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Additional Information

Highlights

- No differences with age were identified in embodiment or its constructs
- No differences with age were identified in proprioceptive drift
- No differences with age were identified in skin conductance or temperature

Abstract

The Rubber Hand Illusion (RHI) is a perceptual illusion that enables integration of artificial limbs into the body representation through combined multisensory integration. Most previous studies investigating the RHI have involved young healthy adults within a very narrow age range (typically 20-30 years old). The purpose of this paper was to determine the influence of age on the RHI. The RHI was performed on 93 healthy adults classified into three groups of age (20-35 years old, N=41; 36-60 years old, N=28; and 61-80 years old, N=24), and its effects were measured with subjective (Embodiment of Rubber Hand Questionnaire), behavioral (proprioceptive drift), and physiological (changes in skin temperature and conductance) measures. There were neither significant differences among groups in any response, nor significant covariability or correlation between age and other measures (but for skin temperature), which suggests that the RHI elicits similar responses across different age groups in the adult phase.

Subjective, behavioral, and physiological responses to the rubber hand illusion do not vary with age in the adult phase

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Abstract

The Rubber Hand Illusion (RHI) is a perceptual illusion that enables integration of artificial limbs into the body representation through combined multisensory integration. Most previous studies investigating the RHI have involved young healthy adults within a very narrow age range (typically 20-30 years old). The purpose of this paper was to determine the influence of age on the RHI. The RHI was performed on 93 healthy adults classified into three groups of age (20-35 years old, N=41; 36-60 years old, N=28; and 61-80 years old, N=24), and its effects were measured with subjective (Embodiment of Rubber Hand Questionnaire), behavioral (proprioceptive drift), and physiological (changes in skin temperature and conductance) measures. There were neither significant differences among groups in any response, nor significant covariability or correlation between age and other measures (but for skin temperature), which suggests that the RHI elicits similar responses across different age groups in the adult phase.

Keywords: embodiment; body-ownership; rubber hand illusion; multisensory integration; aging; skin conductance; skin temperature.

1. Introduction

The Rubber Hand Illusion (RHI) is a paradigmatic experiment that promotes the representation of an external limb within the body schema of a participant, a mechanism referred to as embodiment (De Vignemont, 2011), through synchronous visuotactile stimulation of a participant's real limb (hidden from sight) and the external one (Botvinick & Cohen, 1998). The RHI has been extensively used to manipulate and investigate how the brain integrates afferent multisensory information (touch, vision, and proprioception) to configure a mental representation of the body parts and reachable (peripersonal) space. All existing literature involving healthy participants provides evidence that the body schema is continuously updated (Armel & Ramachandran, 2003; Holle, McLatchie, Maurer, & Ward, 2011; Kalckert & Ehrsson, 2014; Petkova & Ehrsson, 2009) to ready the body for forthcoming movements (Rosenbaum, 2010). This mechanism appears to be not only confirmed but also enhanced after physiopathological changes in the brain (Ding et al., 2017; Llorens et al., 2017; Schmalzl, Kalckert, Ragnö, & Ehrsson, 2014).

As in some neurological pathologies, there is substantial consensus regarding the deterioration of sensory processes with age; for example, in visual acuity (Cerella, 1985; Spear, 1993), motor coordination (Bullock-Saxton, Wong, & Hogan, 2001), auditory perception (Alain, Ogawa, & Woods, 1996), and proprioception (Skinner, Barrack, & Cook, 1984). Moreover, age-related neurophysiological changes have been reported both in localized brain areas and distributed brain networks (Reuter, Behrens, & Zschorlich, 2015; Siman-Tov et al., 2016). Although aging and its derived effects could provide an interesting framework to investigate the embodiment mechanisms, the literature is scant.

The few existing reports on age-related effects in embodiment have evaluated

subjective and behavioral responses using ad-hoc questionnaires and the proprioceptive drift, the spatial incongruence between the perceived location of a limb and its actual location, respectively. A study that compared these two responses to the RHI in three groups of children with different ages (4 to 5, 6 to 7, and 8 to 9 years old) and a group of young adults (mean age 23.9 years old) reported comparable sense of embodiment in all the groups but increased proprioceptive drift in children (Cowie, Makin, & Bremner, 2013), which was hypothesized to be promoted by developmental differences in the brain processes that underlie body-ownership (Bremner, Hill, Pratt, Rigato, & Spence, 2013; Cowie et al., 2013). Another study that involved young adults with a small age range (17 to 24 years old) examined different conditions of movement (active, passive, and asynchronous) during the RHI and also reported no effect of age in the embodiment elicited during the RHI (Dummer, Picot-Annand, Neal, & Moore, 2009). In contrast, the responses of participants in the range of 20 to 60 years old to a modified version of the RHI, where the rubber hand was replaced by a real-time video of the real hand being stroked displayed on a screen, indicated decreased elicited embodiment and increased proprioceptive drift with age (Graham, Martin-Iverson, Holmes, & Waters, 2015). Another study evaluated age-related differences in a group of young adults (17 to 38 years old) during the enfacement illusion, an experiment similar to the RHI. In which a participant's face is stroked in synchrony with a pre-recorded video that shows other individuals being analogously stroked (Tajadura-Jiménez, Longo, Coleman, & Tsakiris, 2012). In line with the previous study, the authors reported that younger participants experienced higher embodiment and suggested that the plasticity of self-face representations reduces with age. Thus, existing reports provide an interesting base of study; however, the absence of studies that involve wider age ranges, comparable controlled conditions, and physiological correlates limit the extrapolation of the

preliminary results.

