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Modifying temporal expectations: Changing cortical responsivity to delayed self-initiated sensations with training

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ABSTRACT

The perceptual system makes a specific prediction regarding the timing of impending, self-initiated sensations to facilitate the attenuation of these sensations. The current study used electroencephalography to investigate whether temporal expectations can be modified with training. Participants underwent a button-press-for-tone task and evoked responses to the tones were measured. Fifty participants were randomly assigned to receive repeated exposure (training) to either immediate tones, or tones delayed by 100 ms. Pre-training, N1 amplitude to delayed tones was significantly larger compared to immediate tones. However, while training to the immediate tone maintained a significant difference in N1 amplitude between the immediate and delayed tones post-training, this difference was eliminated when trained to the delayed tone. This suggests that participants' neural expectations regarding the anticipated timing of self-generated sensations can be modified with behavioural training. This result has implications for alleviating the subnormal sensory attenuation which has been observed in patients with schizophrenia.

1. Introduction

An efficient perceptual system is one that allows an organism to prioritize the processing of externally generated sensations over sensations produced by its own actions (Crapse & Sommer, 2008). It is advantageous to prioritize processing of sensory input from the external world as it is less predictable and thus, may signal novelty or threat in the environment. In contrast, self-generated sensations can be anticipated prior to the incoming sensation. Therefore, self-initiated sensations are typically predictable and inconsequential, and as such, can be effectively ignored. Evidence suggests that one way in which our perceptual system achieves this discrimination between self- and externally-generated sensations is by attenuating the cortical responsivity to self-generated sensations, hence reducing their perceived salience (Blakemore, Frith, & Wolpert, 1999; Crapse & Sommer, 2008; Fletcher & Frith, 2009; Kapur, 2003). An internal forward model of motor control, as shown in Fig. 1, has been formalised to capture this process, whereby a prediction is made about the anticipated sensory consequences of a self-generated action (Wolpert, Ghahramani, & Jordan, 1995; Wolpert & Miall, 1996). According to this model, when a motor command is generated, an efference copy of this signal is concurrently sent, and used, to predict the sensory consequences of that action before they are actually experienced. The actual self-generated sensations (sensory reafference) are compared to the predicted sensations (corollary discharges), and a match between these sensations results in sensory attenuation. This attenuation renders self-produced sensations less salient as compared to less predictable sensations, such as sensations that are externally generated (Blakemore et al., 1999; Blakemore, Wolpert, & Frith, 1998; Wolpert et al., 1995).

Sensory prediction does not simply involve anticipating the phenomenological experience of incoming sensations, but also involves a precise *temporal* prediction regarding those sensations. This was demonstrated by Blakemore et al. (1999) in a study of perceptual modulation of self-generated tactile stimulation. Participants produced tactile stimulation to their right hand by moving a robotic hand with their left hand, and they were required to rate the salience of the tactile stimulation. The tactile sensation was produced immediately, 100 ms, 200 ms, or 300 ms after participants moved the robotic hand, or it was produced automatically without the participant having to make a movement (i.e., externally-generated). It was found that externally produced stimulation resulted in higher ratings of salience compared to immediate self-produced movements of the robotic hand. Thus, with immediate

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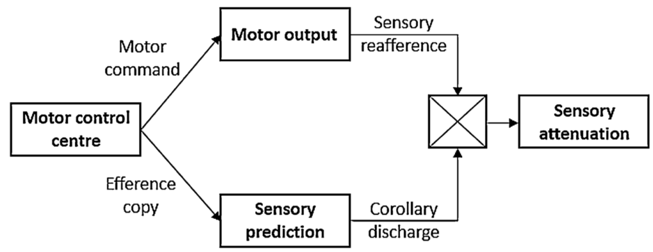

Fig. 1. An illustration of the internal forward model of motor control. The actual self-generated sensations (sensory reafference) are compared to the predicted sensations (corollary discharges), and in the case that the actual and predicted sensations match, the perceived salience and cortical activity evoked by these sensations are suppressed. Image modified from Blakemore et al. (1999).

sensory feedback there was suppression of the salience of self-generated sensations. Critically, participants' ratings of the salience of the self-generated tactile stimulation increased proportionately with increasing delays, such that for the longest delay period (300 ms), the salience of the stimulation was no different to the case in which the robotic hand's movements were externally generated. That is, sensory suppression of self-generated sensations decreased as the delay between action and the resultant sensation increased. This finding suggests that anticipating the sensory consequences of our own actions not only involves a precise prediction about *what* sensations will occur, but also highly specific information about *when* self-generated sensations will occur.

