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Sources of adaptation of inferior temporal cortical responses

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ABSTRACT

Neurons of different brain regions change their response when a stimulus is repeated. In inferior temporal cortex (IT), stimulus repetition typically reduces the responses of single neurons, i.e., IT neurons show repetition suppression. Single unit recordings in IT showed that individual neurons vary in their degree of adaptation effects, ranging from strong suppression to slight enhancement of the response to the repeated stimulus. The suppression is maximal after the peak of the response and then reduces during the further course of the response. Repetition suppression in IT is still present for interstimulus intervals of at least 900 msec. I discuss the contribution of mechanisms that have been proposed to explain adaptation effects of IT responses. Firing-rate dependent response fatigue, e.g., a prolonged hyperpolarization, intrinsic to the recorded neuron cannot explain the stimulus specificity of the adaptation effect. The latter can be explained by synaptic depression or an adapted input from other IT neurons. We observed repetition suppression of IT neurons when adapter and test stimuli were presented at locations that differed by 8 degree of visual angle, suggesting that at least part of the adaptation effect is not inherited from retinotopic visual areas with small receptive fields. We observed no effect of repetition probability on repetition suppression in macaque IT using images of various categories, suggesting a dissociation between top-down expectation effects and repetition suppression. Together, our data agree with the hypothesis that adaptation in IT serves to reduce the saliency of recently seen stimuli, highlighting stimuli that differ from recently presented ones.

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Many brain areas of different species show adaptation: their neural response to a stimulus changes after exposure to that stimulus. The sort of adaptation-induced response changes can depend on the area (Weiner, Sayres, Vinberg, & Grill-

Spector, 2010) and can vary from suppression of the response ("repetition suppression") to enhancement. Repetition suppression is ubiquitous in macaque inferior temporal cortex (IT), the end-stage of the ventral visual

Abbreviations: IT, inferior temporal cortex.

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stream. Indeed, several studies showed that the responses of IT neurons usually decrease with stimulus repetition (De Baene & Vogels, 2010; Kaliukhovich & Vogels, 2011, 2012, 2014; Liu, Murray, & Jagadeesh, 2009; McMahan & Olson, 2007; Miller, Li, & Desimone, 1991; Sawamura, Orban, & Vogels, 2006; Vogels, Sary, & Orban, 1995). This repetition suppression (Desimone, 1996) has aroused recent interest because of the widespread use of adaptation paradigms in human fMRI studies (Malach, 2012), especially (but not exclusively) in ventral stream areas, some of which are likely homologs of monkey IT cortex. In fact, a highly influential paper that introduced the fMRI-adaptation technique dealt with the invariance of object representations in human occipito-temporal areas (Grill-Spector et al., 1999). Despite criticisms of the fMRI-adaptation technique to infer the stimulus selectivity or invariance of neurons (Sawamura et al., 2006; Tolia, Keliris, Smirnakis, & Logothetis, 2005), fMRI adaptation studies are still being performed and even interpreted as if the stimulus selectivity of adaptation effects directly reflects the tuning of neurons [for a very recent example see Glezer, Kim, Rule, Jiang, and Riesenhuber (2015)]. Aside from the relevance for interpreting fMRI adaptation data, the changes in neural responses with adaptation show the impact of stimulus history on the neural representation of a stimulus. Given that stimulus history affects perception (Bar & Biederman, 1999; Muller, Schillinger, Do, & Leopold, 2009; Noudoost & Esteky, 2013), a better understanding of adaptation is necessary to gain a deeper insight into the neural mechanisms of perception (Clifford et al. 2007). Despite the theoretical and practical importance of adaptation, the mechanisms underlying adaptation in IT are still poorly understood.

1. Short-term adaptation: paradigm and phenomenology of adaptation effects

In this paper, I will discuss the underlying mechanisms of adaptation in macaque IT, relating these to observations made in single unit recording studies. I will discuss mainly short-term adaptation studies, in which the stimuli are presented for relatively short durations (as in most fMRI-adaptation studies) and without intervening stimuli (unlike in “priming” – related studies). It is well possible that the mechanisms of short-term adaptation differ at least to some extent from those underlying adaptation following long-duration exposure to stimuli or with long time delays with intervening stimuli present in-between the adapter and test stimuli. Thus, the adaptation paradigm that I will discuss here consists of 300–1000 msec presentations of a stimulus, the adapter stimulus, followed by an interstimulus interval of 300–1000 msec, after which a second stimulus is presented, the test stimulus. The test and adapter stimuli can be either identical (“repetition trials”) or different (“alternation trials”; see Fig. 1 for a typical adaptation protocol). The images are presented when the monkeys are fixating a small target. Fixation of the gaze inside a small electronic fixation window (typically 2° on a side) is required for 300–500 msec before and after the stimulus presentations and during the interstimulus interval in order to obtain a juice reward. Trials in which

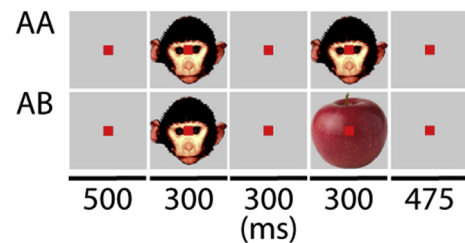


Fig. 1 – A typical short-term adaptation protocol. In this example, two stimuli are shown successively, separated by a 300 msec blank field. Two types of trials are presented to the subject: repetition trials (AA) in which the same stimulus is repeated and alternation trials (AB) in which the two stimuli of a sequence differ. The monkey is required to fixate a target (indicated by the red square, for clarity shown larger than in the actual experiments) during the entire trial. The stimulus presentations are preceded by a baseline fixation interval of 500 msec and followed by a post-stimulus fixation period of 450 msec. A juice reward is given, contingent on successful fixation, at the end of the trial period. Repetition trials and alternation trials consist of different stimuli on different trials, chosen to cause a response in the recorded unit as established in an independent test. The intertrial interval is an order of magnitude longer than the interstimulus interval. In the studies reviewed in this paper, the stimulus duration varied between 250 and 500 msec and the interstimulus interval between 300 and 500 msec.

fixation is broken during the trial (aborted trials) are discarded. Analyses of the eye movements inside the fixation window failed to detect a relationship between eye movements and adaptation effects in IT in all studies we have conducted.

An often ignored issue concerns the visual stimulation condition before the adapter stimulus. In some studies, no stimulus, except for a uniformly illuminated display, is presented in the intertrial interval while in other studies stimuli that are supposed to disadapt the neuron are presented. The latter can vary from sequences of spatially scrambled images [e.g., De Baene and Vogels (2010) – to which IT neurons typically respond poorly (Vogels, 1999)] – to short presentations of full-screen natural images. We do not know whether adaptation effects would differ without these (e.g., as with an empty interstimulus interval). It should be noted though that for some “passive” adaptation mechanisms – such as response fatigue (see below) – the recent stimulus history before the adapter stimulus will impact the response to the adapter and hence test stimuli. In all but a few studies of adaptation in IT, the monkeys were awake during the study and the animals were free to make eye movements during the intertrial interval, implying that the intertrial intervals varied between trials and were constrained only by a lower bound. The intertrial intervals in most studies were at least an order of magnitude longer than the interstimulus interval. In most of our studies, we employed pseudorandomized stimulus presentations in which the adapter stimulus of a trial differed

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