We hypothesized that age-related changes would limit the plasticity of the body-schema reconfiguration, thus restricting the effects of the RHI, and it would be reflected by a decrease in the elicited sense of embodiment, and in behavioral and physiological responses. Therefore, the objective of this study was to investigate the subjective, behavioral, and physiological responses during the RHI in healthy adults at different ages.

2. Methods

2.1. *Participants*

Healthy adults from 20 to 80 years were recruited from the student body, staff, and relatives of three different universities (Universitat de Valencia, Universitat Politècnica de València, and Universitat Jaume I) and a medical center (Servicio de Neurorehabilitación y Daño Cerebral de los Hospitales NISA). Ninety-three volunteers (40 men) agreed to participate in the study. The participants were divided into three groups according to their age: early adulthood, from 20 to 35 years old, $N=41$, mean age=26.83 (SD=4.29); midlife, from 36 to 60 years old, $N=28$, mean age=49.43 (SD=7.67); and mature adulthood, from 61 to 80 years old, $N=24$, mean age=67.54 (SD=5.29). All participants provided written informed consent. Ethical approval was obtained from Universitat de València.

2.2. *Procedure*

The experiment was conducted by two experimenters in three quiet rooms free of distractors that were arranged in the same locations of recruitment. The participants, who were blind to the purpose of the study, were briefly introduced to the experiment and were equipped with a wearable wireless armband, the Q-sensor (Affectiva®, Waltham, MA, USA), which recorded the skin temperature and conductance during the entire

experiment. The participants sat on one side of the table in a comfortable position with both arms resting on the table and palms facing downward; they were instructed to relax and maintain the position for 10 minutes for temperature and skin conductance stabilization. A movable wooden vertical board (50x40x4 cm) was placed in front of the participants' left or right shoulder depending on whether they were right or left-handed, respectively. This shoulder was also covered with a piece of black cloth to avoid direct line-of-sight of the participants with their own non-dominant hand. After the acclimation time, a sex-matched left or right rubber hand was placed in the other side of the frame at 15 cm to the participant's real hand (measured between index fingers) (Aimola Davies & White, 2013; M. P M Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Llorens et al., 2017) and 5.5 cm of the wooden frame. The participants were instructed to stare at the rubber hand, and the experiment was initiated. The fingers and the dorsum of the real and rubber hands were synchronously stroked with two identical small brushes. Strokes of different lengths were provided in a proximal to distal direction at approximately 1 Hz with an unpredictable origin (Marjolein P M Kammers, Rose, & Haggard, 2011; Llorens et al., 2017; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Rohde, Wold, Karnath, & Ernst, 2013). After two minutes, the stimulation was terminated, and the rubber hand was smashed with a hammer, which was hidden until this point.

2.3. Outcome measures

Subjective, behavioral, and physiological responses to the experiment were collected. The subjective assessment of embodiment was conducted after the experiment using the Embodiment of Rubber Hand Questionnaire (ERHQ) (Longo et al., 2008). The behavioral responses were measured with the proprioceptive drift (Tsakiris & Haggard, 2005). The physiological measures included changes in the skin conductance and

temperature (Armel & Ramachandran, 2003; Llorens et al., 2017).

Embodiment of Rubber Hand Questionnaire. The ERHQ is a 10-item Likert questionnaire with scores that range from -3 (strongly disagree) to +3 (strongly agree), which assesses the strength of embodiment elicited during the RHI. Specifically, five items assess body-ownership, the extent to which the rubber hand is owned, three items assess location, the extent to which the rubber hand is aligned with the representation of the real hand, and the remaining two items assess agency, the extent to which the rubber hand can be voluntarily moved. Interestingly, these three factors have been reported to explain up to 79.0% and 76.2% of the variance of embodiment in synchronous and asynchronous conditions, respectively (Longo et al., 2008). Subcomponents of embodiment were defined as the average score of their composing statements. Average scores greater than 0 were considered positive. For the present study, items were translated into Spanish and back-translated by an independent native English speaker to correct conceptual discrepancies. The Cronbach's alphas for the present sample are 0.95 for the ownership, 0.77 for the localization, and 0.90 for the agency factors.

Proprioceptive drift. Participants were instructed to sit in front of the table with the hands on its surface and palms facing downwards. The participants were subsequently instructed to close their eyes and indicate the center of their non-dominant hand, which was about to be or was stimulated during the experiment, with the index finger of their dominant unstimulated hand without making contact, similar to previous studies (Rohde, Di Luca, & Ernst, 2011). The experimenter measured the difference in the perceived position and the actual position of the hand with the help of a ruler. Proprioceptive drift was defined as the difference between these measurements after and before the experiment. Bias towards the rubber hand is believed to indicate a visual dominance over proprioception (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005).

