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ERPs Studies of Short- and Long-Term Habituation in Humans: A Systematic Review

Estudios de ERP de Habituación a Corto y Largo Plazo en Humanos: Una Revisión Sistemática

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Habituation is a type of learning that consists of a decrease in the response to a repetitive stimulus. The traditional view is that habituation comprises two processes: a transitory one called short-term habituation (STH), promoted by stimulus presentations at short intervals, and a more durable one called long-term habituation (LTH), promoted by more spaced repetitions. Due to the importance of time in this distinction and in an attempt to elucidate its underlying mechanisms, several studies have sought to relate habituation to brain activity through the analysis of event-related potentials (ERPs). We performed a systematic review of studies on habituation of ERPs in humans using the PRISMA methodology. A total of 175 articles were evaluated for eligibility and 145 were included. Most of the studies focused on short-term effects, demonstrating habituation in a range of ERP components such as P50, P1, N1, P2, N2, and P3. These studies revealed that STH occurs with intervals ranging from 75 ms to 4 s with an optimal of 500 ms, but it does not with intervals greater than 10 s. There are also some studies showing that the P1, N1, P2, N2, and P3 components exhibit LTH with inter-stimulus intervals between 3 and 10 seconds, but the evidence is yet insufficient to establish a secure conclusion with respect to LTH. We propose that future studies should use a wider range of inter-stimulus intervals with tests of both short-and long-term habituation so that the specific neurophysiological components of each type of habituation could be determined.

Keywords: event-related potential, ERPs, short-term habituation, long-term habituation

La habituación es un tipo de aprendizaje que consiste en una disminución en la respuesta a un estímulo repetitivo. La visión tradicional es que la habituación comprende dos procesos: uno transitorio llamado Habituación de Corto Plazo (HCP), promovido por presentaciones de estímulos a intervalos cortos, y uno más duradero llamado Habituación de Largo plazo (HLP), promovido por repeticiones más espaciadas. Debido a la importancia del tiempo en esta distinción y en un intento por elucidar sus mecanismos subyacentes, varios estudios han buscado relacionar la habituación con la actividad cerebral a través de los potenciales relacionados a eventos (PRE). Realizamos una revisión sistemática acerca de la habituación de PREs en humanos utilizando la metodología PRISMA. Evaluamos la elegibilidad de 175 artículos y se incluyeron 145. La mayoría de los estudios se centran en los efectos a corto plazo, donde se demostró habituación en componentes tales como P50, P1, N1, P2, N2, P3. Estos estudios revelan que la HCP ocurre con intervalos entre 75 ms y 4 s, con un óptimo de 500 ms, pero no con intervalos mayores a 10 segundos. Otros estudios han demostrado que los componentes P1, N1, P2, N2 y P3 exhiben HLP con intervalos entre estímulos de 3 a 10 segundos, pero la evidencia aún es insuficiente para establecer una conclusión segura. Proponemos que los estudios futuros deberían utilizar una gama más amplia de intervalos, con pruebas tanto de habituación de corto como de largo plazo, de modo que se puedan determinar los componentes neurofisiológicos específicos de cada tipo de habituación.

Palabras clave: potencial relacionado a eventos, PREs, habituación de corto plazo, habituación de largo plazo

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La correspondencia relativa a este artículo debe ser dirigida a Johanna Kreither, Facultad de Psicología de la Universidad de Talca, Avda. Lircay S/N, Talca, Región del Maule, Chile. Email: jkreither@utalca.cl

Habituation has been experimentally studied since the first half of the 20th century (Harris, 1943; Humphrey, 1933; Prosser & Hunter, 1936) and several of the behavioral regularities have been identified in a wide range of species (Liang et al., 2019; Rankin et al., 2009; Thompson, 2009; Thompson & Spencer, 1966). Specifically, when a stimulus is presented repeatedly there is a decrease in the amplitude response. If this behavioral modification is not due to sensory or motor changes, it is inferred that a basic form of learning, called habituation, has occurred. The behavioral changes involved in habituation are strikingly similar across the entire phylogenetic spectrum, regardless of the complexity of the organism's nervous system. This evidence supports the hypothesis that habituation would be a first filter mechanism, universal to living beings, from which the most complex cognitive processes are deployed (Kepler et al., 2020).

In humans, habituation has been demonstrated in the startle response (e.g., Ornitz & Guthrie, 1989), heart rate and skin conductance (e.g., Gatchel & Lang, 1974), generally triggered by auditory stimuli. Habituation has been observed in the response curves obtained by presenting series of stimuli with a variety of intervals (Askew, 1970; Laming & McKinney, 1990; Rankin & Broster, 1992). Studies in participants with significant neurocognitive disorders have showed "abnormal or atypical" habituation curves (Blackford et al., 2015; Lloyd et al., 2014; McDiarmid et al., 2017), such as autism (Guiraud et al., 2011), fragile X syndrome (Miller et al., 1999), schizophrenia (Geyer & Braff, 1982), depression (Perry et al., 2001), attention deficit syndrome (Lloyd et al., 2014), post-traumatic stress disorder (Kozarić-Kovačić et al., 2011) and panic attack (Ludewig et al., 2005). Reduced habituation is the most reported phenotype in these disorders, although augmented habituation has also been observed (McDiarmid et al., 2017).