Sensory suppression has also been demonstrated to occur to self-produced auditory stimulation. Auditory self-suppression has typically been investigated using electroencephalography (EEG) by measuring event-related potentials (ERP) elicited by auditory stimuli. In particular, the N1 component of the auditory ERP (a negative component that peaks approximately 100 ms after sound onset) has been the focus of much auditory suppression research given that it largely originates from the primary auditory cortex (Godey, Schwartz, Graaf, Chauvel, & Liégeois-Chauvel, 2001; Zouridakis, Simos, & Papanicolaou, 1998). Notably, it has been established that the amplitude of the N1 component is volume-dependent; that is, softer sounds evoke a smaller N1 amplitude compared to louder sounds (Mulert et al., 2005; Simmons, Nathan, Berger, & Allen, 2011). As self-generated auditory stimuli elicit a smaller N1 amplitude compared to the same stimuli generated externally (Baess, Horvath, Jacobsen, & Schroger, 2011; Bäss, Jacobsen, & Schröger, 2008; Martikainen, Kaneko, & Hari, 2005), this reduction in N1 may reflect a decrease in the salience and perceived intensity of self-generated auditory stimuli.

There is evidence to indicate that N1 suppression depends on temporal predictions about *when* self-initiated auditory sensations will occur (Oestreich et al., 2015; Whitford et al., 2011). In the study by Oestreich et al. (2015), participants either pressed a button to produce a tone, or listened to the same tone being played automatically. The self-generated tones were either delivered immediately after the participant's button-press, or were delayed by 25 ms, 50 ms, 75 ms, or 100 ms. Tones delivered immediately after a button-press elicited a significantly smaller N1 than externally generated tones, indicating sensory suppression to self-generated auditory sensations. Furthermore, Oestreich et al. (2015) found that, as the time interval between button-press and tone increased, the level of N1 suppression decreased. This indicated that the longer the duration between the action and the tone, the less attenuation to the auditory sensation. These findings support the idea that immediate sensory feedback may have a special status in that it is expected by default in response to self-initiated actions. This raises the question of whether the expected timing of incoming self-generated sensations can be altered, such that delayed self-generated events could be anticipated, and effectively suppressed.

Consistent with this idea, evidence suggests that changing the temporal context by exposing participants to delayed self-generated sensory events can result in a shift in perceptual judgements as a result of this experience. Stetson, Cui, Montague, and Eagleman (2006) conducted a study where participants pressed a button, which on a majority of trials, resulted in a flash 35 ms after (immediate), or 135 ms after (delayed) the button-press. They found that participants' judgements of temporal order (i.e., as to whether the key press occurred before the flash) changed depending on the temporal context. After training to expect the 135 ms-delayed flash, participants often perceived flashes occurring 35 ms after the button press as having occurred *prior* to the button press. Thus, it appears as though judgements of temporal contingency adjust to the temporal dynamics of the immediate environment. However, this recalibration process has been investigated only in the context of temporal order judgments; it remains unclear as to whether temporal recalibration modulates sensory attenuation to self-generated actions. If the temporal dynamics of sensory attenuation reflect learning about relationships between actions and sensory feedback, then, given sufficient training, it should be possible to train individuals to exhibit suppression to delayed, self-initiated sensory feedback. Not only would such an investigation provide empirical insights to the way in which our perceptual system functions, but it would also present a potential mechanism for re-tuning breakdowns in the self-suppression mechanism, such as have previously been reported in patients with schizophrenia (Blakemore, Smith, Steel, Johnstone, & Frith, 2000; Ford et al., 2001; Ford, Palzes, Roach, & Mathalon, 2014; Whitford et al., 2011); we return to this idea in the Discussion.

Therefore, the current study used EEG to investigate whether sensory attenuation to immediate and delayed self-generated tones could be modified with training. Participants received approximately 42 min of training on a button-press-for-tone task. For those in Delayed Training Group, a tone was delivered 100 ms subsequent to a willed button-press; for those in the Immediate Training Group, a tone was delivered immediately subsequent to the button-press. Pre- and post-training measures of N1 amplitude to immediate and delayed tones were compared to determine whether training produced changes in the amount of sensory attenuation of the tones. In line with previous research (Oestreich et al., 2015; Whitford et al., 2011), it was expected that prior to training, both groups would exhibit larger N1 amplitudes for delayed, self-generated tones than immediate self-generated tones. It was further hypothesised that repeated exposure to immediate tones should not influence N1 amplitude to delayed tones, such that a significant difference in N1 amplitude would remain between delayed and immediate tones post-training. Most importantly, it was predicted that repeated exposure to delayed tones would result in increased attenuation to the delayed tone, which would suggest a change in sensory attenuation as a function of sensory experience.