Changes in the skin temperature and conductance. A change in the skin temperature was defined as the difference between the mean temperature in the following 5 s after the hammer smash and the 5 s prior to the stimulation, similar to previous work (Llorens et al., 2017; Rohde et al., 2013). A change in the skin conductance was defined as the difference between the maximum peak that occurred between 1 and 5 s after the hammer smash, and the mean value in the second prior to the smash, as described in previous work (Armel & Ramachandran, 2003; Llorens et al., 2017; Ma & Hommel, 2013; Reinersmann et al., 2013). Only variations greater than 0.03 mS were considered meaningful (Armel & Ramachandran, 2003; Llorens et al., 2017; Reinersmann et al., 2013). Changes in both the skin temperature and conductance have been postulated as physiological signs of stress and excitement (Alonzo & Cipriani, 2012).

2.4. *Statistical data analyses*

Chi-squared tests were performed to determine the differences in the percentage of participants who felt the embodiment sub-components. Although Shapiro-Wilk tests showed that our data violated assumptions of normality, parametric tests were used with comparable results. Univariate ANOVA tests were performed to determine the differences in the total embodiment score, proprioceptive drift, and changes in the skin temperature and conductance between the three groups of age. MANOVA tests were performed to determine the differences in the constructs of embodiment (ownership, location, and agency) between the three groups of age. Finally, Pearson correlations were calculated for age and individual scores to embodiment constructs. The α level was set at 0.05 for all analyses (two-sided). All statistical analyses were performed using the software package SPSS 22.0 (IBM, Armonk, NY, USA) for Windows.

3. Results

Differences between groups of age.

The percentage of participants who felt body-ownership was greater than those who felt localization and, overall, agency (Figure 1). Statistical differences between groups were found in the percentage of participants who felt body-ownership ($p=0.038$), but not for localization ($p=0.334$) or agency ($p=0.085$).

No statistically significant differences were identified between the groups for embodiment as a whole ($p=0.889$, $\eta^2=0.003$) or any sub-component: body-ownership ($p=0.406$, $\eta^2=0.020$), localization ($p=0.895$, $\eta^2=0.002$), and agency ($p=0.804$, $\eta^2=0.005$) (Figure 2). Furthermore, no significant differences between groups were identified in the proprioceptive drift ($p=0.080$, $\eta^2=0.076$) (Figure 3) or the changes in the skin conductance ($p=0.070$; $\eta^2=0.070$) or temperature ($p=0.160$, $\eta^2=0.049$) (Figure 4). Age did not covary with any variable. Descriptive statistics are provided in Table 1.

Correlations between age and embodiment measurements.

Age did not significantly correlate with the scores on embodiment ($r=-0.01$, $p=0.943$), body-ownership ($r=0.06$, $p=0.570$), localization ($r=-0.04$, $p=0.691$), agency ($r=-0.11$, $p=0.286$), or proprioceptive drift ($r=-0.16$, $p=0.132$), or the changes in the skin conductance ($r=0.02$, $p=0.874$). However, weak but significant correlations were identified between age and skin temperature ($r=0.25$, $p=0.032$).

4. Discussion

This study examines the role of age in the embodiment processes during the RHI experiment in healthy adults. We hypothesized changes in the self-reported sense of embodiment and the behavioral and physiological measures; however, no significant age-related differences were identified, with the only exception of a weak significant

correlation between age and skin temperature.

The number of participants who felt body-ownership in our study confirms previous reports with similar conditions, which have been reported to vary from 53% (Petkova & Ehrsson, 2009) to 78% (Kalckert & Ehrsson, 2014) in young adults and approximately 60% in the elderly (Llorens et al., 2017). Approximately 40% of the older participants felt a sense of agency over the rubber hand during our experiment, which is also consistent with previous reports (Llorens et al., 2017). Although there were differences between groups, the absence of statistically significant differences and covariability between age and the embodiment sub-components suggests that participants felt the experience with comparable strength independent of their age. More importantly, the older participants reported a higher sense of body-ownership than the other groups, which is not only inconsistent but also contradicts our preliminary hypothesis. However, the heterogeneity within groups, which was evidenced by an increasing variance with age, could explain part of these results.

Behavioral and physiological responses showed analogous results. The absolute values of proprioceptive drift were similar to those reported in similar studies with healthy young adults (Holle et al., 2011; Petkova & Ehrsson, 2009; Riemer, Bublitzky, Trojan, & Alpers, 2015) and failed to reach statistically significant differences between groups. The increase in the skin conductance during the experiment is also supported by previous studies that involved young (Armel & Ramachandran, 2003; Ma & Hommel, 2013) and elderly populations (Llorens et al., 2017). The increase detected in the skin temperature, although contrary to the initial postulation of a limb-specific decrease with the strength of the illusion (Moseley et al., 2008), which has been reported to act both ways (Marjolein P M Kammers et al., 2011), is likewise supported by a recent study with the same procedure in older adults (Llorens et al., 2017). All physiological

measures failed to exhibit significant differences between groups with the only exception of a weak age-dependent correlation in the skin temperature. We hypothesize, however, that this effect could have been motivated by changes in sympathetic sudomotor function with aging (Ferrer, Ramos, Pérez-Jiménez, Pérez-Sales, & Alvarez, 1995) or by a statistical artifact, rather than by the experiment itself.