A characteristic of habituation that has been object of considerable interest among researchers is the time interval between stimuli or Inter Stimulus Interval (ISI). Overall, the evidence obtained from various species and their response systems, indicates that there is an inverse relationship between the ISI and the degree of habituation (e.g., Broster & Rankin, 1994; Buchwald et al., 1965; Clément et al., 2013; Daniels & Davison, 1998; Davis, 1970a; Gatchel & Lang, 1974; Geer, 1966; Laming & McKinney, 1990; Prosser & Hunter, 1936; von Dincklage et al., 2013). For example, Gatchel and Lang (1974) evaluated the habituation of the skin conductance response in humans to a series of 20 stimuli (tone) in 3 groups of people that differed in the mean ISI (20, 60, and 100 seconds). The results showed greater habituation with the 20 s ISI compared to 60 and 100 s ISIs. Other studies, however, show that the magnitude of the response recovers after a period without further stimulation. This phenomenon has been found in a test known as "retention of habituation" or "spontaneous recovery" (e.g., Beck & Rankin, 1997). Systematic investigations of the startle response in humans and rats (Davis, 1970a, 1970b; Gatchel, 1974; Haerich, 1997) and the escape response in nematodes (Rankin & Broster, 1992) showed that the shorter the duration of the interval between stimuli, the faster the decrease in the response throughout the trials, but the weaker the retention of habituation over time. For example, Gatchel (1974) examined the skin conductance response of human to auditory stimuli, one group received 15 stimuli with 20 s ISI and another group received 15 stimuli with 100 s ISI. Greater habituation was observed in the 20 s group compared to the 100 s ISI. However, greater habituation to the 100 s ISI was obtained in a subsequent session conducted 15 minutes later. These opposite effects of the ISI were explained by the existence of two habituation processes: Short-Term Habituation (STH), transitory and favored by short intervals ranging from 2 to 10 s (Broster & Rankin, 1994; Davis, 1970a, 1970b; Haerich, 1997) and Long-Term Habituation (LTH), more permanent and favored by longer ISIs. In fact, habituation is partially retained if tested from 30 min. to 24 hrs. after the habituation session (Beck & Rankin, 1997; Rankin & Broster, 1992).

In a standard session of habituation consisting of several stimuli repetitions, both short and long-term processes might be developing simultaneously. Thus, the observed habituation at the end of the session might very well reflect a mixture of these two processes. Under this assumption, STH could be observed by presenting a pair of stimuli and examining how the decrease in response to the second of them fades when the interval between them is increased (e.g., Wilson & Groves, 1973). Alternatively, LTH would be evident when observing the response to a stimulus presented after the end of the habituation session (e.g., Lozada et al., 1990; Ornitz & Guthrie, 1989; Prados et al., 2020). Naturally, the habituation curve studied in humans would be the result of a combined effect of both processes, a buildup (LTH) and a dissipative (STH) throughout the session. Unfortunately, most of the research in humans, and particularly those for neurocognitive disorders, was limited to the observation of habituation curves. This approach makes the interpretation of the findings difficult since the curves data do not clarify the precise nature of a deficit. This limitation in the study of the STH and LTH explains why there are so many inconsistencies and gaps in this area (e.g., McDiarmid et al., 2017). In addition, habituation studies in humans only have information at the input (stimulus) and output (response) level, lacking the processing mechanisms that account for the behavioral responses in a habituation session. Thus, as the observation of pure short-term and long-term effects is experimentally dissociated, the question about how these effects interact in a habituation session remains.

An alternative approach to evaluate the mechanisms underlying STH and LTH is to examine the neurobiology of the stimulus-response pathway (Bailey et al., 2015; Castellucci et al., 1970; Rankin & Carew, 1987). The cellular and molecular mechanisms involved in various types of habituations have been studied in invertebrates, such as *Aplysia* (Fischer et al., 2014; Glanzman, 2009), *Caenorhabditis elegans* (Giles & Rankin, 2009; Kindt et al., 2007) and *Drosophila melanogaster* (Engel & Wu, 2009). These studies indicate that while both STH and LTH involve a similar decrease in neurotransmitter release at the level of the synaptic terminal of the sensory neurons onto inter or motor neurons (i.e., a pre-synaptic modification). There are differences on the biochemical processes, such as the dopamine receptors in STH and a protein synthesis in LTH (see McDiarmid et al., 2019).

Despite the evidence from Aplysia, Caenorhabditis elegans, and Drosophila melanogaster (Engel & Wu, 2009; Giles & Rankin, 2009; Glanzman, 2009), very little is known about the neurobiological mechanisms underlying habituation in mammals, particularly in humans (Ramaswami, 2014; Wilson & Linster, 2008). Studies in vertebrates suggest that the mechanisms of habituation are more complex than those described for invertebrates. For example, Randlett et al. (2019) studied the startle response of zebrafish to visual stimulus and found that stimulus latency, duration, and probability exhibited poor correlation with habituation curves. Likewise, research with rodents suggests that LTH might depend on changes outside of the stimulus-response pathway, some of them even located at the cortical level (Cooke et al., 2015; Jordan & Leaton, 1982).

These findings highlight the importance of considering multiple habituation processes, and of the use of tools allowing to measure habituation at the behavioral as well as the neural level, in order to establish spatial and temporal distinction of the habituation processes. In human research, functional or electrophysiological techniques emerge as the most appropriate alternatives. Among these, the event-related potentials (ERPs) technique stands out for its great temporal resolution, and for being a direct measure of cortical neuronal activation.

ERPs are obtained from electroencephalography (EEG) recordings while participants perform a task with a variety of stimuli. Unlike behavioral studies, ERPs provide a continuous measurement of the cortical processing occurring between the stimulus and the response execution. This time window is key to understanding both the stimulus triggered cortical activation, processing, and response selection (e.g., Leonard et al., 2013; Luck, 2014; Luck et al., 2000).

Electroencephalography (EEG) records the cerebral electrical activity consisting of the sum of tiny electric fields produced by assembly of pyramidal neurons located in the cerebral cortex (Luck, 2014). During an experimental EEG recording session, participants are exposed to a sequence of stimuli (events) while voltage changes are recorded at various electrodes located on the scalp. The recording traces are then averaged around the stimulus presentations, obtaining distinctive waveforms representing the average neural response to each stimulus type. The waveforms, known as event-related potentials (ERPs), consisting of several positive and negative deflections occur at specific latencies and represent activation in different stages of cortical processing. The typical result of habituation stimulation in ERP studies is a progressive decrease in the amplitude of some of its components (e.g., P50, P1, N1, P2, N2, P3) which correlate with behavioral habituation (e.g., Butler, 1968; Megela & Teyler, 1979). The most studied ERPs in habituation are the early components N1 and P2, and the late component P3 (according to the temporality classification of Kaiser et al., 2020; e.g., Megela & Teyler, 1979).

