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Differentiating aversive conditioning in bistable perception: Avoidance of a percept vs. salience of a stimulus

Gregor Wilbertz[a,*], Philipp Sterzer[a,b,c,d]

[a] Department of Psychiatry and Psychotherapy, Campus Charité Mitte, Charité-Universitätsmedizin Berlin, Berlin, Germany
[b] Berlin Center for Advanced Neuroimaging, Charité - Universitätsmedizin Berlin, Germany
[c] Berlin School of Mind and Brain, Humboldt Universität zu Berlin, Berlin, Germany
[d] Bernstein Center for Computational Neuroscience, Berlin, Germany

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ABSTRACT

Alternating conscious visual perception of bistable stimuli is influenced by several factors. In order to understand the effect of negative valence, we tested the effect of two types of aversive conditioning on dominance durations in binocular rivalry. Participants received either aversive classical conditioning of the stimuli shown alone between rivalry blocks, or aversive percept conditioning of one of the two possible perceptual choices during rivalry. Both groups showed successful aversive conditioning according to skin conductance responses and affective valence ratings. However, while classical conditioning led to an immediate but short-lived increase in dominance durations of the conditioned stimulus, percept conditioning yielded no significant immediate effect but tended to decrease durations of the conditioned percept during extinction. These results show dissociable effects of value learning on perceptual inference in situations of perceptual conflict, depending on whether learning relates to the decision between conflicting perceptual choices or the sensory stimuli per se.

1. Introduction

The perceptual conflict that arises when the visual system is faced with stimuli that are compatible with two mutually exclusive perceptual interpretations usually leads to alternation between the two possible percepts over time. The dynamics of such bistable perception, that is, when perceptual transitions between the two perceptual states occur and how long each state dominates, are partly explained by stochastic processes and noise (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Gigante, Mattia, Braun, & Del Giudice, 2009). However, there are also a number of factors known to bias perceptual competition in a systematic way (Blake & Logothetis, 2002; Brascamp, Sterzer, Blake, & Knapen, 2018). The influence of attention, for example, has been studied for decades (Lack, 1974) and results in perceptual predominance of the attended stimulus or percept (Paffen & Alais, 2011). Other variables that affect perceptual dominance in bistable perception are expectations (Denison, Piazza, & Silver, 2011; Haijiang, Saunders, Stone, & Backus, 2006; Schmack et al., 2013; Sterzer, Frith, & Petrovic, 2008), current needs (Balcetis & Dunning, 2010; Radel & Clement-Guillotin, 2012; Sanford, 1936), and emotional states of the observer (Anderson, Siegel, & Barrett, 2011; Gray, Adams, & Garner, 2009; Stefanucci, Proffitt, Clore, & Parekh, 2008; Sterzer, Hilgenfeldt, Freudenberg, Bermpohl, & Adli, 2011; see Scocchia, Valsecchi, & Triesch, 2014, for a thorough review on top-down effects). Overall, these findings are in line with theories that conceptualize perception as an active inferential process (Brascamp et al., 2018; Friston, 2005; Rao & Ballard, 1999).

* Corresponding author at: Klinik für Psychiatrie und Psychotherapie, Campus Charité Mitte, 10117 Berlin, Germany.
E-mail address: gregor.wilbertz@fu-berlin.de (G. Wilbertz).

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A challenging question both from an empirical and from a theoretical perspective is how negative valence affects perceptual inference. Prioritized access to awareness of negative stimuli has been proposed on the basis of evolutionary considerations (LeDoux, 2000; Ohman & Mineka, 2001) and was empirically supported using a variety of paradigms (Alpers & Gerdes, 2007; Carlson & Reinke, 2008; Coren & Russell, 1992; Milders, Sahraie, Logan, & Donnellon, 2006; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Yang, Zald, & Blake, 2007) [but also criticized (Gray, Adams, Hedger, Newton, & Garner, 2013; Stein, Seymour, Hebart, & Sterzer, 2014; Yang & Blake, 2012)]. In regard to attentional selection, it was shown that stimuli associated with negative feedback – although their avoidance may sometimes also be beneficial for the subject – capture attention (Anderson, 2017). In binocular rivalry – a form of bistable perception that occurs when two incompatible images are presented to the two eyes (Blake & Logothetis, 2002; Brascamp et al., 2018) – Alpers and colleagues showed that a previously neutral stimulus predominates perception after a classical fear conditioning procedure (Alpers, Ruhleder, Walz, Muhlberger, & Pauli, 2005). Similarly, Gayet and colleagues showed that fear-conditioned stimuli broke into awareness faster during continuous flash suppression, a variant of binocular rivalry (Gayet, Paffen, Belopolsky, Theeuwes, & Van der Stigchel, 2016). It seems that in these cases a previously neutral stimulus – through its association with fear – gained affective salience, hence attracted more processing resources and therefore tended to capture attention and dominate perception.