The absence of differences indicates comparable behavioral and physiological responses in all groups. The similar responses in the proprioceptive drift detected in our study contradict the age-related differences reported in a previous study (Graham et al., 2015). However, the dependence of this test on the proprioceptive integration, which has been determined to decline with age (Skinner et al., 1984), may affect the results. Nevertheless, it is important to highlight that the assumption of this measure as a valid correlate of embodiment is not always supported, not even in the previously discussed study (Graham et al., 2015). First, significant drift effects have been detected in conditions where participants denied illusory feelings of ownership (Holle et al., 2011). Second, whether the increase in the skin conductance is a direct effect of the embodiment mechanisms during the experiment or a threat to a human-like arm remains controversial (Ma & Hommel, 2013). Finally, previous reports suggest no evidence of hand cooling (Llorens et al., 2017; Rohde et al., 2013) or contradicting results with the perceived ownership over external limbs (Hohwy & Paton, 2010). Importantly, the relationship between the subjective perceptions of embodiment and the physiological and behavioral responses elicited during the RHI has been reported to be more complex than one-to-one (Llorens et al., 2017).

The absence of statistical differences between groups of age and the absence of covariability between age and any other measure suggest, however, that the embodiment mechanisms are present and persist with age with comparable strength but with

increasing variance. The differences in the perceived embodiment reported by a previous study may be explained by the inclusion of a group of children (Cowie et al., 2013). Although our study involved individuals within a wide age range, all participants were adults (age>20). In light of the results, one could conjecture that embodiment may be altered by brain changes associated with puberty and adolescence (Giedd et al., 1999; Sisk & Foster, 2004). In adult stages, when these processes are thought to decay, embodiment may remain stable, as shown in our study. However, an age-related decline of embodiment has been reported in participants from 21 to 60 years old after an experimental variation of the RHI, in which the rubber hand was projected on a screen embedded horizontally in a table (Graham et al., 2015). The differences in the age ranges of the participants and the methodologies of both studies may explain the differential results. The dependence of the embodiment mechanisms with age may require further studies to be untangled.

Furthermore, embodiment is not only the result of multisensory integration; an interplay between bottom-up and top-down influences is necessary for bodily synthesis and self-attribution of the fake hand (Tsakiris & Haggard, 2005; Constantini & Haggard, 2007; Haans, Ijsselsteijn & De Kort, 2008). Our data suggest that these processes may be not deteriorated with aging.

The limitations of the study must be taken into account when analyzing the findings. First, in contrast to the current study, most previous studies registered the physiological recordings in the unstimulated hand because of limitations in the instrumentation (Armel & Ramachandran, 2003; Hohwy & Paton, 2010; Holle et al., 2011; Marjolein P M Kammers et al., 2011; Ma & Hommel, 2013; Moseley et al., 2008; Rohde et al., 2013). Although this issue may limit the comparability of the results, a previous study using the same methodology did not show significant differences

between measurements in both arms in healthy volunteers (Llorens et al., 2017). Second, the absence of an asynchronous condition and neuroimaging data prevented an analysis of the effects of the incongruence of the stimulation and the neural correlates in the elicited responses, respectively. Finally, the increasing variance in the subjective responses with age could mask other effects. However, although traditional null hypothesis significance testing methods, such as those used here, cannot guarantee the null hypothesis, the wide age range of the participants, the controlled conditions of the study, and the inclusion of both subjective and physiological responses to the RHI support that the sense of embodiment and its behavioral and physiological correlates do not vary with age.

5. Conclusions

In contrast to the scant literature, our results showed that there is no subjective, behavioral, or physiological evidence of an age-dependent alteration in embodiment processes in the adult phase.

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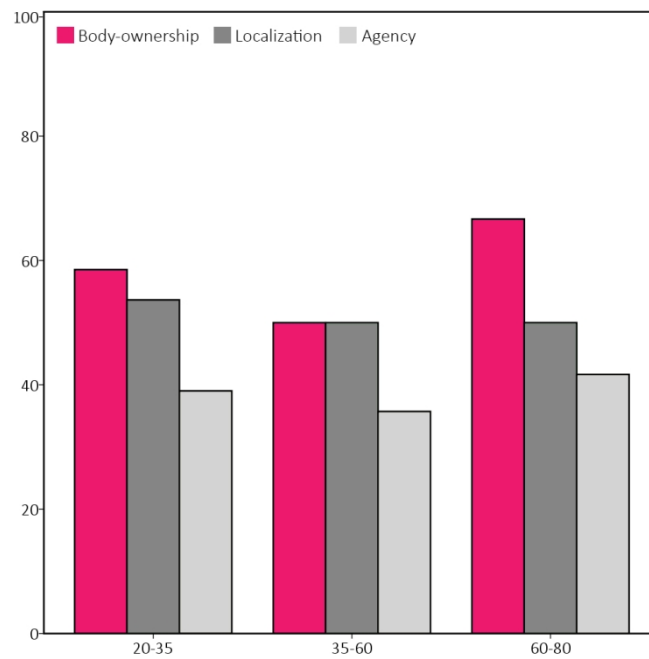
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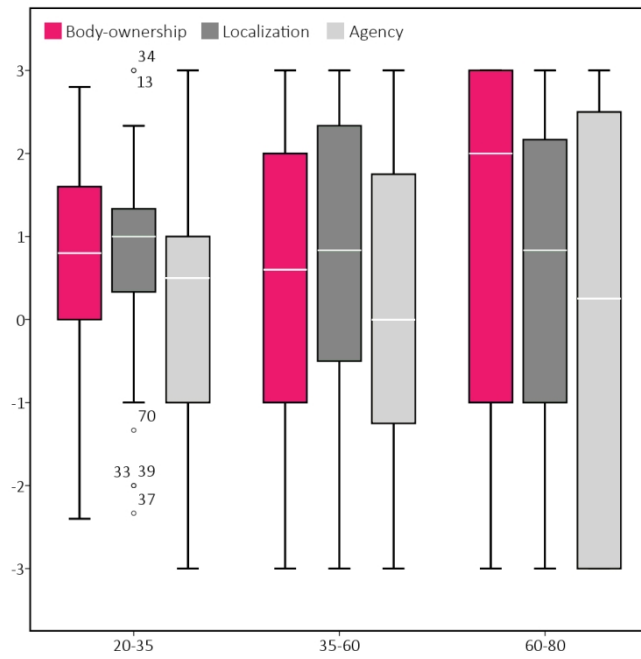
9. Figures

