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# Action-Shaped Perception. Towards a reunification of two systems.

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# Summary

In this dissertation I investigated the relationship between action and perception in the processing of Space, Time and Numerosity. In the first chapter the most prominent literature on the topic is reviewed to introduce the conceptual framework in which the experimental paradigms were developed. In 2003 Vincent Walsh proposed A Theory of Magnitude (ATOM) which posits that space, time and numerosity share a common processing mechanism rooted in our need for information about the spatial and temporal structure of the external world. According to Walsh, we could learn about the association between the fundamental magnitudes through our interaction with the environment, as in real-life settings they often correlate with each other (for instance, a higher number of items takes up a larger space and requires a longer time to be retrieved).

One of the functional consequences of the ATOM theory would be a perceptual interference across magnitudes, which would result in judgments regarding one magnitude being biased by another irrelevant one. In the second chapter of this thesis, I demonstrate that the interaction between duration and numerosity is task-dependent: participants' judgments about stimulus duration were influenced by stimulus numerosity only when tested with a discrimination task. This suggests that the cross-magnitude interaction predicted by the ATOM Theory does not occur at the processing level, but it is dependent by the kind of task (ie. comparisons) the observer is required to perform. This, in turn, suggests that the interplay between time and numerosity occurs at a later stage after perceptual processing as for example, at the decisional level.

In chapter 3 I report evidence for a new cross-modal after-effect, revealing that the metric with which the visual system computes the relative spatial position of objects is shared with the motor system. A few seconds of mid-air self-produced tapping movements (adaptation) yielded a robust compression of the apparent separation of dot pairs subsequently displayed around the tapping region. As the influence of tapping on numerosity and duration perception had been previously demonstrated, these results offer clear evidence for a generalized interaction between the motor system and the processing of perceptual magnitude information in line with the ATOM Theory predictions (see above).

After demonstrating the influence of upper-body movements on magnitude perception, Chapter 4 is dedicated to the investigation of the influence of lower-body movements on the perception of duration and numerosity. As already reported in previous literature, I found that running

systematically interferes with duration perception as it causes an overestimation of perceived time. However, in order to overcome some of the discrepancies in the existing literature that might be caused by methodological differences, I applied a standardized motor paradigm to different time ranges and sensory modalities. This allowed me to generalize the effect induced by running on duration perception across visual and auditory modalities and across sub-second and supra-second duration ranges. On the other hand, I found no distortion of numerosity judgments because of running, suggesting that this effect does not generalize across magnitudes.

Lastly, I focused on the importance of Peripersonal (PPS) and Extrapersonal (EPS) space in the investigation of the relationship between action and perception, which is often overlooked, but remains a vital component in the theoretical framework of ATOM theory. Indeed, action needs proximity with its target, and there is evidence of perceptual networks dedicated exclusively to PPS. As is often the case with magnitude perception, time has been the first domain investigated while taking into account the influence of stimulus distance. One of the research lines carried out during the PhD was aimed at generalizing the effects of PPS and EPS on time to numerosity perception. My results clearly indicate numerosity perception relies less on stimulus distance than time does, with participants showing the same perceptual precision and accuracy in both EPS and PPS.

In the last chapter I applied the psychophysical methodologies I got familiar to during the PHD to study perception in a virtual reality (VR) environment that allow to test perceptual processes in highly ecological settings to make VR always more important in future research of perceptual neuroscience. This study was conducted in collaboration with the Center for Applied Neuroscience of the University of Cyprus where I spent 7 months during my period abroad. My aim was to validate in VR a paradigm that has been replicated multiple times in real world settings to measure the size of participants’ PPS. Following this, I also experimented a tool-training method aimed at reshaping participants’ PPS. My results show that, similarly to real world settings, a short period of tool-training is sufficient to cause a significant enlargement of the PPS. This result is of primary importance, as it shows for the first time that PPS in Virtual Reality has similar characteristics of Peripersonal space as measured in real life settings, thus offering evidence towards a valuable validation of VR as a tool to study the characteristics of Peripersonal space.

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# Publications

Parts of the thesis have been included in the following peer-reviewed journal publications.

Experiment in Chapter 3 was included in the following publication:

**Petrizzo, I.**, Anobile, G., & Arrighi, R. (2020). Motor adaptation distorts visual space. *Vision Research*, *171*, 31-35, https://doi.org/10.1016/j.visres.2020.04.007

Experiment in Chapter 4 was included in the following publication:

**Petrizzo, I.**, Anobile, G., Chelli, E., Arrighi, R., & Burr, D. C. (2022). Visual duration but not numerosity is distorted while running. *Brain Sciences*, *12*(1), 81, https://doi.org/10.3390/brainsci12010081

Experiment in Chapter 5 was included in the following publication:

**Petrizzo, I.,** Chelli, E., Bartolini, T., Arrighi, R., & Anobile, G. (2023). Similar effect of running on visual and auditory time perception in the ranges of milliseconds and seconds. *Frontiers in Psychology* 14, https://doi.org/10.3389/fpsyg.2023.1146675

Experiment in Chapter 6 was included in the following publication:

**Petrizzo, I.**, Castaldi, E., Anobile, G., Bassanelli, S., & Arrighi, R. (2021). Time and numerosity estimation in peripersonal and extrapersonal space. *Acta Psychologica*, *215*, 103296, https://doi.org/10.1016/j.actpsy.2021.103296

# Declaration

I, the author, declare that the work presented in this thesis is my own and has not been submitted for a degree at any other institution.

# Chapter 1

# Introduction

# 1. Introduction

## 1.1 A Theory of Magnitude

Action and perception might appear to be in opposition, as one is the requirement for being active and the other could be mistaken for passively witnessing the surroundings. This is however far from being an accurate description of the two. Perception is rarely a passive phenomenon and action is not merely an automatic reaction. Action, every action that we perform, even the most instinctual, requires designing preparation of a motor plan. As the number of actions we carry out on each given day is almost immeasurable, it is evident that the motor preparation needs to be as effortless and efficient as possible. The first step to each action is to determine which, and even if, an action is indeed required. For this reason, it is crucial to correctly perceive and encode the characteristics of the targets of our action, such as their position in space, their size, if they are moving and at which speed, and even their number in case we plan to interact with an ensemble. A logical way of organizing the stages that get from perception to action would be to have all the key magnitudes that characterize the environment (when, where and how many) being processed close to each other and then to be able to promptly feed this information to the motor cortex in order to plan the motor response.

More than twenty years ago Vincent Walsh (2003) proposed this line of reasoning to formulate the ATOM Theory or A Theory Of Magnitude. The hypothesis at the core of the ATOM Theory was straight-forward: space, time and numerosity share a common processing mechanism rooted in our need for information about the spatial and temporal structure of the external world (Fig.1). According to Walsh we learn about the association of the fundamental magnitudes through our interaction with the environment, as in real-life settings they often correlate with each other: for instance, a higher number of items takes up a larger space and requires a longer time to be retrieved.

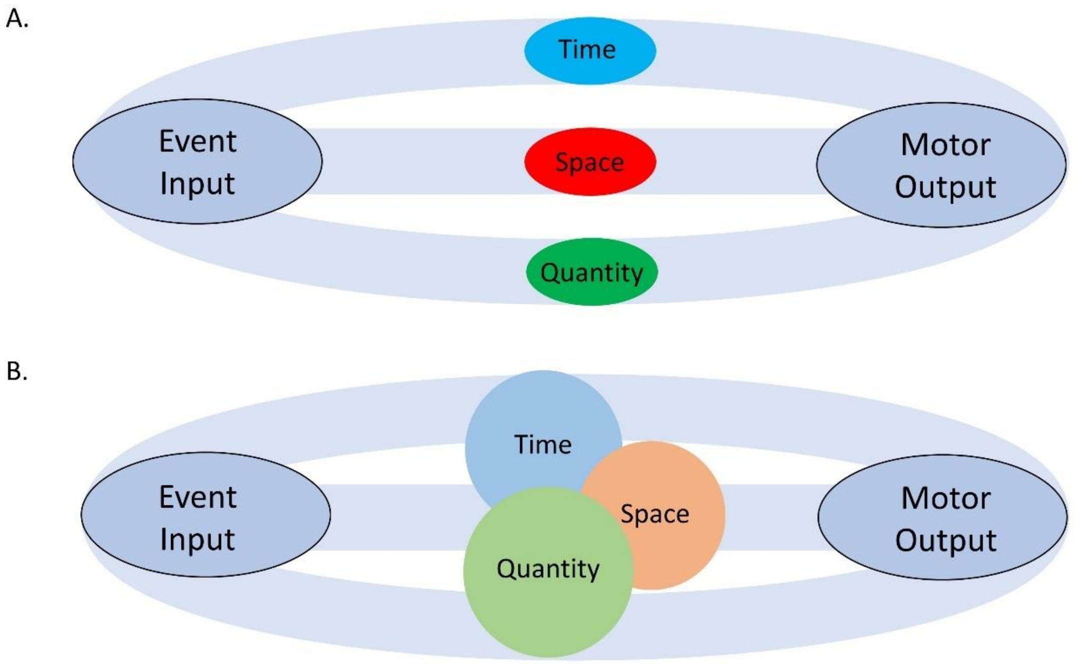

**Figure 1. Comparison of two schemas for processing time, space and quantity. (Reproduced from: Walsh, 2003)**
**A.** The three magnitudes could be analyzed separately and compared according to their own individual metrics
**B.** In a generalized magnitude system as suggested here magnitudes would be computed according to a common metrics

If our brain encodes space, time and numerosity by leveraging on the same brain areas and we also learn from ecological experience that these magnitudes often covary, it would then be expected to find that these magnitudes interfere with each other and are difficult to ignore even when they are irrelevant to the task at hand.