In the last 40 years, Robert Barry, and his collaborators (e.g., McDonald & Barry, 2020), inspired by Sokolov's theoretical proposal (1963a, 1963b), have aimed at the search for the best cortical analog of the habituation of the orientation reflex. Their results suggest that the components of the Late Positive Complex (LPC: P3a, P3b, nP3 and SW) have a differential sensitivity to habituation. More specifically nP3 (novelty P3), a subcomponent of P3 between 360-450 ms after the stimulus onset reflects the effects of the loss of novelty due to stimuli repetition (e.g., Barry et al., 2020; Barry, De Blasio et al., 2016; Barry, Steiner et al., 2016; MacDonald & Barry, 2014; Rushby et al., 2005).

ERPs represent a unique opportunity to determine the electrophysiological mechanisms of STH and LTH, and thus complement the behavioral studies of habituation. This review aims to describe the evidence on ERPs for STH and LTH in humans. Specifically, what are the types and features of the ERPs that represent

STH and LTH in humans and the evidence on the role of ISI. We focused on those studies that explicitly manipulated the ISI to evaluate the ERPs habituation.

To do this, we focused our search on 3 habituation protocols traditionally used to evaluate STH and LTH at the behavioral level. The first one called the *s1/s2 procedure* consisting of a 2 stimuli temporal sequence—S1 followed by S2—evaluates whether the smaller response to s2 relates to the ISI (e.g., Whitlow, 1975). Originally, this protocol allows the assessment of STH in its purest state. The second protocol, called *intra-session* evaluates the habituation in response to a repetitive stimulus (e.g., Gatchel & Lang, 1974). The third protocol, called *inter-session* or *habituation retention*, evaluates the response to the habituated stimulus after the intra-session protocol has ended (e.g., Prados et al., 2020). If the stimulus occurs after a considerable time from the end of the intrasession protocol, the reduced response observed can be attributed to LTH in its purest state. If the cortical mechanisms involved in STH and LTH are different, then the behavioral habituation would be expected to correlate with changes in several ERPs. Thus, the response curve obtained with the intra-session protocol, or *intra-session analysis*, is the result of a combined effect of STH (dissipated) and LTH (accumulated) processes throughout the session. The changes in ERPs components with the s1/s2, intra-session and inter-session protocols will provide evidence on the relative contribution of both STH and LTH processes to behavioral habituation.

Method

Search strategy

The literature search was developed according with the PRISMA methodology (Moher et al., 2009), incorporating the use of the Web of Science (WoS) and Google Scholar (GS) databases as a search strategy, with no restriction on the time range used for searching for both search engines. The WoS search was complemented with GS to retrieve the most indirect information, both academic and non-academic (Haddaway et al., 2015). The key words were: “habituation and ERP”. The literature search began in September 2019 and ended in October 2019. For a broader search of the s1/s2 protocol, a literature update was performed between October 2020 and November 2020 using "sensory gating" as keyword. The s1/s2 protocol is typically used to study sensory gating. Thus, the latter search strategy was chosen to gather more studies with the s1/s2 protocol.

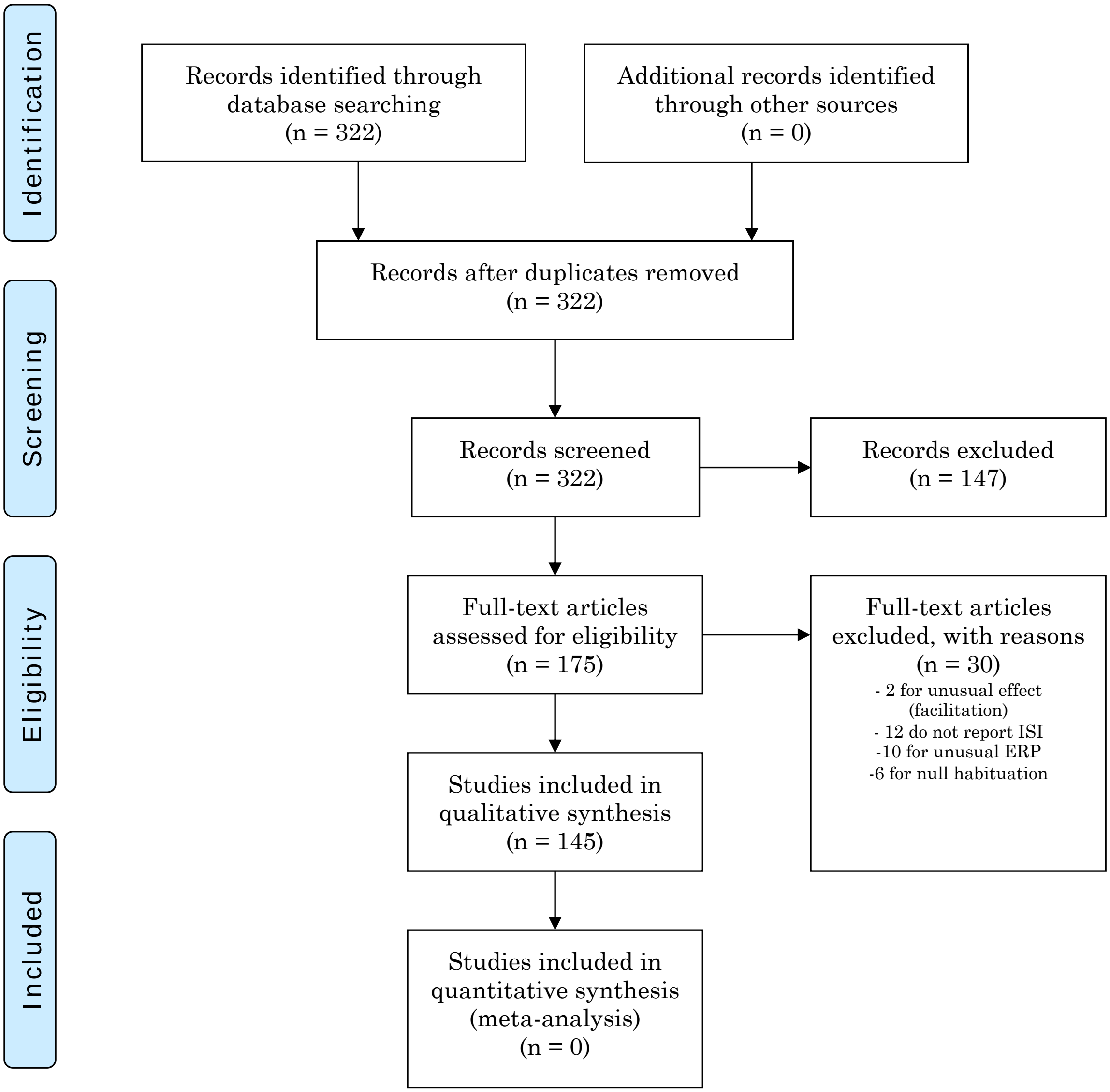
All studies identified were screened and assessed for eligibility. The articles included were in English or Spanish, reported an ISI fixed or variable and showed habituation of at least one ERP component. Studies on clinical samples with a control group were included. We excluded case studies, systematic reviews and meta-analyzes, ERP components that did not have replicability over time (Luck, 2014), and studies which showed an increase or facilitation of the response with short duration ISIs because its poor replicability over time (e.g., Budd & Michie, 1994; Wang et al., 2008). One of the authors of this review was in charge of the data collection and screening process. The included studies were reviewed by two independent reviewers. The systematic review was not registered.