Figure 1. Percentage of participants who felt body-ownership, localization, and agency.



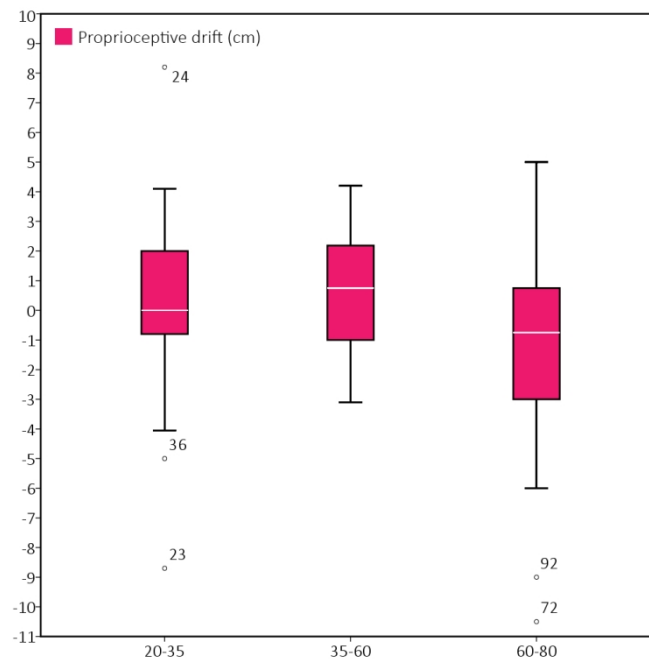
The figure shows the percentages of participants who felt body-ownership, localization, and agency in the three groups of age.

Figure 2. Self-reported embodiment scores



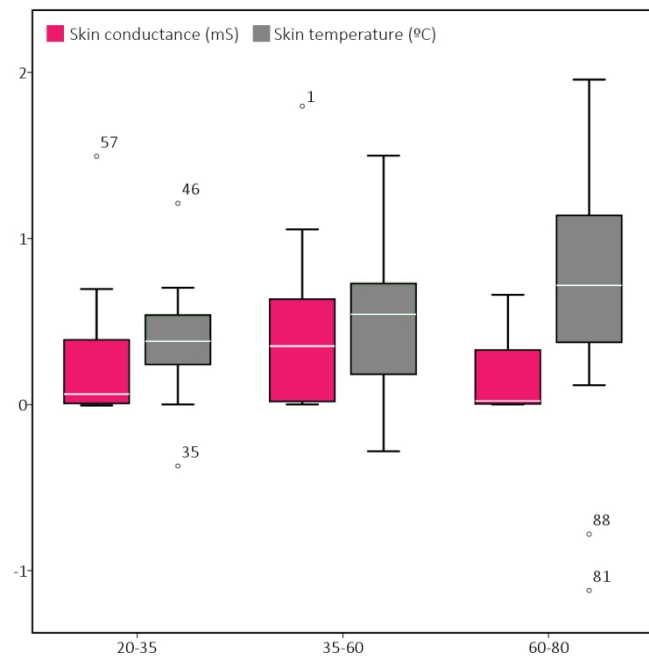
The figure shows the mean scores for the perceived body-ownership, localization, and agency in the three groups of age.