We can refer to this phenomenon as cross-magnitude interaction and the literature of the past century is scattered of such examples, even before the ATOM theory was formally proposed. Indeed, the encodings of different magnitudes often share some common properties. For instance, most magnitudes obey to the Weber Law. The Weber Law states that the minimum perceptible change in stimulus intensity is proportional to the intensity of the stimulus (Ekman, 1959) or that sensitivity proportionally increases with increasing of stimulus intensity (Haigh et al., 2021). This has been proved to apply to the three core magnitudes, with judgments following the Weber Law for duration (Grondin et al., 2001; Ren et al., 2020), numerosity (Anobile et al., 2014;

Ditz & Nieder, 2016), space (Ganel et al., 2008; Morgan & Watt, 1989) and even motion perception (Zanker, 1995).

## 1.2 Cross-dimensional interactions between magnitudes

One of the most cited examples of an association between space and numerosity is the SNARC effect (Spatial Numerical Association of Response Codes): large numbers are responded to faster with the right-hand key whereas small numbers are responded to faster with the left-hand key (Dehaene et al., 1993). Even though this association has been proved to hold only under specific circumstances (relatively small Arabic numerals used with participants whose primary language is written left to right) it still shows how the mental representation of numbers relies on spatial cues to improve efficiency, in this case reaction times (Dehaene et al., 1993). Indeed, within the variables mentioned, the SNARC effect is strong enough to cause a shift in attention to the space, with participants detecting targets in the left visual field when they are preceded by a low digit (presented in the center of the screen) compared to a high digit (Fischer et al., 2003), and errors in the bisection of a string of digits or letters, with left-ward errors occurring for low numbers and right-ward errors for high numbers (Calabria & Rossetti, 2005; Fischer, 2001). These reports suggest the organization of numbers on a mental number line in which the space on the left is associated with smaller numbers and the space on the right with larger numbers. This organization is also reflected in hemispheric asymmetry in number processing: when comparing two stimuli that are fairly distant from each other in terms of their numerical value, participants show a left visual field advantage for smaller number, which results in faster reaction times (Lavidor et al., 2004).

Our perception is not only influenced by contextual information but also by previous events to the one that is being encoded. What we perceived before is just as important as what we are currently perceiving. A clear example of this is the phenomenon of perceptual adaptation. The first account of this phenomenon was the motion after-effect as described by Addams (1834) after observing a waterfall: after a period of adaptation to the downward motion of the water the rocks on the side of the cascade appeared to be moving upwards. The accepted explanation of this phenomenon is that the repeated exposure to a direction of motion “fatigues” a class of neurons, causing a rebound effect in the opposite direction when the visual system is presented with a neutral stimulus. This characteristic of the visual system has been used for centuries as a tool to test perception as an indirect tool to target a specific group of neurons. This led to the speculation that, if space and numerosity share similar neural circuits, adapting to one magnitude should theoretically also affect the perception of the other.

Interestingly, it has been demonstrated that adapting to size subsequently induced a distortion in the perception of the numerosity of the stimulus presented after, while leaving perception of density untouched (Zimmermann & Fink, 2016), suggesting that space and numerosity share at least partially overlapping neural resources. This finding is further supported by neuroimaging studies which investigated tuned responses to visual object size and numerosity in the bilateral posterior parietal cortex. Harvey et al. (2015) characterized size and numerosity maps in the same subjects and found that they largely overlapped and that preferences were correlated among recording sites within both maps. Even though many other properties of size and numerosity representation differ, suggesting that they result from two separate mechanisms, they clearly share some neural resources pointing to a generalization across quantities of magnitude processing. The interaction between the two magnitudes, however, seems to be asymmetrical, with space influencing numerosity to a greater extent than the opposite. This is often true for cross-magnitude interaction and might point to a hierarchical organization of their saliency. It has been suggested that space could be the foundation for all other magnitudes, especially those that are more abstract such as time and numerosity (Bonn & Cantlon, 2012): a theoretical proposal termed Metaphoric theory (Lakoff & Johnson, 2008). It is also worth to notice that some dimensions are more environmentally and culturally salient than others, and this might lead to have a stronger mapping in the magnitude system, which in turn would influence the asymmetry of their relationship. The existence or non-existence of interactions between magnitudes per se might not be enough to rule in favor of against the ATOM Theory.

Indeed, space is also able to interfere with time perception. The kappa effect, for instance, is a temporal perceptual illusion in which in perceiving a sequence of consecutive stimuli, participants tend to overestimate the elapsed time between two successive stimuli as the distance between the two increases (Cohen et al., 1953). One might argue that the kappa effect arises from the participants belief that the two sequentially presented stimuli are in fact the same stimulus moving in space, and since traveling longer distances requires more time this belief biases their judgement. However, also an influence of the size of stationary stimuli on time discrimination has been reported (Xuan et al., 2007). Using the duration reproduction method it has been demonstrated that the length or the distance travelled by a stimulus influences duration, with longer/further stimuli being reproduced as having a longer duration than shorter ones, however the opposite influence has not been found (Casasanto & Boroditsky, 2008). Even the implicit modulation of magnitudes related to space, such as length and volume, influences time perception, with words representing longer/heavier objects being perceived as lasting longer (Ma et al., 2012). While the reported results seem to be quite robust, as they have been demonstrated with multiple paradigms, it is still to be determined when and where the interaction between magnitudes occurs. Indeed, these results might stem from two different processes: the irrelevant quantity might directly affect the perception of the stimuli of the relevant dimension, or the interference might occur at the decisional level, with the irrelevant dimension biasing participants judgment regarding the relevant magnitude. To this aim, some have proposed to attempt to replicate cross-dimensional interferences using different paradigms, under the assumption that if the interference occurs at the perceptual level, the same results should be obtained from different procedures. Following this line of reasoning Yates et al. (2012) tried to investigate the effect of size influence on duration judgments by directly comparing a task in which participants had to perform a discrimination judgment (which stimulus last longer) with an equality judgment (do the two stimuli have the same duration). Their results show that, while the discrimination task nicely replicates previous reports of larger stimuli being judged as lasting longer, with the equality task participants judged larger stimuli as being shorter (Fig. 2). The authors speculate that when participants are asked to make an equality judgment they might be influenced also by the irrelevant magnitude and make the judgment in a more abstract sense. When the larger stimulus is also the larger ones its spatial dimensions are the same, in the sense that they are congruent with each other. On the other hand, when the small stimulus lasts longer its dimension are incongruent, and thus different. This might lead to a rise in the proportion of same responses for those stimuli whose dimension are congruent with each other, which, in turn, would result in the observed results, the same that we would observe if indeed smaller stimuli were perceived to last longer. While this study cannot provide a definitive answer for the presented results, it still proposes an interesting methodological approach to the investigation of the cross-magnitude interferences proposed by the ATOM Theory.

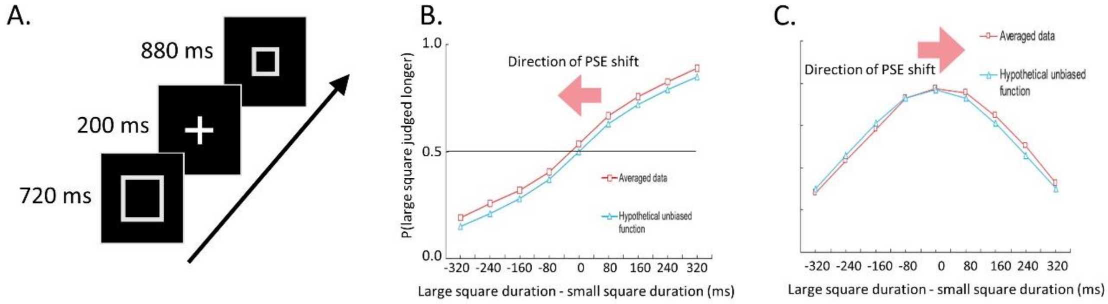

**Figure 2. Cross-dimensional interaction between size and duration investigated with two paradigms.**

**A.** Sample sequence of stimuli for the discrimination and the equality judgments. In the incongruent condition the first stimulus was presented for 720 ms and the second for 880 ms. The task for the discrimination was to judge which of the two squares was shorter/longer. The task for the equality was to judge whether the two squares had the same or different durations.

**B.** Averaged data for the discrimination task showing proportion of responses in which the large square was judged longest as a function of the duration difference between the squares (large square duration minus small square duration). A hypothetical unbiased function is shown for comparison purposes. This hypothetical function was modeled on the averaged data but rotationally symmetrical around the point (0, 0.5).

**C.** Averaged data for the equality task showing proportion of responses in which the squares were judged as equal in duration as a function of the duration difference between the squares. The hypothetical unbiased function was modeled on the averaged data but symmetrical around the line x=0.

(Adapted from: Yates et al., 2012).

Subsequent reports (Rammsayer & Verner, 2014) have tested this effect with yet another method, and indeed found that larger stimuli are judged to last longer when participants are required to reproduce the duration of the presented stimulus. This result challenges Yates’ (2012) interpretation of the cross-magnitude interference acting at a decisional level but still does not cast definitive light on inter-task differences in cross-magnitude interferences.

A possible step further in this direction would be to test whether also other cross-dimensional interactions in duration judgments are modulated by the task employed. Another magnitude that has been repeatedly reported to influence duration is numerosity. With a simple Stoop paradigm Dormal et al. (2006) have shown that when comparing the duration of two sequences of flashing dots the numerical cues interfered with their duration processing. A similar effect using a comparison task was found also for digits (Shukla & Bapi, 2021) and simultaneously presented dots (Javadi & Aichelburg, 2012; Xuan et al., 2007). The effect also appears to be task-resistant: the duration of a stimulus consisting of dots is overestimated for large numerosity also when a verbal estimation task is employed and reproducing the duration of a digit via keypress is influenced by the numerosity represented by the digit (Chang et al., 2011). On top of this, the influence of numerosity represented by digits seems to affect sensory accuracy, but not precision, suggesting that the change in perceived duration because of numerosity influence is not the mere result of a lower sensory precision (Shukla & Bapi, 2021). However, despite the cited evidence, the influence of numerosity on duration is far from being definitively demonstrated. Lambrechts et al. (2013) used to investigate this issue a task in which participants were presented with two anchor stimuli, one for the lower limit of the range presented and one for the upper. On each given trial participants had to judge whether the presented stimulus was closer to the upper or lower anchor. Surprisingly they found that stimulus duration influenced numerical and spatial judgments, while the former was resilient to interference from the other two magnitudes. Vicario et al. (2011) have shown that digits numerical magnitude affects performance in a duration bisection task, but only when digits of different magnitudes are intermingled in the same experimental block. This finding is relevant as it suggests that the implicit comparison of size differences across displayed numbers, rather than the numerical size itself, seems to be a key factor underlying this interaction. Even when we examine the relationship between time and numerosity in a cross-adaptation paradigm, results show that while adaptation to time slightly distorts numerosity perception of an array of dots, there is not enough evidence to prove the opposite (Tsouli et al., 2019).

