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# Defensive activation during the rubber hand illusion: Ownership versus proprioceptive drift

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ABSTRACT

A strong link between body perception and emotional experience has been proposed. To examine the interaction between body perception and anticipatory anxiety, two well-established paradigms were combined: The rubber hand illusion (RHI) and the threat-of-shock paradigm. An artificial hand and the participants' own hand (hidden from sight) were touched synchronously or asynchronously, while either threat-of-shock or safety was cued. Potentiated startle reflexes and enhanced skin conductance responses were observed during threat as compared to safety conditions, but threat conditions did not interact with illusory body perceptions. Thus, defense system activation was not modulated by altered body representations. Physiological responses increased with the sense of ownership for the artificial limb, but not with proprioceptive drift towards its location. The results indicate that ownership ratings and proprioceptive drift capture different aspects of the RHI. The study presents a new approach to investigate the relationship between body representations and emotional states.



## 1. Introduction

The interaction of bodily signals and emotional states is of particular relevance for the understanding of anxiety- and pain-related disorders. Already the James–Lange theory stated a close relationship between physiological feedback and emotion processing, modulating the level of anxiety (James, 1884; Lange, 1887). This notion received much support (Craig, 2002; Pollatos, Kirsch, & Schandry, 2005; Wiens, 2005), for instance, in the somatic marker hypothesis (e.g., Damasio, 1999) and embodiment theories (e.g., Niedenthal, 2007), stating that bodily sensations are an important source for emotional experiences. This becomes apparent in various psychosomatic disorders, as enhanced attention to bodily signals can trigger anxiety, and conversely, psychological distress can severely impair body perception (Hiller, Rief, & Brähler, 2006).

The anticipation of aversive events is important to prepare the organism for fast reactions in potentially dangerous situations. In fear conditioning studies, the anticipation of electric stimulation is associated with potentiated startle reflex and enhanced activation of the autonomous system (Hamm, Greenwald, Bradley, & Lang, 1993; Lipp, Sheridan, & Siddle, 1994). These findings have been interpreted from the perspective of the motivational priming hypothesis, assuming preparatory activation of defensive response programs during threatening conditions (Lang, Bradley, & Cuthbert, 1997). Importantly, the actual experience of aversive events is no prerequisite for aversive anticipation. The mere verbal instruction about aversive contingencies is sufficient to establish triggers that provoke defensive responding (e.g., Bradley, Moulder, & Lang, 2005; Bublatzky, Gerdes, & Alpers, 2014; Bublatzky, Guerra, Pastor, Schupp, & Vila, 2013; Grillon, 2002; Grillon, Ameli, Woods, Merikangas, & Davis, 1991) and facilitates sensory processing of external threat cues (e.g., Baas, Milstein, Donlevy, & Grillon, 2006; Bublatzky, Flaisch, Stockburger, Schmälzle, & Schupp, 2010; Bublatzky & Schupp, 2012; Cornwell et al., 2007). Moreover, anticipatory anxiety may be elicited by somatic sensations as emphasized in the etiology of panic disorder (e.g., palpitation signaling a heart attack; Bouton, Mineka, & Barlow, 2001; Pané-Farré et al., 2014). For instance, the anticipation of interoceptive threat (e.g., expected hyperventilation or dyspnea) has been shown to activate defensive systems in participants prone to anxiety disorders (Alius, Pané-Farré, Löw, & Hamm, 2015; Melzig, Michalowski, Holtz, & Hamm, 2008; von Leupoldt, Chan, Bradley, Lang, & Davenport, 2011). Thus, defensive mobilization may be triggered by internal and external

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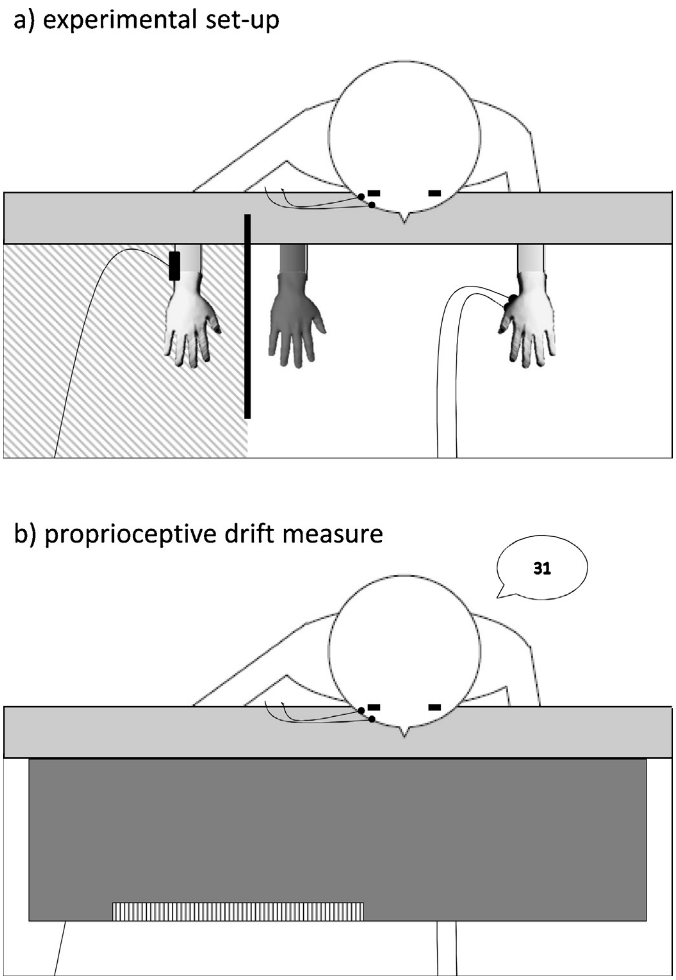