Contrary to these considerations, however, there is also evidence that aversive conditioning can bias perception in the other direction, i.e., towards avoidance of the perception of stimuli previously associated with negative consequences. In a recent study, we used monetary losses to punish participants for enduring perception of one of two stimuli during binocular rivalry and observed a relative decrease of its perceptual dominance (Wilbertz, van Slooten, & Sterzer, 2014). Similar results were reported by Marx and colleagues who decoded the participants' perceptual alternations from eye tracking measurements in order to rule out potential response biases (Marx & Einhauser, 2015). Moreover, they could show that this effect – though it scaled with attention – cannot be explained by attention alone, since punished percepts decreased even when they had to be attended.

The decrease of aversively conditioned percepts observed by Wilbertz et al. (2014) and Marx et al. (2015) seems at odds with the notion of increased affective salience as outlined above. It is in fact an intriguing puzzle how the brain might possibly solve the aversion problem considering two opponent goals: (a) to prioritize perception of stimuli that signal harm, and (b) to avoid negative consequences of perceptual choices, which would include the suppression of perceptual choices that are associated with negative outcomes. The puzzle might be resolved by a differentiation between two types of conditioning that takes into account the precise object of aversive association (Wilbertz et al., 2014): In Pavlovian/classical conditioning a neutral stimulus (CS) is repeatedly paired with a biologically relevant stimulus (US). Because the CS allows the organism to prepare for the US, the CS becomes relevant itself and triggers a conditioned response (CR; Domjan, 2005). In binocular rivalry, increased perceptual dominance of conditioned stimuli may reflect this conditioned response. Because this type of conditioning is based on the association of the aversive US and one of the rivaling stimuli (CS), we call it *stimulus* conditioning. In contrast, conditioning may result in the opposite effect if not the stimulus itself is paired with the negative outcome but the choice of a stimulus. Critically, this choice need not comprise a motor act but may also be a perceptual inference process that results in the selection of a stimulus for conscious awareness, such as in binocular rivalry. The perceptual dominance of a given stimulus may hence decrease if its selection in the process of perceptual inference is paired with aversive consequences. Because this type of conditioning is based on the association between an aversive stimulus and the choice of a percept, it is here called *percept* conditioning. Such percept conditioning would be in line with the law of effect, which states that responses are reduced if they have aversive consequences (Thorndike, 1907), and could thus be regarded as a type of instrumental learning (Wilbertz et al., 2014). Importantly, the term "instrumental learning" usually refers to overt behavior involving motor actions (O'Doherty, Cockburn, & Pauli, 2017). However, as we have argued previously (Wilbertz et al., 2014), perceptual inference includes the active selection of sensory information (Hohwy, 2017; Hohwy, Roepstorff, & Friston, 2008) and may hence be subject to instrumental conditioning, similar to motor acts.

In order to test these putatively different effects of *stimulus* (or classical) conditioning and *percept* (or instrumental) conditioning directly, we designed a binocular rivalry experiment with two groups of participants. One group received stimulus conditioning and the other group percept conditioning. Critically, the effect of each type of conditioning on binocular rivalry was assessed in analogous ways. We hypothesized that stimulus and percept conditioning would have opposite effects on dominance durations: Stimulus conditioning was expected to lead to an increase in dominance of the conditioned stimulus, whereas percept conditioning was expected to lead to a decrease in dominance of the conditioned stimulus. To minimize any conditioning-related response bias associated with the subjective report of perception (Erdelyi, 1974; Firestone & Scholl, 2015; Walter, 1978), we used an objective assessment of perceptual states based on probe detection (Alpers & Gerdes, 2007; Balcetis, Dunning, & Granot, 2012; Chong, Tadin, & Blake, 2005; Lack, 1974; Nguyen, Freeman, & Wenderoth, 2001; Yu & Blake, 1992). The continuous probe detection binocular rivalry task (Wilbertz et al., 2014) was further optimized by including ongoing adaptation of probe visibility. As a control, we also measured skin conductance responses as well as subjective stimulus valence (ratings) and expected equally strong conditioning effects on these measures in both groups.

2. Materials and methods

2.1. Participants

Sixty volunteers were tested and randomly assigned to either *stimulus* conditioning (group 1) or *percept* conditioning (group 2). The data of four participants were discarded from further analysis because they did not experience binocular rivalry as indicated by the absence of any perceptual alternations during baseline blocks. The final sample consisted of $N = 56$ participants (28 per group,