Taken together, these mixed findings seem to suggest that, while some sort of shared representation between time and numerosity exists, the parameters and causes of this interplay are far from being determined. One of the reasons for the discrepancies of the results in the literature is the everchanging methodology employed. Several different tasks, numerosity and duration ranges, as well has sensory modality have been used, which makes it difficult to directly compare evidence from different studies. For this reason, in the second chapter of this work, I decided to investigate the cross-dimensional interference of numerosity on time by having the same participants perform different tasks while maintaining the stimuli used unchanged among paradigms.

### 1.3 Action and perception

In the previous paragraph I focused on the inter-play between magnitudes in both interference and adaptation paradigms. Even though the cross-dimensional interaction between magnitudes has been postulated by the ATOM Theory (Walsh, 2003) as a functional consequence of the Magnitude System, it is not the primary focus of it. The relationship between magnitudes and their sharing of the same neural resources would not be an accident of evolution, but a functional development of the cerebral cortex in order to efficiently interact with the environment. Indeed, a shared mechanism processing quantitative information in multiple dimensions may be beneficial in providing a unique interface between the perceptual and the motor systems, sub-serving the transfer of sensory information between them. In line with this idea, voluntary movements performed during the presentation of visual stimuli can affect perceived duration.

One of the most beknown examples of action influencing perception is the chronostasis illusion, which refers to the phenomenon we can observe if we perform a saccade onto the seconds hand of a clock: the hand appears to freeze for a moment before starting to move along the usual pattern. This is a general phenomenon that characterizes the first visual stimulus perceived after an eye movement (Yarrow et al., 2001), and extends to a variety of eye movements (Yarrow et al., 2004). Duration distortion is not only limited to stimuli presented at the landing point of saccades but also to stimuli presented close to saccadic onset. Indeed, duration is strongly compressed around the time of saccades: subjects judge two bars flashed 100ms as being much closer in time to each other, up to half of the true value of the interval (Binda et al., 2009; Morrone et al., 2005). The compression of events happening around the time of saccades is not limited to duration, but, in line with a common magnitude system, also extends to spatial position (Morrone et al., 1997; Ross et al., 1997) with targets being localized as closer to the saccades landing point than they really are, and even more strikingly, while well before or after the saccade numerosity estimation is veridical, close to saccadic onset there is a large and systematic underestimation of number (Binda et al., 2011). The effect is not caused by image motion per se, but by the voluntary eye movement, as neither space, time nor number is affected by simulating the saccade with a fast mirror motion (Binda et al., 2009, 2011; Morrone et al., 1997). While voluntary eye motion influences perception we can also find evidence of the opposite: indeed, there have been reports that the processing of numerosity, for instance, influences both saccades latencies (Fischer et al., 2004) and amplitude (Pressigout & Dore-Mazars, 2020).

Eye movements are of paramount importance to visually explore the environment; however, they are not the primary effectors we use to interact with the space around us. It is thus not surprising that there have been several reports of the interaction between magnitude perception and hand movements. Hands are used to grasp and explore objects in the space, as well as being a very useful vessel to keep track of the number of items in the surroundings. Indeed, there has always been a tight connection between hands and number processing, and many studies indicate that the use of fingers is a cornerstone for the understanding and development of number concepts (Berteletti & Booth, 2015; Crollen et al., 2011). This account is compatible with the results of a recent study on swiping movements in which movement amplitude depended on number magnitude (Fischer et al., 2018). Furthermore, number magnitude also influences other hand motions, with larger numbers associated with faster initiation of opening grips, power grasps and larger maximal finger aperture (Andres et al., 2004, 2008; Lindemann et al., 2007; Moretto & di Pellegrino, 2008).

Similarly to eye movements, also action can influence perception: for instance observing fingers depicting grip closing impacts the processing of number magnitude (Badets & Pesenti, 2010) and random number generation (Badets et al., 2012).

Hand action influence on magnitude is not limited to numerosity but has also been documented for other magnitudes. For instance, an effect like the saccades chronostasis described above, has been reported for voluntary hand-movements (Park et al., 2003). Also, when participants are asked to move a robotic arm while judging the duration of auditory intervals, they judge stimuli as lasting longer if the robotic arm is applying viscosity to their movement (De Kock et al., 2021). On the other hand, if fast circular hand movements are performed during duration perception, this causes a compression of the perceived duration of the interval separating two sequentially presented stimuli (Yokosaka et al., 2015). Some authors have tried to make a broader generalization and claim that perceived duration is biased towards the duration of concurrent actions (Yon et al., 2017). Even when the durations to judge are presented just before the initiation of hand movements, participants report a compression of perceived duration (Tomassini et al., 2014). This phenomenon has also been observed for the third main magnitude proposed by the ATOM Theory, which is space. There have been indeed some studies suggesting that tactile stimuli was systematically mislocalized in the direction of the movement (Dassonville, 1995; Maij et al., 2011; Watanabe et al., 2009).

While all the above examples are referred to the interference between action and magnitude perception when they are happening at the same time, there have been reports of an inference happening even after the end of the voluntary movement. Anobile et al. (2016) used the adaptation phenomenon described in paragraph 1.2 to investigate the relationship between action and numerosity perception. Participants were required to perform a series of mid-air taps for several seconds and then judge the numerosity of a visual stimulus presented near the tapping region. Motor adaption reliably distorted perceived numerosity: after a short period of adaption to rapid tapping participants underestimated the number of stimuli presented near the tapping region, while adaptation to slow tapping caused overestimation. Interestingly this effect generalized across format, by distorting both simultaneously and sequentially presented dots or the perceived numerosity of a series of auditory tones (Anobile et al., 2021; Togoli et al., 2020). This effect is extremely spatially selective, as the distortion would occur only if the stimulus to judge was presented in an area of radius 12° around the tapping location (Anobile, Domenici, et al., 2020).

Crucially, this motor adaption paradigm has also been expanded to the time magnitude, where a similar effect has been found: rapid tapping induced a time underestimation of the perceived duration, while slow tapping produced an overestimation (Anobile, Domenici, et al., 2020).

At the beginning of this paragraph, I described a motor induced distortion of magnitude that generalizes to both space, time and numerosity (Binda et al., 2009, 2011; Morrone et al., 1997). However, the interaction between magnitude perception and the motor adaptation introduced above has not been fully generalized as only the effects of motor adaptation on time (Anobile, Domenici, et al., 2020) and numerosity (Anobile, Arrighi, et al., 2016) have been investigated so far (see Fig. 3). For this reason, in the third chapter of this thesis I decided to apply the same paradigm to space perception: I tried to determine whether adaptation to fast hand tapping induced an underestimation of the perceived separation between two dots simultaneously presented around the tapping location.

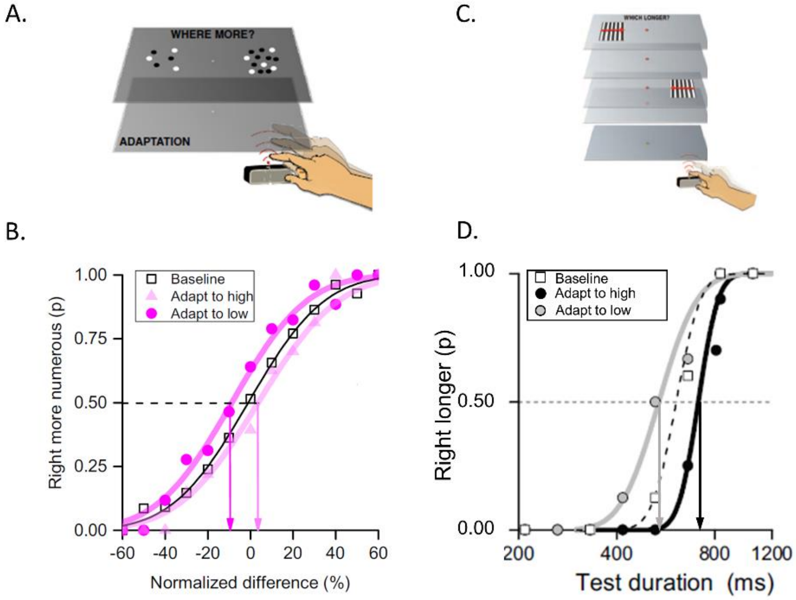

**Figure 3. Hand-tapping effect on numerosity and durations (Adapted from: Anobile, Arrighi, et al., 2016; Anobile, Domenici, et al., 2020)**

**A. Motor adaptation paradigm.** During the motor adaptation phase, participants made a series of midair tapping movements below a screen, with the hand floating above an infrared motion-tracking device. After 6 s of tapping, a stop signal appeared and was followed by two clouds of dots presented simultaneously: that on right was chosen at random between 5 or 20 dots, that on the left differed by a random value within the range ± 5 dots (capped between 5–20). Subjects indicated which stimulus appeared to be more numerous.

**B. Motor adaptation effects on perceived numerosity.** Psychometric functions for pooled data (6 subjects) for numerosity judgments. The curves indicate the proportion of trials when the test (presented on the right, the same side of tapping) was seen as more numerous than the unadapted stimulus (presented on the left), as a function of the numerosity difference (normalized by the averaged of the two stimuli). Adaptation to slow tapping shifted the curve leftwards, showing that subjects were biased to perceive the stimulus as more numerous that it was; and adaptation to fast tapping shifted it rightwards. The point where the best-fitting curves pass 50% is considered the point of subjective equality (PSE).

