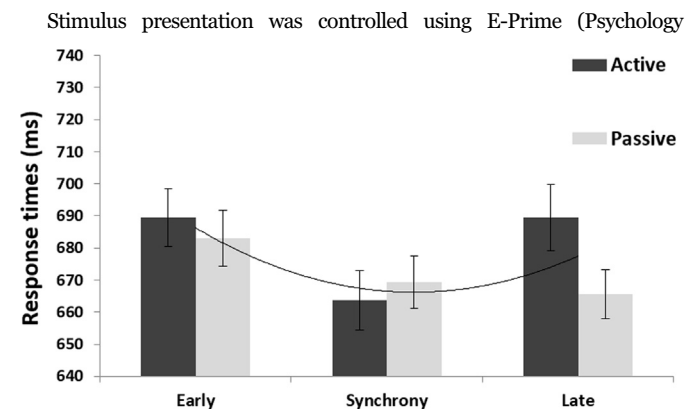Stimulus presentation was controlled using E-Prime (Psychology

Fig. 2. Response times (in milliseconds) to auditory targets for the Active (dark grey bars) and Passive task (light grey bars). There was a significant quadratic effect of Time as in synchrony targets were faster compared to when targets were presented early or late across both tasks. This is represented by the thin solid trend line. Error bars are standard error of the mean.