Figure 3. Proprioceptive drift

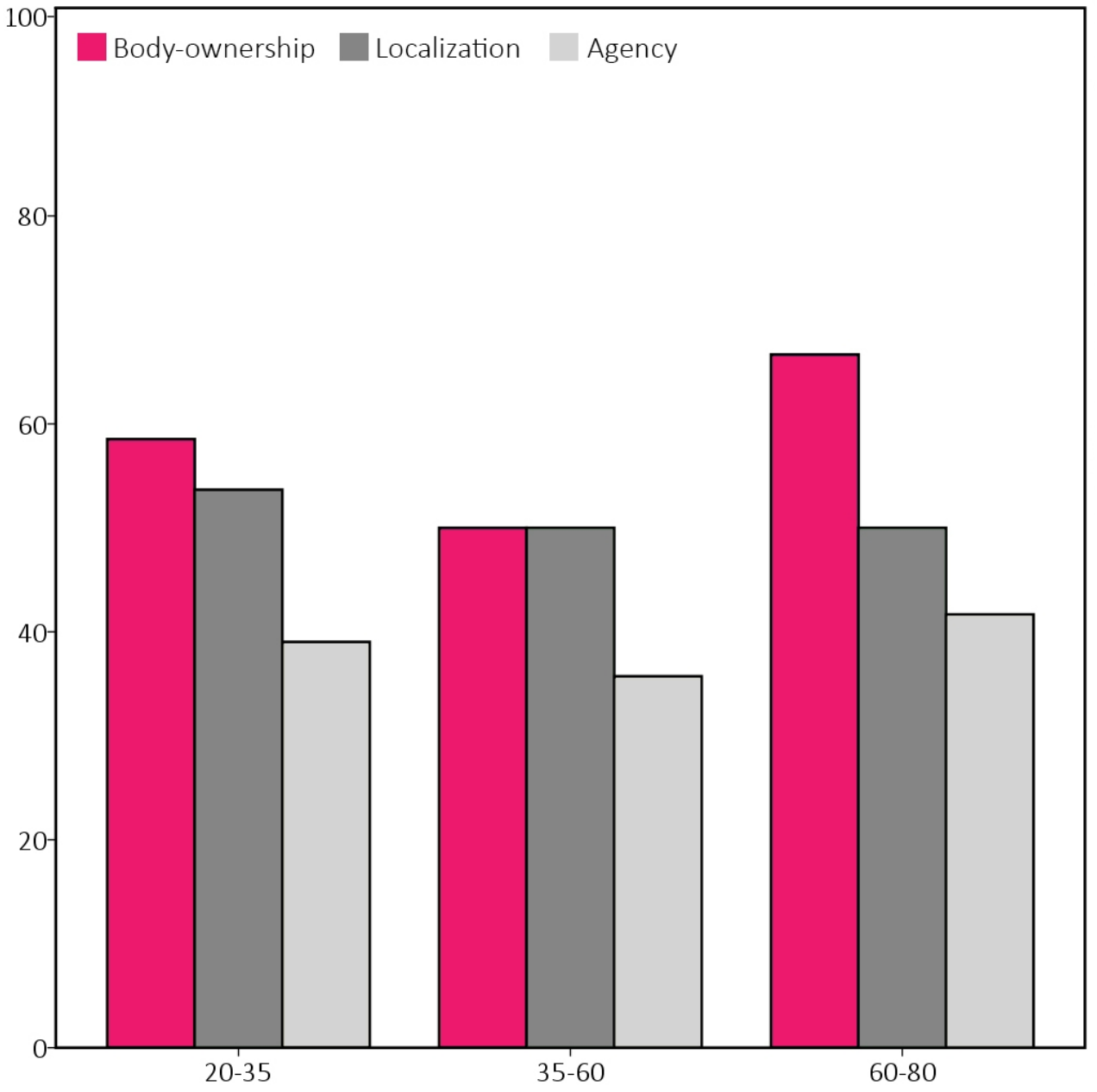


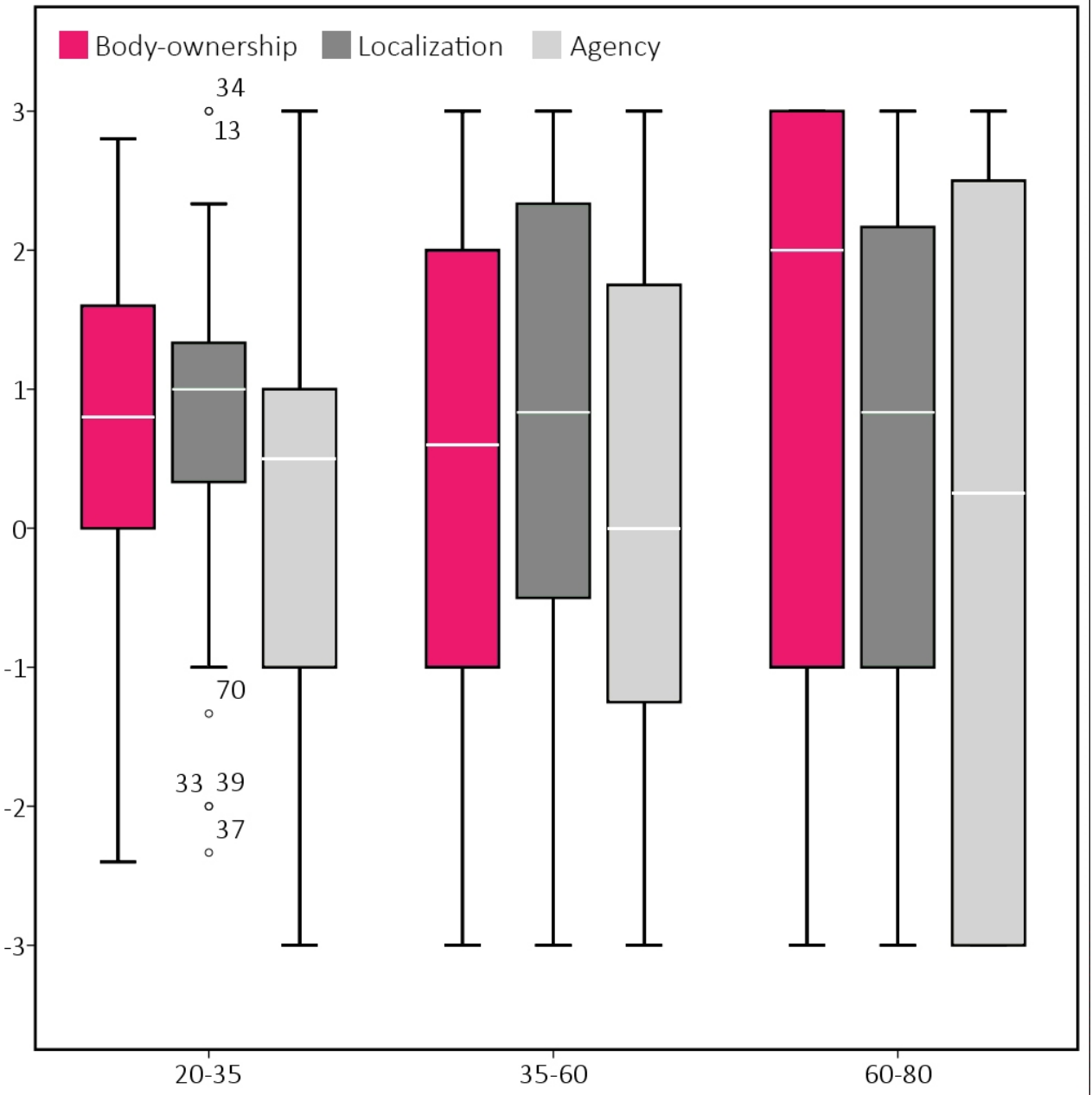
The figure shows the mean proprioceptive drift in the three groups of age.