**C. Motor adaptation paradigm.** During the motor adaptation phase, participants made a series of midair tapping movements below a screen, with the hand floating above an infrared motion-tracking device. After 6 s of tapping, a stop signal appeared and was followed by two drifting gratings presented sequentially: the test (variable numerosity) at the point of tapping and the reference (600-ms duration) at the opposite position. Subjects indicated which stimulus appeared to last longer.

**D. Motor adaptation effects on perceived duration.** Sample psychometric functions for representative observers for discrimination judgments. Shifts between curves reveal adaptation, with points of subjective equality (PSE; the physical test magnitude corresponding to 0.5 proportion of "longer" or "faster" responses) moving away from the physical duration. Rightward shifts show that after adaptation to fast tapping the reference stimuli was perceived as lasting less.

Hands and fingers are without a doubt the key effectors to grasp and perform fine-tuned movements, and their link with magnitudes such as numerosity is more evident. However, if we learn about the association between magnitudes through the observation that they often correlate with each other in the environment one of the first examples of this that might come into mind is that it takes more time to travel a longer distance and a higher number of steps. Thus, it is not surprising that the interaction between magnitude and lower-body movements has been studied before. If the ATOM Theory was indeed true, one might expect the influence of motion on perception to generalize to all the effector in both the upper and lower body. The most investigated magnitude for lower-body motion is without a doubt duration, which has been investigated with an impressive number of types of movement and tasks. While one must admit that the focus for the previous authors was not on the interaction between motion and magnitude per se, but on the effect of physical exercise on duration. However, I will take the evidence from these studies to further the discussion about the validity of the ATOM Theory. The results found in the past literature point in the direction of a strong bond between lower-body motion and duration, with action usually causing an overestimation of perceived time. This result has been found for both cycling (Edwards & McCormick, 2017; Lambourne, 2012; Tonelli et al., 2022) and running (Kroger-Costa et al., 2013; Sayalı, Özoglu, et al., 2018) and for both very short (Kroger-Costa et al., 2013; Lambourne, 2012; Tonelli et al., 2022) and longer intervals (Edwards & McCormick, 2017; Sayalı, Özoglu, et al., 2018). The efforts of investigating the influence of physical activity or lower body motion on magnitude perception have primarily focused on time perception alone, while there are no reports of physical activity influencing other magnitudes. For this reason, in Chapter 4 of this thesis I investigate the effect of lower body movement on numerosity perception. This was achieved by replicating the time generalization task used by Lambourne et al. (2012) which showed a clear effect of physical exercise on perceived stimulus duration (Fig. 4). However, I opted to switch the cycling with a running paradigm, in which participants were asked to perform the task while running on a treadmill at a speed sufficient to achieve 80% of their maximum heart rate adjusted for their age (Tanaka et al., 2001a). Having confirmed previous results of a time overestimation induced by physical activity, I followed with an experiment in which the same subjects were tested in a condition in which they had to encode and decode a standard numerosity as opposed to duration.

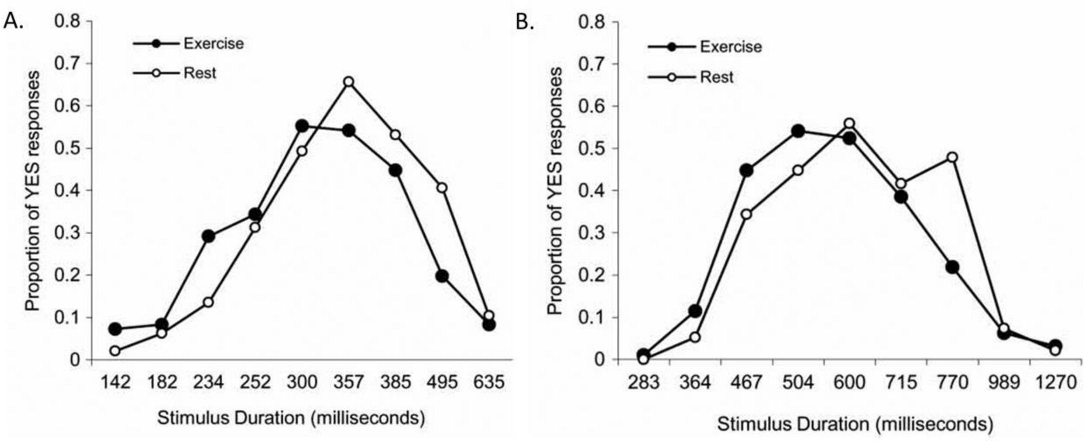

**Figure 4. Generalization gradients for temporal generalization task performed during exercise and rest. (Reproduced from: Lambourne, 2012)**
Proportion of yes responses plotted against stimulus duration for the rest and exercise conditions and the different stimulus ranges (300 ms (A), 600 ms (B)).

Interestingly, Tonelli et al. (2022) tried to expand the effect of time overestimation induced by cycling to the third fundamental magnitude, and asked participants to perform a distance judgment by estimating the distance between two simultaneously presented stimuli the authors found no effect of physical activity on estimated distance. This result suggest that this magnitude might be more resilient to influence of co-occurrent lower-body motion. On top of this, this study also provides an expansion of previous results regarding the distortion of perceived duration. Indeed, the authors found that while physical activity produced an overestimation of durations in the subsecond range, as predicted by the existing literature, durations in the suprasecond range were left relatively unaffected. In the discussion the authors speculate that this result is in line with the speculation that there are two different systems devoted to the perception of durations in the millisecond (Buonomano & Karmarkar, 2002) and the seconds range (Gibbon, 1977). The millisecond range would be more fundamental for motion and motor coordination and thus be more prone to being distorted by physical activity. However, this result is partly at odds with previous reports of duration overestimation induced by physical activity for much longer duration (Edwards & McCormick, 2017; Sayalı, Özoglu, et al., 2018). These mixed results might be caused by the major change in both physical activity paradigms and duration perception tasks that can be found across studies. This consideration does not only apply to the possible distinction between subsecond and suprasecond time perception, but also to whether physical activity distorts time perception across sensory modalities. Indeed, to the best of my knowledge, the only study in which the auditory modality was investigated provided mixed results, which running affecting duration perception in a classification task but not in a time generalization task. While it is undeniable that physical activity interacts with duration perception at some level, it is still unclear to which sensory modality and duration ranges this interaction generalizes. For this reason, in Chapter 5 I investigated this by using the standardized running task also employed in Chapter 4 and systematically varying stimuli duration between the subsecond and suprasecond range and the presentation modality, by running an experiment in which subjects had to judge durations presented in the visually and one in which participants had to perceive duration aurally.

## 1.4 Peripersonal and Extrapersonal Space

As already mentioned above the ATOM theory suggests that we learn about the association between magnitudes through motor interactions with the environment (Walsh, 2003). An apparent consequence of this suggestion is that we can only directly interact with magnitudes that are places in our reaching space. Indeed, the distinction between what we can and cannot reach is of primary importance for defining efficient motor plans that allow us to interact with the environment. It is thus not surprising that in Rizzolatti et al. (1981) discovered in the periarcuate neurons of monkeys the existence of multi-modal neurons that only fire if a stimulus is placed near the body of the animal. The authors named this area the Peripersonal space, that can be operationally defined as everything that lies within arm's reach. All that lies beyond arms reach, on the other hand, falls in the Extrapersonal space. Interestingly, one of the predictions of ATOM was that if magnitude systems originate in the need to compute space, time and size for action, they should behave differently towards stimuli that are within or out the Peripersonal space (Bueti & Walsh, 2009). Despite the relative easiness of testing magnitude perception at different distances, to the present day there are only a few studies that have tried to investigate this. One example comes from the investigation of the phenomenon known as pseudo-neglect. When asked to bisect a horizontal line, neurologically healthy individuals tend to provide leftward biased responses, this is effect is proposed to show a default leftward bias in spatial attention (McCourt & Jewell, 1999). Interestingly, however, this attentional bias attenuates progressively with distance: when asked to perform the bisection task in EPS, subjects' responses shift rightward not leftward (Longo & Lourenco, 2010; McCourt & Garlinghouse, 2000), suggesting a possible dissociation between space perception in Peripersonal and Extrapersonal space. A similar effect involving number line bisection has been found with digits, with again a reduction in the left-ward bisection bias as stimulus distance increases (Longo & Lourenco, 2010). However, these two examples might be argued to reflect a mere shift in attention, and not a genuine change in magnitude perception as a function of the stimulus being within or outside of the Peripersonal space. A more explicit way of testing this possible dissociation would be to use a task such as reproduction or estimation. Indeed, Anelli et al. (2015), asked participants to reproduce half of the duration of a stimulus that could be placed either in the Peripersonal or the Extrapersonal space. As perceived size automatically changes as a function of viewing distance, the authors also controlled for this variable in order to be able to rule out a possible spurious effect induced by the influence of perceived distance on duration. Their results show that while duration reproduction was quite accurate when participants were tested in Peripersonal space, duration were significantly overestimated when stimuli were presented in the Extrapersonal space, regardless of stimulus size (Fig. 5). This result is quite interesting, as it might suggest that there are two different systems dedicated to the perception of magnitude based on their relevance for action. However, to further support this hypothesis this result would need to be extended also to other relevant magnitudes. For this reason, in Chapter 6 I tried to replicate this novel finding on duration perception and also try to expand this effect to another fundamental magnitude: non-symbolic numerosity. Participants were asked to reproduce half of the duration of stimuli that could be presented either in the Peripersonal or Extrapersonal space and, in a separate experiment, to estimate half of the numerosity of a cloud of dots that could be presented at different viewing distances.