Data extraction

A total of 323 potentially relevant studies were identified (205 records from the search "habituation and ERP" and 117 records from the search "sensory gating"). Figure 1 shows the search process overview and results included in each search strategy. Finally, the bibliographic search resulted in the inclusion of 145 studies.

Figure 1

Flow Chart showing the Literature Selection Process according to PRISMA Guidelines (Moher et al., 2009).



Results

The reviewed studies on STH and LTH in humans evaluated exogenous sensory components triggered by stimulus presentation and endogenous components that reflect task dependent neuronal processes. Table 1 shows the main ERPs components reported in the reviewed studies, organized according to the stimulus type (i.e., auditory, visual, tactile, etc.) and habituation protocol (s1/2, intra-session, and inter-session). The numbers inside the table represent the studies reviewed. In the following paragraph, we present an overview of the ERP components.

Table 1

Components of ERPs examined in Human Habituation Studies according to Stimulation for each Protocol

		Evidence of habituation											
Pt	St	P50	P1	N1	P2	N2	P3	P3a	P3b	nP3	SW	LPC	N4
S1/S2	Auditive	11,12,14,15,19 20-22,30,35,36 39,42,4348,49 50,52,54-62 65-70,77-79 81-83,86,90 93,113,115-117 119,120,122,123 125,129,135 140,142,143	53,80 123	10,13,31,46,47 65-68,80-82 117,119,120,125	10,31,46,47 65-68,81,82 117,119,124							81	
	Tactile	4,5,29,81	26	24-28,81	81		26					81	
	Visual		45			45							
Intra-session	Auditive	99,100	84,85	3,6,9,10,16-18 23,32,33,38,41 44,73,76,84,85 87,91,94,98,99 100,102-105 109,111,114 118,130,138 141	9,17,18,33,41 44,73,76,84,85 87,91,94,97,98 101-105,109-111	23,76,84 85,94,105 110,111,126	9,51,76,92 105,118,126 139,145	71,108 112	8,72,74 108	7,8,71,72,74 107,108	71,72,74,108 144	106,108,121	109
	Tactile		2	40,44	34,40,44, 124,128	1,34,124,128	1,134						1
	Visual		63	44,63,75 96,127,131	44,63,75 131,127	63	37,63,75 136,137		127				
Inter-session	Auditive		88	88,89,95,133	88,89,95,133	88	95						
	Tactile				64	64							
	Visual			132	132								