**Fig. 1.** Depiction of the experimental set-up during (a) the induction of the RHI, and (b) the assessment of proprioceptive drift. Strokes are applied to the artificial hand (black) and the participant's own right hand (white), which is hidden from sight (black bar). A shock electrode is attached to the participant's right hand, EDA sensors to the left hand and EMG sensors below the right eye. To assess proprioceptive drift, a board displaying a ruler is placed horizontally above the hands and participants indicate the number corresponding to the perceived location of their 'own right index finger'.

information, however, little is known about the mutual impact of aversive anticipation and the integration of bodily signals.

Accurate representations of the own body are essential to organize behavior. Seen from this perspective, the integration of bodily sensations – such as visual, tactile, and proprioceptive signals – provides an internal body representation which is strongly related to emotional and cognitive processes of self-consciousness (Cash & Brown, 1987; Costantini & Haggard, 2007; Kilteni Maselli, Kording, & Slater, 2015). An established method to induce alterations in body perception is the rubber hand illusion (RHI; Botvinick & Cohen, 1998), in which an artificial hand is placed visibly in front of the participant, while the corresponding own hand is hidden from sight (Fig. 1a). Synchronous stroking of the artificial and the unseen own hand elicits an illusory sense of ownership over the artificial hand, which is not experienced during asynchronous stroking (Botvinick & Cohen, 1998). This sense of ownership is usually assessed by RHI questionnaires, including items such as 'It seemed like the artificial hand was part of my body' (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). Perceived ownership is often accompanied by a hand-localization bias: The spatial position of the participants owns hand seems to be closer to the artificial hand after synchronous as compared to asynchronous stroking. This bias is generally referred to as proprioceptive drift (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Tsakiris & Haggard, 2005). Self-reported sense of ownership and behavioral measures of proprioceptive drift have often been used interchangeably as indicators for the RHI, but recent research suggested independent underlying processes (Holle, McLatchie, Maurer, & Ward, 2011; Honma, Yoshiike, Ikeda, Kim, & Kuriyama, 2014; Rohde, Di Luca, & Ernst, 2011).

As an intriguing demonstration of the illusionary capability, the RHI is qualified by defensive system activation when the artificial body part is threatened (Armel & Ramachandran, 2003; Ehrsson et al., 2008). For example, a needle stabbing the artificial hand has been associated with higher skin conductance responses (SCRs) during the illusion as compared to asynchronous stroking condition (Ehrsson et al., 2008). Moreover, in these studies, autonomous system activation increased with the strength of the illusion as revealed by sense-of-ownership ratings (Armel & Ramachandran, 2003) or proprioceptive drift (Ehrsson et al., 2008). It remains unclear whether defense activation in this procedure occurs because of, or despite of, the illusion. More specifically, does defensive responding depend on threatening the artificial body part, or is it a general defense mechanism regardless of body integration/representation processes as manipulated by the RHI.

The main goal of the present study was to explore the mutual impact of body illusions and aversive anticipation on defensive system activation. For this purpose, the RHI was induced during prolonged periods of instructed threat of shock or safety while eye-blink startle responses and electrodermal activity were recorded. Previous studies have reliably revealed potentiated startle reflexes during instructed threat as compared to safety conditions (e.g., Bradley et al., 2005; Bublatzky et al., 2013, 2014; Grillon, 2002; Grillon et al., 1991). Building upon this, it was hypothesized that an altered experience of the own body, as induced by the RHI, results in pronounced defense system activation. Assuming an increased perception of bodily signals during the RHI (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007), altered body experience may exert synergistic effects on defensive reflex activity. Here, threat-potentiated startle reflexes may be specifically pronounced during the RHI as illusory extended body-experience by itself may trigger defensive activation. Alternatively, impaired body perception during the experience of the RHI (e.g., feelings of loss of the own hand; Longo et al., 2008; Moseley et al., 2008) may lead to reduced defensive responding. Finally, crossmodal attentional interference may reduce startle responses during the RHI, because visual and tactile attention directed at the artificial and own hand might impede auditory startle probe processing. Such attentional shifts – from the visual/tactile to the auditory domain (startle probe) – have previously been shown to inhibit defensive reflex activity (cf. Anthony & Graham, 1985; Filion, Dawson, & Schell, 1998). Regarding autonomous system activation, enhanced SCRs have been found both under conditions of instructed threat and when threatening the artificial hand during the RHI (Bradley et al., 2005; Ehrsson et al., 2008). Thus, concurrent activation of defense system by threat-of-shock and RHI may operate simultaneously but independent from each other (i.e., additively enhanced SCRs), or exert synergistic effects (i.e., threat-enhanced SCRs specifically during the RHI). Finally, to account for potential variation of the threat-of-shock manipulation, the stability of threat effects was tested across the time course of the experiment (cf. Bublatzky et al., 2014).

## 2. Methods

### 2.1. Participants

Thirty-eight healthy students (11 males, mean age 21, all right-handed) from the University of Mannheim participated for course credit. Questionnaire scores were within a normal range for Anxiety Sensitivity Index (ASI-3, mean = 18.2, sd = 8.6),