While in animal models the border between PPS and Extrapersonal space can be accurately measured using in-vivo single-cell recording (Rizzolatti et al., 1981), in humans a behavioral approach has to be adopted. One of the most widely used methods to capture the boundary between Peripersonal and Extrapersonal space is a visuo-tactile detection task designed by Canzoneri et al. (2012). In this task participants are presented on each trial with a looming auditory stimulus that gives the illusion of an approaching object.  Following a predetermined delay, a tactile stimulus is delivered to the hand as a vibration and participants are instructed to react to this as fast as possible, while ignoring the auditory stimulus. If the vibration is delivered when the sound is perceived as being in the PPS then reaction times are significantly reduced. The operational definition of PPS using this auditory-tactile detection task can be summarized as the maximum distance at which the auditory stimulus can still facilitate the detection of the tactile stimulus. One of the characteristics of PPS neurons is that they are multimodal (Rizzolatti et al., 1981) and are thus able to signal both auditory and visual stimuli. The auditory-tactile detection task can even be adapted to use visual stimuli to facilitate the vibration detection. However, delivering ecologically accurate looming visual stimuli posits some technical challenges. These challenges can be overcome by using stimuli presented in Virtual Reality (VR), a relatively novel approach that has however provided promising results (Buck et al., 2020; Serino et al., 2018)(Fig. 5).

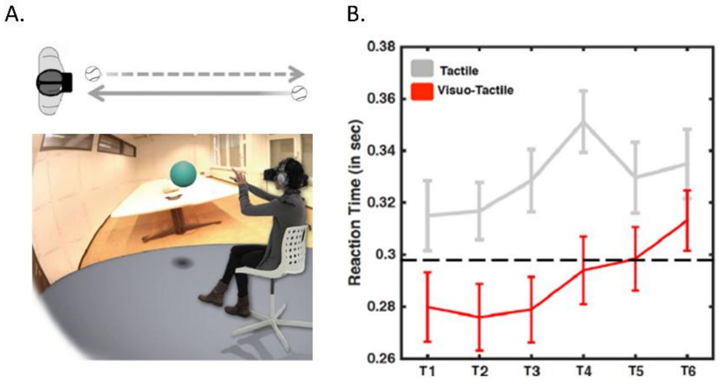

**Figure 5. Peripersonal space measuring in a Mixed Virtual Reality Environment (Adapter from: Serino et al., 2018)**

**A.** In the visuo-tactile detection task, by means of an head mounted display, looming virtual stimuli are visually presented being overimposed in an online recording (or prerecorded video) of the external environment and of the participant's body within the scene.

**B.** Averaged reaction times (RTs) (error bars represent SEM) to tactile stimulation as a function of temporal delays for unimodal tactile (gray) and visuo-tactile trials (red). Visuo-tactile stimuli induced a stronger modulation of tactile RT, as compared to unimodal tactile stimuli, depending on temporal delays, that is on the position of the virtual ball in space at the time of tactile stimulation. The PPS boundary is identified as the distance at which the visual stimulus induced significantly faster RT as compared to the fastest unimodal tactile RT (as indicated by the dashed line).

The operational definition of the Peripersonal space, the space that we can reach, might be considered somewhat ambiguous, as the space that we can reach can change based on whether, for instance, our movements are restricted, or in case we use a tool. Tool-use is an ability not unique to humans, and has for instance been documented in a variety of primates (Boesch et al., 2000). Indeed, there have reports that the receptive fields of neurons dedicated to the perception of stimuli placed in Peripersonal space are not static but can reshape in order to take into account modifications in our range of action. When monkey are instructed to use a tool in order to retrieve food that has been placed in the distance the receptive field of the Peripersonal neurons has been reported to elongate in order to respond also to areas that are now part of the reaching space as a consequence of tool use (Iriki et al., 1996).

A similar phenomenon has also been reported in humans, with specific kinds of training that expand the space we can act on, resulting in faster reaction times also for stimuli that would normally fall into the Extrapersonal space (Canzoneri et al., 2013). Moreover, a prolonged period of training can induce long-term reshaping of the Peripersonal space, as it has been documented for tennis players who exhibit greater Peripersonal space while holding a racket (Biggio et al., 2017). However, it is not clear which aspect of the training (e.g. merely holding a tool, using that tool to act in Extrapersonal space, or the direction of motion) is responsible for triggering the reshaping. For this reason, in the 7th and last experimental chapter of this thesis I investigated the reshaping of Peripersonal space in a Virtual Reality setting in which participants extension of Peripersonal space was measured before and after completing different types of trainings.

# Chapter 2

# The interaction between time and numerosity perception is task dependent

# 2. The interaction between time and numerosity perception is task-dependent

## 2.1 Introduction

In the last few decades, much research has been dedicated to investigating whether the human brain encodes different perceptual dimensions such as duration, size or numerosity via single or via multiple and functionally independent magnitude representations. Indeed, it has been pointed out that the brain frequently needs to process quantitative inputs from different dimensions such as space, time and number at the same time, and these magnitudes often correlate with each other. Just as the longer the distance to walk, the longer the time needed to reach the destination and the more steps to get there. The ATOM Theory (Walsh, 2003) proposes that a shared neural and functional mechanism of magnitude representation might be an efficient interface to combine perceptual information with the programming and execution of the motor routines needed to interact with objects in the environment.

Indeed, several studies have reported similarities between the perception of space, time, and number. For example, the discrimination of temporal, numerical and spatial magnitude follows the same psychophysical law - Weber's law - with the just noticeable difference (JND) between two stimuli being proportional to the overall intensity level (Allan & Kristofferson, 1974; Gibbon, 1977; Killeen & Weiss, 1987). Furthermore, the distance effect reported in numerical judgements, according to which the higher the numerical distance between two numbers, the easier to discriminate between them, also occurs for quantitative judgements of other dimensions such as length (Dormal & Pesenti, 2007; Fias et al., 2003) and duration (Droit-Volet et al., 2004). Other similarities have been reported regarding the effects of contextual information. After observing a fast-moving visual stimulus for a few seconds (motion adaptation), the perceived time (Burr, Ross, et al., 2011; Johnston et al., 2006), numerosity (Fornaciai et al., 2018) and apparent position (Whitney & Cavanagh, 2003) are all robustly compressed. Similarly, eye movements have been reported to distort perceived time, space, and numerosity with a strong compression of all these dimensions at the time of the saccadic onset (Binda et al., 2011; Morrone et al., 2005). Recently, it has been shown that the interaction between action and perception also occurs for other effectors, as the repetitive execution of hand routines (motor adaptation) compresses or extends the perceived time, space, and numerosity depending on the number of movements executed (Anobile, Cicchini, et al., 2016a; Anobile, Domenici, et al., 2020; Anobile et al., 2021; Maldonado Moscoso et al., 2020; Petrizzo et al., 2020).

A possible consequence of a shared processing of different perceptual dimensions might be the existence of interference effects amongst them when they get presented together, even when the information from a given dimension is not relevant to accomplish the task. For example, observers that must select the more numerous between two visual arrays of dots in which the number of dots and the area occupied by dots are congruent (i.e. the more numerous array also has a greater area), or incongruent (i.e. area is kept constant so that the more numerous array has smaller individual elements than the less numerous one), are slower and less accurate in the incongruent trials (Nys & Content, 2012).

Another class of interference effect regards the interplay between spatial and temporal information processing. Several studies reported that larger stimuli are perceived as lasting longer than smaller ones (Rammsayer & Verner, 2014, 2015; Xuan et al., 2007). However, it appears that while irrelevant spatial information cannot be ignored when making judgments about stimuli duration, the opposite is not necessarily true as the performance of participants that are asked to evaluate the spatial extent of growing lines is not influenced by the duration of lines (Casasanto & Boroditsky, 2008).

In addition, several studies have also reported a strong interplay between the perception of time and numerosity. Leveraging on evidence collected in animal studies, it has been suggested that time and numerosity might be represented via a shared representational mechanism in which an ‘internal accumulator’ represents the numerosity or duration of events/objects by summing up the impulses yielded by a generator (Meck & Church, 1983). This common code for time and numerosity seems to be supported by studies showing that in rats and human infants, a numerical rule can be generalized into the temporal domain and vice versa (de Hevia et al., 2012; Meck & Church, 1983). These findings are complemented by psychophysical evidence showing that in human observers, the numerosity of visual stimuli interferes with the judgement of their duration (Dormal et al., 2006). Nonetheless, it is worth noting that robust asymmetric effects have also been reported for the interaction between time and numerosity: when participants judge the numerosity, the duration of the stimuli does not significantly affect numerosity estimates (Dormal et al., 2006). In addition, emotional stimuli affect time and number in opposite ways, as these have been reported to yield overestimating temporal estimates but *under*estimation of numerical estimates (Hamamouche et al., 2018).

Even more critical for the idea of a shared magnitude mechanism are reports documenting asymmetric or conflicting effects for the different dimensions. For example, in two recent studies, space, time and number were pitted against each other, and participants were asked to judge the duration, the numerosity or the spatial extent of visual stimuli. One of these studies reported a significant interference of numerical and spatial information on temporal judgments (Dormal & Pesenti, 2013), while in the other study temporal judgments were not affected by space or number, even though temporal information yielded significant distortions of numerical and spatial judgments (Lambrechts et al., 2013). In addition, some studies failed to find any signature of cross-dimensional interference. For instance, in an estimation task of auditory signals, perceived numerosity was not found to affect temporal estimates (Agrillo et al., 2010) while, in another experiment, no interference between numerosity and duration was reported in high working-memory load tasks (Bi et al., 2014).

Here we hypothesize that the current empirical discrepancies could be related to crucial methodological differences among the studies, and that specific experimental paradigms might be more prone to induce cross-dimensional interference effects than others. This idea finds support in the results of a study by Yates et al. (2012). These authors found that in a discrimination task similar to that used by Xuan (2007), the perceived size of visual stimuli significantly affected temporal judgments, so that larger stimuli were estimated as lasting longer, thus replicating previous results. However, when participants were required to judge whether the same stimuli had the “same or different” duration, thus eliciting a direct semantic instantiation of the concept of “magnitude”, the opposite effect was found with larger stimuli being judged as lasting shorter.