Note. The numbers inside the table represent the studies reviewed. [1] Akın, G., & Güdücü, Ç. (2019). [2] Angel et al. (1985).[3] Annanmaki et al. (2017). [4] Bak et al. (2011). [5] Bak et al. (2014). [6] Barry et al. (1992). [7] Barry et al. (2011).[8] Barry et al. (2020). [9] Bourbon et al., (1987). [10] Boutros et al. (2006). [11] Boutros, Overall, et al. (1991). [12] Boutros, Zouridakis et al. (1991). [13] Brockhaus-Dumke et al. (2008). [14] Brinkmeyer et al. (2011). [15] Broyd et al. (2013). [16] Budd et al. (1998). [17] Butler (1968). [18] Butler et al. (1969). [19] Cabranes et al. (2013). [20] Cardenas et al. (1993). [21] Cardenas et al. (1997). [22] Carrillo-De-La-Peña et al. (2015). [23] Castrén et al. (2003). [24] Chang et al. (2012). [25] Chan & Davenport (2008). [26] Chan & Davenport (2009). [27] Chan, Cheng, Hsu et al. (2015). [28] Chan, Cheng & von Leupoldt (2015). [29] Chan et al. (2012). [30] Chen et al. (2011). [31] Chien et al. (2019). [32] Clearwater et al. (2008). [33] Davis et al. (1966). [34] de Tommaso et al. (2015). [35] Dolu et al. (2001). [36] Edgar et al. (2003). [37] Elton et al. (1983). [38] Ethridge et al. (2016). [39] Fein et al. (1994). [40] Fruhstorfer (1971). [41] Fruhstorfer et al. (1970). [42] Ghisolfi et al. (2006). [43] Ghisolfi et al. (2004). [44] Gjerdingen & Tomsic (1970). [45] Gjini et al. (2008). [46] Gmehlin et al. (2011). [47] Gooding et al. (2013). [48] Gumenyuk et al. (2013). [49] Hall et al. (2011). [50] Hazlett et al. (2015). [51] Hirano et al. (1996). [52] Holstein et al. (2013). [53] Hunter et al. (2008). [54] Hunter et al. (2015). [55] Hutchison et al. (2013). [56] Jessen et al. (2001). [57] Johannesen et al. (2008). [58] Jin et al. (1998). [59] Karkal et al. (2018). [60] Kathmann & Engel (1990). [61] Lamberti et al. (1993). [62] Lemvigh et al. (2020). [63] Lehtonen (1973). [64] Lev et al. (2012). [65] Lijffijt et al. (2012). [66] Lijffijt, Lane et al. (2009). [67] Lijffijt, Moeller, Boutros, Burroughs et al. (2009). [68] Lijffijt, Moeller, Boutros, Steinberg et al. (2009). [69] Luo et al. (2019). [70] Lu et al. (2007). [71] MacDonald & Barry (2014). [72] MacDonald et al. (2015). [73] Maclean et al. (1975). [74] MacDonald & Barry (2017). [75] Megela et al. (1977). [76] Megela & Teyler (1979). [77] Micoulaud-Franchi et al. (2012). [78] Micoulaud-Franchi et al. (2014). [79] Micoulaud-Franchi et al. (2015). [80] Miller et al. (2018). [81] Montoya et al. (2006). [82] Müller et al. (2001). [83] Nagamoto et al. (1989). [84] Nelson & Lassman (1968). [85] Nelson & Lassman (1973). [86] Neylan et al. (1999). [87] Öhmant et al. (1972). [88] Öhman & Lader (1972). [89] Öhman et al. (1975). [90] Oranje et al. (2013). [91] Özesmio et al. (2000). [92] Pan et al. (2000). [93] Park et al. (2015). [94] Prosser et al. (1981). [95] Putnam & Roth (1990). [96] Regtvoort et al. (2006). [97] Ritter et al. (1968). [98] Rosburg & Sörös (2016). [99] Rosburg et al. (2006). [100] Rosburg et al. (2004). [101] Rosburg et al. (2007). [102] Rosburg et al. (2010). [103] Roth et al. (1976). [104] Roth & Kopell (1969). [105] Roth & Kopell (1973). [106] Rushby & Barry (2007). [107] Rushby & Barry (2009). [108] Rushby et al. (2005). [109] Rust (1977). [110] Salamy & McKean (1977). [111] Sambeth, Maes, Quiroga et al. (2004). [112] Sambeth, Maes, Quiroga, Van Rijn et al. (2004). [113] Sánchez-Morla et al. (2013). [114] Schoenen et al. (1995). [115] Shaikh et al. (2015). [116] Shan et al. (2013). [117] Shen et al. (2020). [118] Simons et al. (1987). [119] Sklar & Nixon (2014). [120] Smith et al. (2010). [121] Steiner & Barry (2011). [122] Tecellioğlu et al. (2015). [123] Teo et al. (1997). [124] Torta et al. (2012). [125] Van Tricht et al. (2015). [126] Van Sweden et al. (1994). [127] Verbaten et al. (1986). [128] Vossen et al. (2011). [129] Waldo et al. (1995). [130] Walpurger et al. (2003). [131] Wastell & Kleinman (1980a). [132] Wastell & Kleinman (1980b). [133] Weber (1970). [134] Webster et al. (2004). [135] Williams et al. (2011). [136] Woestenburg et al. (1981). [137] Woestenburg et al. (1983). [138] Woods & Elmasian (1986). [139] Woods et al. (1980). [140] Yadon et al. (2009). [141] Yagcioglu & Ungan (2008). [142] Yee & White (2001). [143] Zhu et al. (2017). [144] Zimmer & Demmel (2000). [145] Zimmer (2002). Pt = Protocols. St = Stimuli.

As shown in Table 1, most studies (*n* = 123) reported habituation in ERP components evoked by auditory stimulus (e.g., clicks and tones; MacDonald & Barry, 2017; Shen et al., 2020), such as the P50, a positive peak between 40 and 90 ms after stimulus (Chang et al., 2011) and long latency components such as N1, P1, and P2 (Luck, 2014; Pratt, 2012). The long-latency components are strongly influenced by high-level processes, such as attention and arousal (Luck, 2014). Specifically, N1 has several subcomponents: 1) a frontocentral that peaks around 75 ms and it is likely generated in the auditory cortex on the dorsal surface of the temporal lobes, 2) a vertex of the maximum potential of unknown origin that peaks around 100 ms, and 3) a component that peaks around 150 ms, likely generated in the superior temporal gyrus (Luck, 2014; e.g., Budd et al., 1998). In addition, some studies report habituation of N2, a central negativity reaching a peak approximately 250 ms after the onset of the stimulus (Carretié et al., 2004). Finally, some studies report habituation of the P3 component, a large centroparietal deviation with a peak of approximately 300 ms after stimulus onset, which varies directly with stimulus certainty (Barry, Steiner, et al., 2016; Polich, 2012). It has been proposed that P3 represents a "Late Positive Complex" (LPC) consisting of an early frontocentral P3a (220-280 ms), followed by a parietal P3b (310-380 ms) and a late slow-wave (SW), and the third subcomponent of P3, late frontal (360- 450 ms), called Novelty P3 (nP3) (Barry et al., 2020; MacDonald & Barry, 2020).

Habituation was also reported for ERP components evoked by visual stimuli such as brief flashes (e.g., Lehtonen, 1973), checkerboard patterns (e.g., Wastell & Kleinman, 1980a) and word pictures or geometric figures. For visual stimuli, P1 is larger at the occipital electrode sites, starts 60 to 90 ms after the stimulus onset and peaks between 100 and 130 ms; N1 has an early subcomponent (100 to 150 ms) and two later subcomponents: 1) it arises from the parietal cortex and 2) it arises from the occipital cortex between 150 to 200 ms after the stimulus onset; and P2 that follows N1 at the anterior and central scalp sites. Habituation on ERP components from cortical somatosensory areas has also been reported with somatosensory stimuli (Pratt, 2012) by electrical simulation (e.g., Bak et al., 2014), air puff (e.g., Akın & Güdücü, 2019) and heat pulses (e.g., de Tommaso et al., 2015; Lev et al., 2012). In summary, habituation has been shown in ERP components P50, N1, P1, P2, P3, and N4.