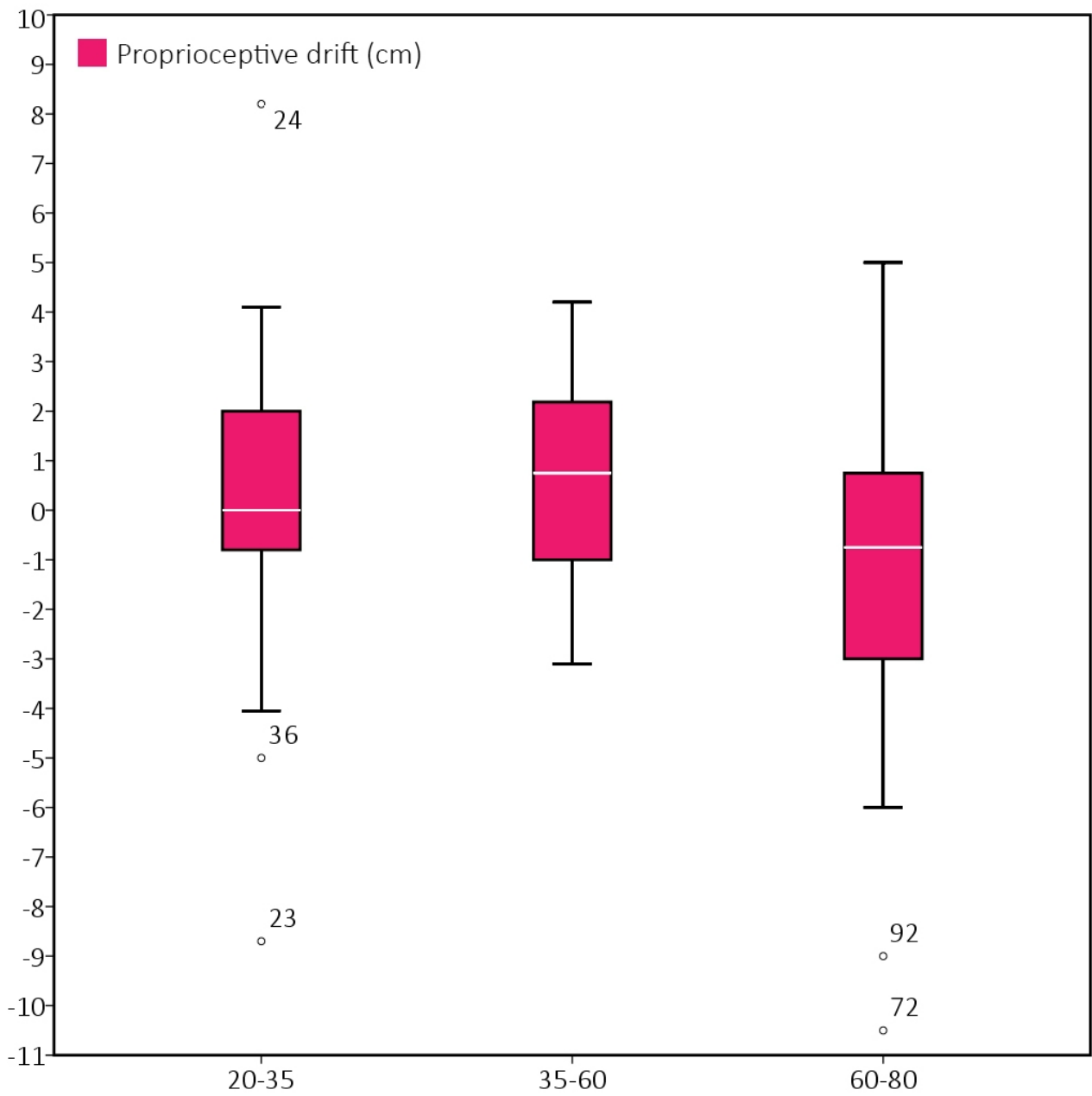
Figure 4. Skin conductance and temperature