The main goal of the present study is to test whether, in line with recent evidence in the study of the space-number association (Pinto et al., 2019, 2021), the use of magnitude-related response codes, e.g. “shorter” vs “longer” plays a crucial role in triggering and guiding the functional interaction between time and numerosity perception, in a way similar to that documented by Yates et al. (2012) for the interaction between size and duration. In four different experiments, we asked participants to discriminate or estimate the duration of visual stimuli (dots arrays) while manipulating the numerosity of the set, despite this information being completely irrelevant to the task. In two discrimination tasks, participants indicated which one out of two sequentially presented stimuli had the longer duration either by indicating its position in the sequence (first or second; Experiment 1) or its color (red/green vs blue/yellow; Experiment 4). In Experiment 2, participants provided equality judgments by indicating whether the two sequential stimuli had the same or different duration. Finally, perceived duration was also measured via a task in which the temporal duration of dot arrays had to be reproduced via key press (Experiment 3).

The rationale of the study is as follows: if the perception of duration and numerosity relies on basic bottom-up shared neural/functional mechanisms, we expect the interaction between these two dimensions - in the form of biases induced by stimulus numerosity on duration estimates - to occur in all experiments. In contrast, if the interplay between the perception of duration and numerosity is guided top-down by the type of task participants are engaged in, and the use of magnitude-related response codes like “shorter” vs “longer”, equality judgements and reproduction tasks would be likely to reveal inconsistencies in the cross-dimensional interactions. If this were the case, one should conclude that cross-dimensional interactions do not arise because the magnitude of time and numerosity dimensions is processed together at the perceptual level and automatically coded in a bottom-up fashion by a shared magnitude system. Rather, one should conclude that cross-dimensional interferences are induced “top-down” by task-related processes such as the way sensory inputs are classified through response codes, represented in short-term memory and matched against each other for decision making. We anticipate that the sets of experiments from the present study reveal a highly specific interaction between time and numerosity only in discrimination tasks where the use of contrasting “shorter” vs “longer” responses provide a top-down magnitude coding bias. These results suggest that the occurrence of cross-dimensional interferences is not task-independent and that, therefore, it is imprudent to generalize the functional and theoretical implications of these interferences without considering the task conditions at the origin of these interferences.

## 2.2 Methods

### 2.2.1 Stimuli

All experiments were carried out in a dimly lit and sound-attenuated room with stimuli presented on the monitor of an iMac (5120 x 2880 resolution, refresh rate 60Hz) subtending 60° x 34° at the subject view distance of 57 cm. Visual stimuli were created via the PsychToolbox routine for MatLab (v. R2016b, Mathworks, Inc.) and consisted of clouds of dots (each element had a diameter of 0.2°) inscribed in an invisible circular area of 12° diameter centered on the monitor screen. In all conditions but Experiment 4, the dots in the set were half white and half black to keep the mean luminance identical to the mid-grey background. In experiment 4, the two clouds of dots in the sequence were colored differently, blue/yellow or red/green. The request for the participants was to indicate the color (not the position in the sequence as in Exp 1) of the stimulus lasting longer.

### 2.2.2 Subjects

A total of 23 participants took part in the experiments (mean age 28.07±7.2, 9 males). Thirteen of them participated in Experiments 1, 2 and 3; 20 participated in Experiment 4 with a subgroup of 8 participants that participated in all experiments. All observers had normal or corrected-to-normal vision and provided written informed consent before starting the experiments. The experimental procedures were approved by the local ethic committee (“Commissione per l’Etica della Ricerca”, University of Florence, 7 July 2020, n. 111) and by the Ethics Committee of the Fondazione Santa Lucia IRCCS (Date 12/12/2020 / No. CE/PROG.895).

### 2.2.3 Experiment 1 – Time discrimination

In a two-alternative forced choice (2AFC) task, participants were asked to indicate which of two sequentially presented clouds of dots (500ms of ISI) had a longer duration. Participants were required to press the "a-key" to indicate the first and the "s-key" to indicate the second stimulus in the sequence (Fig. 1A). In all trials the reference stimulus contained 24 dots and had a duration of 800ms. The duration of the test stimulus varied from trial to trial and was selected according to an adaptive staircase QUEST (Watson & Pelli, 1983) with the range of duration constrained between 400 and 1600 ms. Two different experimental conditions, measured in separate sessions, were defined by the numerosity of the test: low numerosity condition (12 dots) and high numerosity condition (48 dots). After the presentation of the two visual stimuli, a color change of the central fixation point prompted the participants to provide a response, then, after a pause of 500 ms, a new trial automatically started. The presentation order of test and reference was randomized across trials while the order of experimental conditions (defined by test numerosity) was counterbalanced across participants. For each subject, in each condition, we collected 3 sessions of 30 trials, for a total of 90 trials per condition.

### 2.2.4 Experiment 2 – Equality Task

Participants were required to compare two visual stimuli presented sequentially and indicate whether their duration was identical (response "same") or not (response "different"; see Fig. 2A) by using a computer keyboard. Stimuli and procedure were the same as in Experiment 1 with the exception of the sampling procedure of the test duration, which was defined by a logarithmically spaced distribution ranging from 400 to 1600 ms in eleven steps rather than by an adaptative staircase. Similarly to Experiment 1, the presentation order of test and reference was randomized across trials, and the two experimental conditions defined by high or low test numerosity were presented in separate sessions. For each subject, in each condition, we collected 3 sessions of 66 trials (each duration randomly presented 3 times), for a total of 198 trials per condition.

### 2.2.5 Experiment 3 – Reproduction Task

In this experiment, participants were required to reproduce the duration of a visual stimulus (a cloud of dots) by holding down the spacebar on a computer keyboard (Fig. 3A). As in Exp 1 and 2, test stimulus numerosity was either 12 or 48 dots (tested in separate sessions), and the test duration ranged between 400 and 1600 ms demarking 5 different intervals: 400, 600, 800, 1200, 1600. Participants were required to reproduce the perceived interval as accurately as possible soon after the offset of the visual stimulus. No time constraint was applied to interval reproduction.

### 2.2.6 Experiment 4 – Time discrimination task for colored stimuli

Experiment 4 was identical to Experiment 1, but the visual stimuli were colored, not achromatic. In each trial, the dots of one cloud (randomly test or reference and first or second in the sequence) were 50% red and 50% green while those of the other were 50% yellow and 50% blue (Fig. 9A). Participants were instructed to indicate the color of the stimulus that lasted longer by responding with a key press. Please note that this procedure required to identify the more numerous stimulus via a color label and not by its position in the sequence. This controlled for the possibility that cross dimensional interferences reported in Exp 1 were prompted by the ordering information exploited to accomplish the task.

### 2.2.7 Data Analysis

For Experiment 1 and 4 (time discrimination) the proportion of trials in which the test appeared as “longer” than the reference was plotted against the test duration and fitted with a cumulative Gaussian error function separately for the two test numerosity conditions (high and low). The 50% point of the error functions indicates the point of subjective equality (PSE). The width of the Gaussian function (standard deviation) was taken as an index of sensory precision (see Fig. 7A).

In Experiment 2 (equality-task) perceptual accuracy was measured by plotting the proportion of trials in which the test was judged as having the same duration of the reference, as a function of the test stimulus physical duration (examples in Fig. 8A). Data were then fitted with Gaussian functions, with the peak indicating the physical duration of the test stimulus to have it perceptually matched to the reference (PSE). The standard deviation of the best-fitting function was instead taken as an index of perceptual precision.

In Experiment 3 (time reproduction), for each duration, we calculated the mean standard deviation of reproduced duration for each test duration, indicating observers' accuracy and precision respectively.

Statistical significance was tested via frequentist repeated measures ANOVAs and t-tests, whenever the sphericity assumption was violated, the Greenhouse–Geisser correction was applied. We also performed repeated measures bayes-factors t-test along with the frequentist t-test. A BF10=1 indicates that there is no evidence for either hypothesis, while a BF10 higher than 1 suggest evidence for the alternative hypothesis, with the robustness of the evidence increasing as the BF10 increases. Evidence of H0, on the other hand, is suggested with a BF10 lower than 1, in this case a lower BF10 indicates stronger evidence for H0. All statistical analyses were performed with MatLab 2016b (The Mathworks, Inc., Natick, MA, USA) and Jasp Software (version 0.14.1; JASP Team, Amsterdam, The Netherlands).

## 2.3 Results

### 2.3.1 Experiment 1: Duration discrimination

Participants were required to discriminate the duration of two clouds of dots. In each trial the duration of the reference (randomly presented as first or second) was fixed and equal to 800 ms while the duration of the test varied according to an adaptative QUEST algorithm (Watson & Pelli, 1983) capped between ± 0.3 log unit (Fig. 6A). We designed two experimental conditions (tested in separates sessions): in the low numerosity condition, the numerosity of the test was half than the reference (12 vs 24) while in the high numerosity condition it was twice as much (48 vs 24). Fig. 6B shows the results of the aggregate data obtained considering all participants. The proportion of "test longer" responses is plotted as a function of test duration for both, the low and high test numerosity conditions. The 50% point of the Gaussian distribution represents the point of subjective equality (PSE), that is, the physical duration of the test to be perceptually matched to the duration of the reference. A leftward shift of the curve relative to reference duration indicates a bias to overestimate the duration of the test relative to an ideal observer while a rightward shift indicates underestimation. More importantly, the relative position of the curves for the high and low numerosity condition provides a quantitative estimate of the distortions induced by stimulus numerosity on time perception. When the test stimulus was more numerous than the reference (N 48 vs 24), its perceived duration was overestimated (PSE=771 ms) relative to the condition in which the test numerosity was lower than the reference (N 12 vs 24, PSE= 864 ms). It is worth to be noted that this 100ms difference between the high and low experimental condition was induced by the relative difference in numerosity between test and reference despite such dimension was completely not informative to accomplish the temporal task. Fig. 6C shows individual data with the PSEs in the low numerosity condition plotted against the PSEs in the high numerosity condition. It is clear from inspection that for most participants, PSEs in the low numerosity condition were larger than the high numerosity condition to indicate that stimuli of larger numerosity were perceived to last longer. To statistically test for this difference, individual PSEs were used in both, frequentist and Bayesian paired samples t-test. The frequentist analysis revealed a significant difference between high and low numerosity condition (t(12)=3.002, p=0.01) in line with the Bayesian analysis (Bf10=5.35) that indicated substantial evidence in favor of an interference between the perception of duration and numerosity.