The ERPs components that show habituation also correlate with other mental processes which could also impact on habituation (more on this will be described in the discussion). Specifically, P50 correlates with arousal levels (de Lugt et al., 1996), with sensory filtering or the inhibition of irrelevant stimuli (Jones et al., 2016), and a P50 reduced habituation is observed in various disorders such as autism, major depression, schizophrenia, and Parkison's disease (e.g., Buchwald et al., 1992; Franks et al., 1983; Kisley et al., 2003; Teo et al., 1998; respectively). N1 correlates with spatial attention, orientation response, perceptual matching with a previously experienced stimuli and processing of unexpected stimuli (Luck et al., 1990; Sur & Sinha, 2009). Besides, P1 correlates with spatial attention and gating to stimulus location (Luck et al., 2000), P2 correlates with attentional processing of visual stimuli, and N2 correlates with processing of deviant stimuli and stimulus classification (Sur & Sinha, 2009). Finally, P3 correlates with stimuli processing and task relevance evaluation (Cortese, 2012), working memory update, event categorization, attentional resources allocation, and attention reorientation (Polich, 2007).

The studies comparing the role of ISI in human's STH and LTH (*n* = 25) are relevant. Table 2 shows the habituation studies according to the ERP experimental setting s1/s2, intra-session and inter-session, and the ISI values (see Figure 2). The color rectangle indicates the ISI that exhibited significant habituation (black) or null (gray). A synthesis of the main features and experimental findings for each stimulation protocol is detailed below.

Table 2

Intervals between Stimuli examined in Habituation Studies according to Stimulation and ERPs for each Protocol

Pt	Studies	St	ERPs	Intervals between stimuli (ms)																													
				775	1150	2200	2250	2260	3300	4482	5500	6600	6630	7750	8800	9900	9982	11000	11200	11250	11800	11982	22000	33000	33982	44000	55000	66000	77000	77982	88000	110000	116000
S1/S2	Nagamoto et al. (1989)	C	P50	■	■						■																						
	Cardenas et al. (1997)	C	P50					■			■							▨					▨										
	Teo et al. (1997)	C	P1				■				■							▨															
	Dolu et al. (2001)	C	P50				■				■			▨				▨															
	Bak et al. (2011)	EP	P50				■				■							▨															
	Bak et al. (2014)	EP	P50								■							▨															
Intra-session	Davis et al. (1966)	T	N1, P2								■							■						■		▨	▨	▨	▨				
	Nelson & Lassman (1968)	T	P1, N1, P2, N2				■				■							■					■	■		■		▨			▨	▨	
	Ritter et al. (1968)	T	P2																				■									▨	
	Roth & Kopell (1969)	T	N1, P2								■							■					■										
	Nelson & Lassman (1973)	T	P1, N1, P2, N2							■							■					■			▨					▨			
	Roth et al. (1976)	T	N1, P2											■									■	▨									
	Woods et al. (1980)	T	P3						■			■				▨			▨														
	Woods & Elmasian (1986)	T, SS	N1			■									■																		
	Bourbon et al. (1987)	T	N1, P2, P3										■							■													
	Budd et al. (1998)	T	N1															■						■								▨	

(continues)

Table 2 (Conclusion)

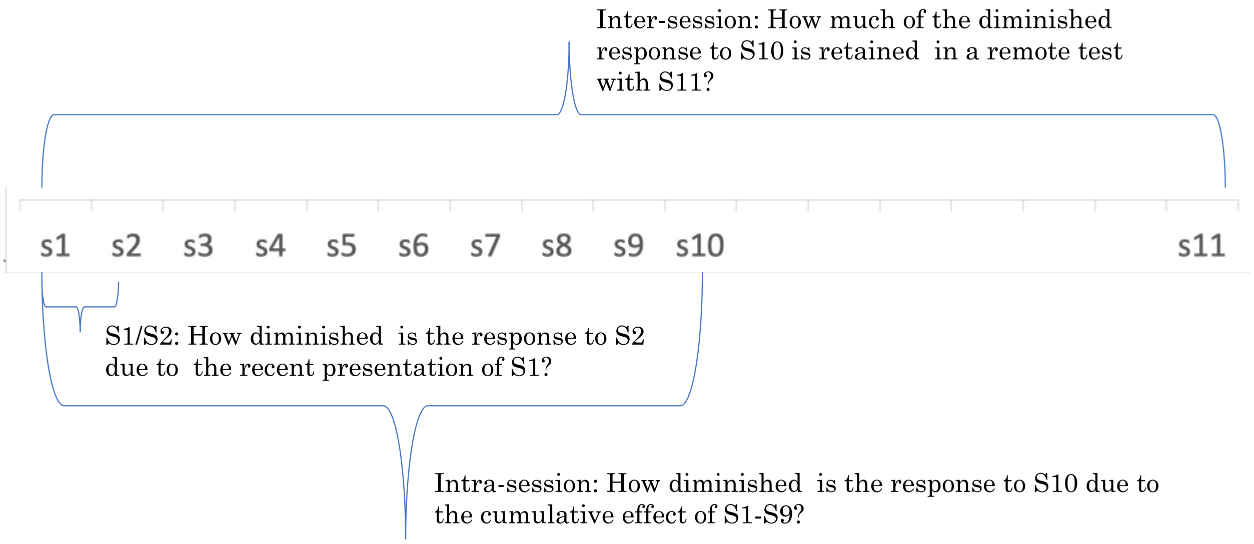
Intervals between Stimuli examined in Habituation Studies according to Stimulation and ERPs for each Protocol

Pt	Studies	St	ERPs	Intervals between stimuli (ms)																													
				775	1150	2200	2250	2260	3300	4482	5500	6600	6630	7750	8800	9900	9982	11000	11200	11250	11800	11982	22000	33000	33982	44000	55000	66000	77000	77982	88000	110000	116000
Intra-session	Rosburg et al. (2010)	T	N1, P2									■							■		■												
	Fruhstorfer et al. (1970)	C	N1, P2															■						■									
	Lehtonen (1973)	F	N1, N2, N3, P1, P2, P3								■							▒					▒	▒		▒	▒	▒					
	Wastell & Kleinman (1980a)	IC	N1, P2								■							■					■	■									
	Angel et al. (1985)	Tc(P)	P1								■							■					■			■					▒		▒
	Akın & Güdücü (2019)	Tc(A)	N2, P3, N4																				■			■					▒		
	Gjerdingen & Tomsic (1970)	T, EP, V, F	N1, P2								■							■					▒				▒					▒	
Inter-session	Öhman & Lader (1972)	C	P1, N1, P2, N2																					■								■	
	Öhman et al. (1975)	C	N1, P2																					■								■	