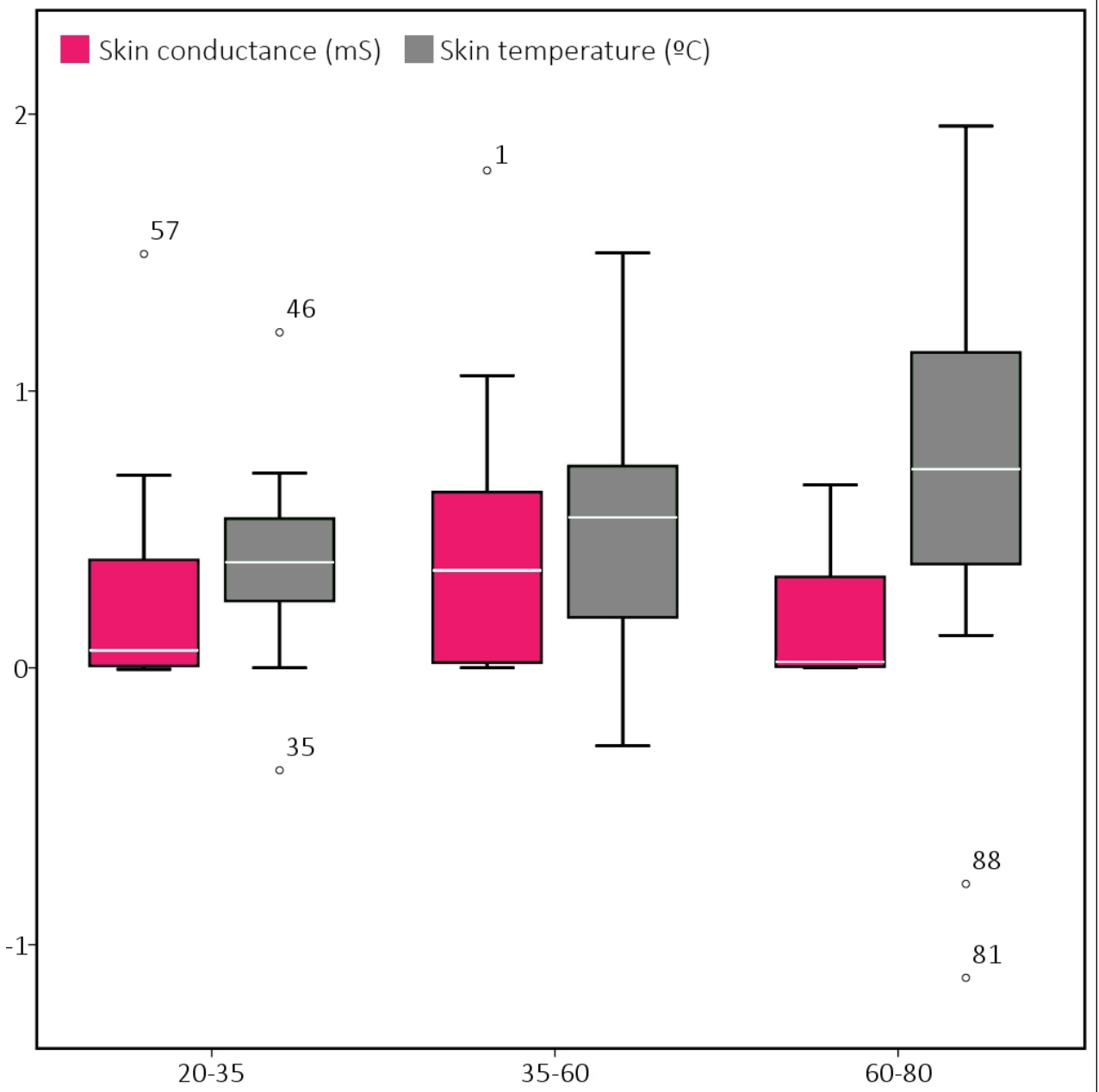


The figure shows the mean variations in the skin conductance and temperature in the three groups of age.









Tables

Table 1. Subjective, behavioral, and physiological responses to the Rubber Hand Illusion

	Group	Group	Group	Significance
	20-35	35-60	60-80	
Embodiment	0.40±1.27	0.70±1.64	0.54±2.03	P=0.798
Body-ownership	0.49±1.34	0.71±1.71	0.94±2.27	P=0.725
Localization	0.59±1.34	1.05±1.65	0.51±2.02	P=0.676
Agency	-0.09±1.48	0.16±1.91	-0.43±2.55	P=0.359
Proprioceptive drift (cm)	-0.05±3.02	0.65±2.25	-1.68±3.53	P=0.072
Skin temperature (°C)	0.38±0.27	0.48±0.41	0.63±0.67	P=0.192
Skin conductance (mS)	0.23±0.33	0.40±0.44	0.18±0.26	P=0.102

The table shows the responses of the participants to the Rubber Hand Illusion. Data are expressed in terms of mean ± standard deviation.