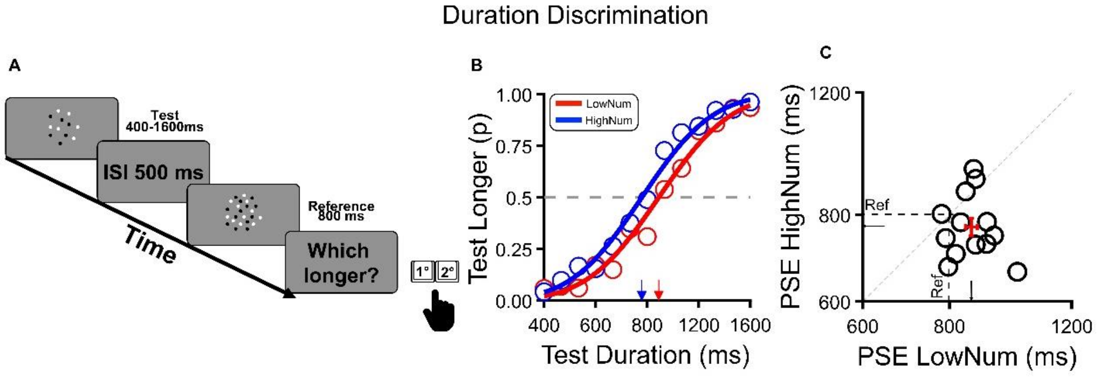

**Figure 6. Experiment 1: Time discrimination task.**

**A.** Participants were asked to indicate which of two clouds of dots presented sequentially lasted longer. In all trials, the reference stimulus consisted of 24 dots and had a fixed duration of 800ms. The test stimulus had a variable duration, between 400 to 1600 ms, and its numerosity was either 12 (low numerosity) or 48 (high numerosity) with the two conditions tested in separated sessions.
**B.** Aggregate data about the proportion of "test longer" responses plotted against test duration. The 50% point of the best-fitting cumulative gaussian curves indicate the PSEs, that is the physical duration of the test stimulus to perceptually match a reference of 800 ms. Different test numerosity conditions are plotted in different color: low numerosity (N=12) in red and high numerosity (N=48) in blue respectively.
**C.** Individual PSEs (open circle) for each participant in the low numerosity condition (x-axis) plotted against the high numerosity condition (y-axis). Dots falling below the bisection line (dashed, diagonal line) indicate a higher PSE in the low numerosity condition compared to the high numerosity condition, and thus a positive covariation between perceived numerosity and duration with more numerous stimuli perceived as lasting longer than their physical duration (and vice-versa). The filled circle indicates the PSE ± S.E.M.

### 2.3.2 Experiment 2: Equality (same or different) task

In Experiment 2 participants were asked to judge whether two stimuli in a sequence had the same or different duration. Alike Experiment 1, we designed two experimental conditions: in the low numerosity condition the variable (test) stimulus was 12 (half of the reference), in the high numerosity condition 48, twice than the reference (see Fig. 7A). Figure 7B shows the results for the aggregate data averaged across all participants with the proportion of "same" responses plotted against the test duration. The mean of the best-fitting Gaussian curve indicates the physical duration of the test to be perceived as being identical to the reference (800 ms). In both experimental conditions, the peak of the Gaussian curves was found to be very close to 800 ms and indeed rather similar to each other (765ms and 760ms for the high and low test numerosity condition respectively) to suggest that when engaged in equality, not discrimination tasks, observers were able to encode visual stimulus duration regardless of their numerosity. In other words, the processing of stimuli duration and numerosity turn out in being independent to each other in equality judgements, with no sign of any cross dimensional interference effect. Such a claim turned out in being fully supported by both frequentist and Bayesian paired samples t-test. The former revealed that the difference amongst the two experimental conditions was far from being significant (t(12)=0.48, p=0.64), and the latter indicated a complete lack of evidence to support the existence of an interaction between the perception of numerosity and stimuli duration (Bf10=0.308).

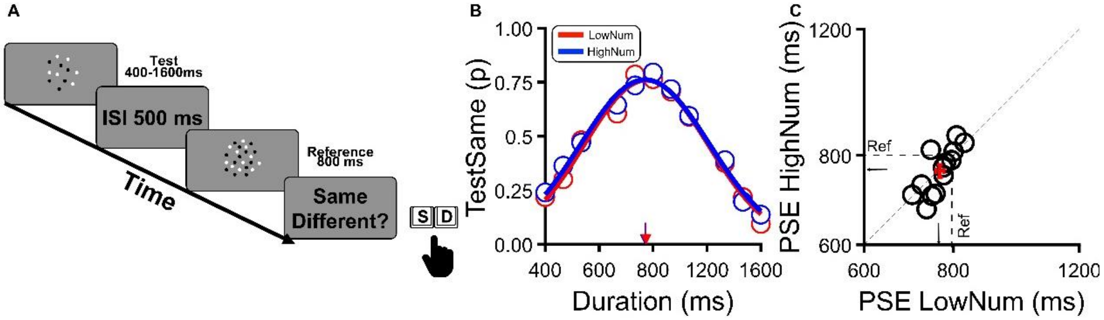

**Figure 7. Experiment 2: Equality (same/different) task.**

**A.** Participants were asked to indicate if two stimuli presented sequentially had the same or different duration. All the characteristics of the two stimuli, test (variable) and reference (fix) were identical as in Exp 1.

**B.** Results fo the aggregate data. The probability to perceive the test stimulus as lasting the same as the reference (800 ms) plotted against several test durations for the low numerosity condition (N test=12) and high numerosity condition (N test =48) in red and blue respectively. Continuous colored curves indicate the best-fitting Gaussian to the data. The peaks of the Gaussians (indicated by arrows on the x-axis) indicate the PSEs, that is, the physical test duration needed to perceptually match the reference (800ms).

**C.** Individual PSEs (allow dots) for each participant in the high numerosity condition plotted against PSEs for the low numerosity condition. The central cross represents the average perceived duration and error bars ± 1 S.E.M.

### 2.3.3 Experiments 3: Time reproduction

In this experiment, participants were asked to estimate the duration of a stimulus (array containing either 12 or 48 dots) displayed on a monitor screen and then reproduce it, as accurately as possible, by holding down a response key (Fig 8A). The averaged reproduced intervals for the 5 tested durations (400, 600 800, 1200 and 1600 ms) are shown in Fig. 8B for the low (N12) and high (N48) numerosity conditions. As it is clear from inspection, duration reproduction was quite accurate for all intervals (429, 602, 749, 1009 and 1241ms for low and 440, 601, 742, 1023 and 13200ms for high numerosities respectively) with rather no difference between high or low test numerosity. Of particular interest are the reproduction data for the 800ms as this matched the reference duration in Exp 1 and 2. Figure 8C shows individual data for time reproduction in the low numerosity against the high numerosity for 800ms. Almost all datapoints are scattered along the diagonal, veridical line to suggest that the reproduction of the observed interval was not significantly affected by stimulus numerosity a pattern of results that also generalized to the other tested durations (those shorter or longer than 800 ms). We ran a two-way repeated measures ANOVA with test numerosity (low or high) and 6 durations (400, 600, 800, 1200 or 1600ms) as factors. We found a significant effect of duration (F(1.53, 18.36)=302.76, p<0.001) indicating that participants responses covaried with interval magnitude with longer durations being reproduced as lasting longer and vice versa. However, the factor numerosity (F(1,12)=0.11, p=0.75) and the interaction between duration and numerosity (F(2.83, 33.92)=0.61, p=0.60) was found to be largely not-significant. A Bayesian analysis ran by collapsing together the data for the five different durations, nicely complemented these results. Again, no evidence was found for an interference of stimulus numerosity on duration estimates (Bf10=0.29).

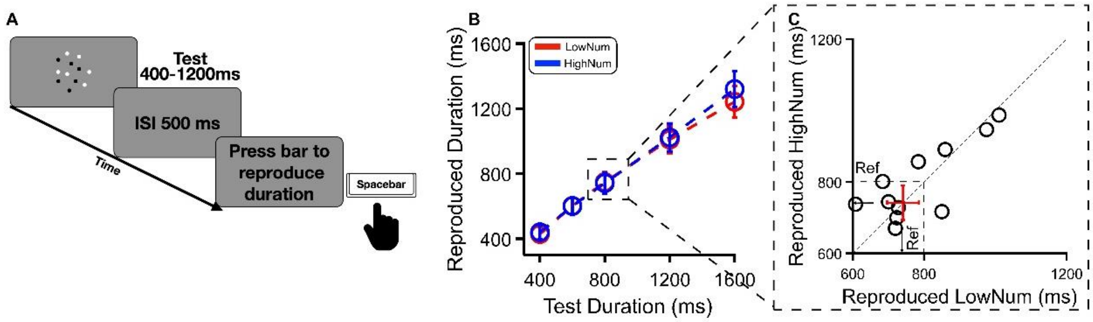

**Figure 8. Experiment 3. Time reproduction.**

**A.** Participants were asked to press a key on the keyboard to reproduce the duration of a clod o dots displayed at the center of the monitor. As in Exp 1 and 2 two different experimental conditions were designed: in the high numerosity condition the test stimulus comprised 48 dots while in the low numerosity condition numerosity was equal to 12 (tested in separated sessions).