Note. In each stimulation protocol, the studies are sorted out according to the stimulation (in the order of auditory, visual, and tactile). The black cells indicate the intervals with which habituation was reported and the gray cells mark the examined intervals with which null habituation was obtained. Pt = Protocols. St = Stimuli. C = Clicks. EP = Electrical Pulses. T = Tones. SS = Speech Sounds. F = Flashes. IC = Illuminated Chessboard. V = Vibration. Tc(P) = Tactile (Pressure). Tc(A) = Tactile (Air).

Figure 2

Intra and Inter-Session Squamae



S1/S2 protocol

Table 2 upper panel shows the "S1/S2" protocol (*n* = 6) used to evaluate the filtering of redundant sensory stimuli, or "sensory gating", in a control population and its alterations in a population with specific disorders (schizophrenia and Parkinson, e.g., Nagamoto, et al., 1989; Teo et al., 1997, respectively), and their brain correlates (e.g., Bak et al., 2011). The "S1/S2" protocol, where a trial consists of two identical stimuli with ISIs of 500 ms and a 10 s time interval between sessions. The second ERP size, relative to the first, indicates the response recovery extent which indicates the neuronal reserve available to respond. The amplitude of the positive component P50 to the second stimulus (S2) is reduced compared to the one evoked by S1. Specifically, S1 excites a set of sensory neurons generating P50, and simultaneously activates a set of interneurons that inhibit the excitatory response to S2 (Anokhin et al., 2007). This inhibition is evidenced by the difference in the response amplitude to S2 and S1 or by a ratio consisting of the amplitude of S2 divided by the S1 amplitude; less common is the use of a habituation percentage ((1-S2 / S1) x 100; e.g., Teo et al., 1997).

As shown in Table 2, the studies with the S1/S2 protocol used auditory stimulation (*n* = 4) with ISIs of 500 ms. Robust evidence shows a P50 suppression with ISIs equal to, or less than 500 ms (e.g., Cardenas et al., 1997, see the black rectangles in Table 2). With longer intervals such as 1 or 2 s, no reduction of S2 was reported (e.g., Dolu et al., 2001, gray cells in Table 2).

Regarding S1/S2 protocol brain correlates, higher activity in the hippocampus and claustrum was observed with response reduction, which suggests that these brain areas are involved in the P50 suppression (Bak et al., 2011, 2014). It is common to find a poor response suppression in certain disorders (Nagamoto et al., 1989; Teo et al., 1997), that account for alterations in sensory processing; although there is suppression evidence in patients with schizophrenia at very short intervals such as 75 ms (Nagamoto et al., 1989).

Intra-session protocol

Table 2 central panel shows the studies that used the intra-session protocol (*n* = 17). Most of the studies (*n* = 13) use auditory stimuli of short duration (≤ 300 ms) and a few used visual and tactile stimuli (*n* = 4).

Regarding the ISI effect, Gjerdingen and Tomsic (1970) found out that the ISI function with ERP amplitude is similar for tactile and auditory stimuli. However, visual stimuli resulted in a less pronounced slope to 1 and 2 s ISIs, relative to the other sensory modalities.

Short-term habituation occurs for components between 100 and 300 ms and the N1 component is particularly sensitive to ISI (Callaway, 1973; Davis et al., 1966). A negative relationship between N1 amplitude and ISI was demonstrated (e.g., Davis et al., 1966; Nelson & Lassman, 1968; Woods et al., 1980) varying according to the stimulus intensity (Nelson & Lassman, 1973). Davis et al. (1966) showed a negatively relationship between the N1-P2 amplitude and ISI. The N1-P2 maximum amplitude was obtained with ISIs between 6 and 10 s. For regular ISIs, the response amplitude is approximately 50 % for 3 s, 25 % for 1 s, and 17 % for 0.5 s. The magnitude of the evoked vertex response (N1-P2 peak-to-peak) is a linear function of the logarithm of ISI from 0.5 s to 10 s (Nelson & Lassman, 1968).

In summary, the habituation of the response is faster and greater for frequent stimuli (Akın & Güdücü, 2019; Angel et al., 1985; Bourbon et al., 1987; Budd et al., 1998; Davis et al., 1966; Fruhstorfer et al., 1970; Gjerdingen & Tomsic, 1970; Lehtonen, 1973; Nelson & Lassman, 1968, 1973; Ritter et al., 1968; Rosburg et al., 2010; Roth & Kopell, 1969; Roth et al., 1976; Wastell & Kleinman, 1980a; Woods & Elmasian, 1986; Woods et al., 1980). As shown in Table 2, a wide range of ISIs have been explored with the intra-session protocol. The findings suggest a decrease in the ERP component amplitude with ISIs between 200 and 4000 ms (black in the Table 2) for N1, P1, N2, P2, P3, N3 and N4 components. Whereas for ISIs greater than 4 s no habituation was reported (gray in Table 2).

Inter-session protocol

As shown in tables 1 and 2, the intra-session protocol is used in most of the ERP studies in humans. Unfortunately, the inter-session protocol, together with its contribution from mnemic phenomena, have not been thoroughly applied.

As seen in the lower panel of Table 2, we identified only a couple of habituation studies with an inter-session stimulation protocol. These studies were characterized by presenting auditory stimuli such as very short duration clicks (1 ms) at moderate intensity (70 dB). The ERPs evaluated were P1, N1, P2, N2. As can be seen in Table 2, only two intervals between stimuli, 3 s and 10 s, have been evaluated, and habituation has been reported with both (see black cells).

Öhman et al. (1975) presented click trains and evaluated the effect of the interval between stimulus trains on auditory event related potentials (N1-P2). They used 20 trains of five click stimuli each, one ms long. The average time between these trains (inter-session) ranged randomly from 24 to 36 s. The ISI for each train was three or 10 s. For intra-session comparisons, the results showed that the N1-P2 component amplitude decreased exponentially within the stimulus train when a regular three-seconds ISI was used. With an irregular ISI of three seconds, the change in amplitude is lower while ten seconds the amplitude remains stable for both regular and irregular intervals. These observed changes were concomitant for ERPs and reaction times within a stimulus train.

On the other hand, in the case of the ERPs average between trains (inter-session), the ISI regularity was not critical since similar long-term changes were found for the regular and irregular three and ten second stimulation in the ISI regarding the ERPs amplitude and latency and their reaction times. However, the relationship between ISI and the habituation rate is not always direct. For example, when people focus their attention on stimuli, instead of receiving them "passively", a steeper habituation slope for longer ISIs (10 s intra-session) than short (3 s intra-session) is observed (Öhman & Lader, 1972).

Discussion

The habituation temporal course requires further study at theoretical and basic levels. The focus of this review assumed that in a standard repeated stimulation habituation protocol, i.e within a train of stimuli, both transient and permanent processes are operating simultaneously. According to the behavioral and neurobiological evidence from non-humans, short and long-term processes are based on different mechanisms (McDiarmid, et al., 2019). The outcome of the present review indicates the literature on human habituation of ERP partially agrees with this view of habituation, but also that the critical research has still to be done.

This review indicates that the human ERPs components evaluated in STH and LTH protocols triggered by auditory stimuli consist of both early (e.g., P50, P1) and late (e.g., P3) components. Moreover, except for the P50 observed with the s1/s2 protocol, there are no protocol specific components. However, the ERPs observed in human STH and LTH protocols (e.g., N1, P1 and P3) are modulated by complex cognitive processes and physiological factors that may also contribute to ERPs amplitude reduction. For example, the P50 decrease observed in response to S2 relative to S1 might result from ignoring irrelevant/repetitive stimuli. This is consistent with a smaller P50 reduction in a population with attentional disorders (e.g., schizophrenia, Nagamoto et al., 1989). Furthermore, the sensitivity of N1 to ISI has been interpreted as a recovery period for N1 neural generators (Budd et al., 1998; Callaway, 1973; Nelson & Lassman, 1968, 1973). Accordingly, there is no ERP amplitude reduction was observed for very long ISIs (10 s; Budd et al., 1998; Ritter et al. 1968) and is no gradual ERP amplitude reduction for ISIs of any length (the maximum decrease is reached in the second trial, e.g., Rosburg et al., 2010; Rosburg & Sörös, 2016). Thus, it is essential to determine if a response reduction is unequivocally as accounted for habituation. Specifically, it should be verified if the protocol satisfies the habituation features described by Thompson and Spencer (1966) and Rankin et al. (2009) that distinguish habituation from alternative processes, which are described below in the experimental design considerations. This is a critical issue (Roemer et al., 1984; Rosburg & Sörös, 2016) that has been ignored in most studies reviewed, except the ERPs studies that used standardized ERP and behavioral protocols (Barry et al., 2020).

Regarding the studies that explicitly manipulated the ISI, the S1/S2 studies indicate that the function that relates the response level to S2, as a function of the ISI, appears to be linear and that its optimal interval is $\leq$ 500 ms. In addition, we explored whether it might covariate with the magnitude of intra-session habituation obtained in a short-term habituation protocol with multiple stimulus presentations. The results show that the range of optimal intervals to obtain intra-session habituation is much wider (between 200 to 4000 ms) than those necessary to obtain a S1/S2 effect. Although there was no direct comparison between these two protocols of habituation, the variability of ISI that triggered intra-session habituation suggests that it might be, in part, based on LTH process.

In summary, the evidence suggests that stimuli repetition leads to a transient reduction of some sensory components (e.g., N1) that correlate negatively with the time interval between stimuli; and that in each protocol (S1/S2, intra-session or inter-session) there is an optimal time interval for habituation. Besides, the evidence suggests no correlation between the habituation in the S1/S2 protocol and intra-session protocol, the latter reaching greater habituation with longer intervals. However, no study has focused on comparing the effects of the time interval between stimuli on both protocols. Furthermore, given the few ERP studies with the inter-session protocol, there is no evidence to conclude that the lack of correlation between S1/S2 and intra-session effects is due to a long-term habituation process.

Because the evidence reviewed is not conclusive, we outline four issues for the design of ERP experiments that will reveal the contribution of short and long-term processes to habituation. First, designs should consider a wide range of intervals between stimulus repetitions in the order of seconds (e.g., 2, 4, 8, 16, 32 and 64 seconds) and hours between sessions of repetition of stimuli (e.g., 24 hours), to determine the function that relates habituation to stimuli time interval. Second, to distinguish habituation from other processes, such as sensory adaptation or motor fatigue, the response decrease should include: (a) a generalization/specificity test by examining the response to a novel stimulus, (b) dishabituation by evaluating the response to the habituated stimulus after a distractor and (c) spontaneous recovery by evaluating the response after a time without stimulation (McDiarmid et al., 2017; Rankin et al., 2009).

Third, in order to validate the ISI/ERPs function that involves STH and LTH processes, the experimental design should include at least one behavioral measure meeting the main characteristics of habituation, such as an exponential decrease in the response that is specific to the stimulus (e.g., skin conductance, MacDonald & Barry, 2020). Fourth, the experimental design should include the nP3 component evaluation that fulfills the main features of habituation. Following Barry and his collaborators (Barry et al., 2020), the experimental design should include a novel stimulus after the habituation session, the trial-by-trial analysis of the response, and a principal component analysis (PCA) technique (Dien, 2010, 2012) to extract the LPC components (i.e., P3a, P3b, nP3 y SW).

The consideration of the all the aforementioned factors for experimental design will allow elucidate the contribution of the short and long-term mechanisms that underlie this form of learning in order to study human habituation.

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