**B**. Results for aggregate data. Reproduced test durations are plotted as a function of physical stimulus duration with the low (N12) numerosity condition and the high numerosity (N48) condition colored in red and blue respectively. Open symbols represent average reproduced duration for each tested interval ± 1 S.E.M.

**C**. Reproduced duration for the 800ms interval for each participant in the low plotted against the high numerosity condition (open symbols). The central cross indicates the average perceived duration across all participants ± 1 S.E.M.

### 2.3.4 Experiments 4: Duration discrimination without ordering response

The main result of the battery of tests presented above is that perception of time and numerosity just interact in the duration discrimination experiment whilst they were found to be independent in the equality (same/different) and reproduction tasks. Given that the very same intervals and visual stimuli were exploited in all experiments, it is likely that the selective effect reported in time discrimination is related to the procedures followed to accomplish these tasks. Indeed, in the duration discrimination experiment observers were required to indicate which stimulus, whether the first or second lasted longer with this ordering code that might have induced to exploit all available quantitative information, and thus even the difference in numerosity between the test and the reference. To test for this hypothesis, we devised a new version of Exp 1 in which test and reference stimulus were colored differently and participants did not indicate the position of the longest stimulus in the sequence but just its color. In details, test and reference could either consist of a cloud of red and green dots or alternatively blue and yellow dots with the colors of the two stimuli counterbalanced across trials. Fig. 9 shows the results of the aggregate data across all participants. Alike in Figure 2.1B, the proportion of "test longer" responses are plotted against test duration with the low and high numerosity conditions (test numerosity one half or twice than the reference) displayed as separated curves. The results indicate that when the test was more numerous than the reference, its duration was overestimated as indicated by a PSE of 781ms. However, the opposite holds true for the low numerosity condition with a PSE achieved for a test physical duration of about 840 ms. Again this was confirmed by both a frequentist paired-samples t-test (t(19)=5.66, $p<0.001$) and a Bayesian approach (Bf10=1262). This result perfectly matched the result of Experiment 1, to support the idea that in discrimination tasks an interplay between perceived numerosity and duration occurs despite the response code used by the participants.

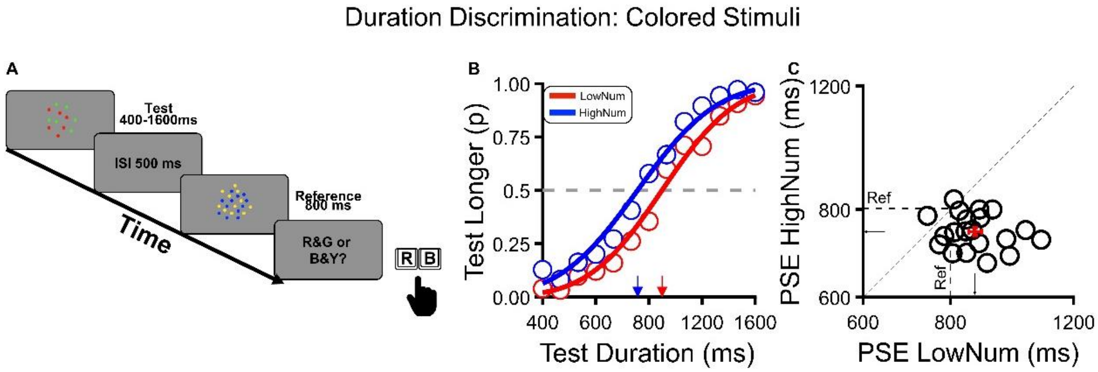

**Figure 9. Experiment 4. Time discrimination with colored stimuli.**

**A.** Duration discrimination with colored stimuli. All procedures were identical to the discrimination task of Exp 1 but the test and reference stimuli were colored differently: red/green or yellow/blue (color assignment counterbalanced across trials). In each trial, participants were required to indicate the color (not the position in the sequence) of the stimulus that lasted longer.

**B.** Aggregate data. Proportion of "test longer" responses plotted against test duration (open symbols) and best-fitting cumulative Gaussian functions to the data (solid lines). The 50% point of the psychometric function (indicate by arrows) represents the PSE. The rightward shift of the curve for the low numerosity condition (red) relative to the high numerosity condition (blue) indicates an interference effect of stimulus numerosity on duration estimates with more numerous stimuli perceived to last longer and vice versa

**C.** Individual PSEs in the low numerosity condition (test numerosity=12) plotted against those measured in the high numerosity condition (N=48). Almost all datapoints are displaced below the diagonal line to indicate that PSEs in the low numerosity were longer than in the high numerosity condition and thus, that less numerous stimuli were perceived to last shorter and vice versa.

To better achieve a quantitative estimation of the interference between the perception of stimuli duration and numerosity in the four different tasks, we measured for each of them the perceived/reproduced duration matching an interval of 800ms for both, the high and low numerosity condition. The results shown in Fig. 9A indicate a clear interaction between perceived duration and numerosity in both discrimination tasks. Regardless participants indicating the longer stimulus by reporting its position in the sequence (ordering information, Exp.1) or its color (Exp.2), in both discrimination tasks the perceived duration of the test in the high numerosity condition (N=48) was about 100ms longer than in the low numerosity condition (test numerosity half than the reference, N=12). On the contrary, neither in the equality (same/different) nor in the duration reproduction task, stimuli numerosity affected duration estimates. In the equality task, the test was matched to an 800ms reference when its physical duration was slightly shorter (40-50ms) to indicate a small bias to overestimate the duration of the variable stimulus. Similarly, participants on average reproduced a visual stimulus lasing 800 ms demarking an interval of about 740ms. More importantly, a change of a factor of 4 in test numerosity (from 12 to 48) did not significantly affect duration estimates neither in the equality nor in the reproduction tasks. This pattern of results was supported by a 3X2 ANOVA with Task (Discrimination, Same or Different and Time Reproduction) and Numerosity (High or Low numerosity) as factors. We found that while neither of the main factor was significant (Task: F(1.1, 13.1)=1.99, p=0.18, Numerosity: F(1,12)=2.96, p=0.11), their interaction was highly significant (2,24)=8.34, p=0.002) suggesting a that the effect of numerosity on duration perception is modulated by the task used. Indeed, a series of post-hoc test confirmed that the only significant interaction between Task and Numerosity is the one for the Discrimination Task employed in Experiment 1 (t=3.9, p=0.006, Bonferroni corrected). These results are graphically represented in Figure 10A, where average Perceived Duration is plotted against Numerosity (High or Low) for the 4 different experiments.

### 2.3.5 Sensory precision

One possibility to account for the task dependent interaction between perceived numerosity and duration, might be in terms of differences in difficulty between the tasks. For example, to discriminate between the duration of two stimuli might have been more difficult than categorizing them as identical or different and this, in turn, might have automatically prompted the observers to leverage on all available quantity information and contaminate duration estimates with numerosity information. To test for the hypothesis that cross-dimensional interactions (i.e time and numerosity) depends on task difficulties, we measured averaged response precision for the purely perceptual tasks (Discrimination and Same/Different) under the plain assumption that the more difficult the task, the lower the average response precision. In details, we retrieved the standard deviation (SD) of the best fitting psychometric curves defining the probability of perceiving the test stimulus as longer against its physical duration in Exp1. Then, we measured the SDs of the best-fitting Gaussian curves in Exp 2 representing the probability of a same responses against the relative duration of the test and reference. Before matching the values across the two experiments, we first measured whether in any of them the SDs differed between the high and low numerosity condition. As no statistically significant difference was observed (both p-values higher than 0.2) we averaged SD values between the high and low numerosity to obtain a single estimate for each experiment. As shown in Fig. 9B, despite a rather consistent variability between subjects, the average SDs were found to be very similar in the two experiments and averaged around 350ms. The lack of difference between participants' response precision – that we used to index task difficulty – was also supported by a paired-samples t-test (t(12)=0.6, p=0.53). In other words, despite perceived numerosity and duration interacted in the discrimination but not the equality (same/different) task, the difficulty of the two turned out in being rather identical to suggest that neither the complexity is a critical factor to define the interference effects between the two perceptual dimensions.

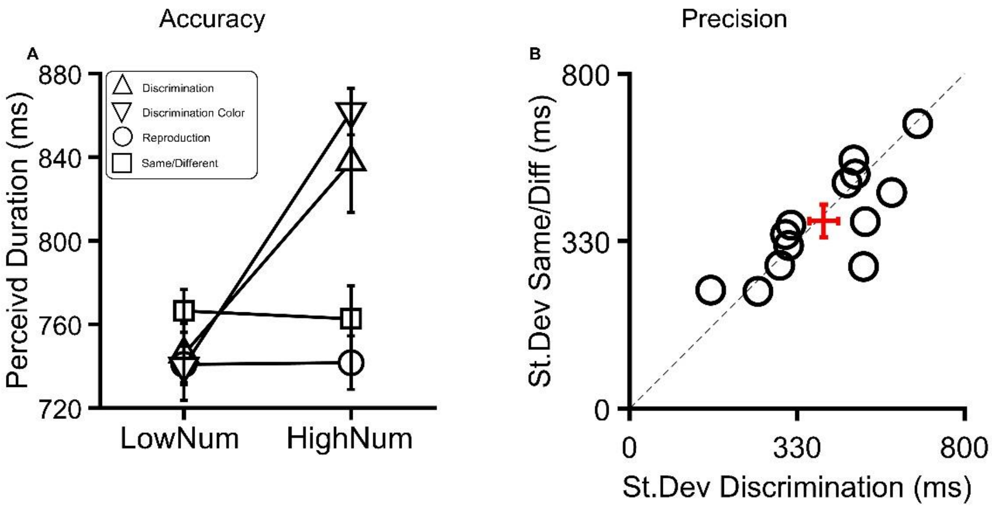

**Figure 10. Accuracy and Precision**

**A. Matching duration estimates across the 4 experiments.** Test stimuli estimates to match an 800ms interval in the time discrimination, same/different and reproduction task for the condition in which test numerosity was 12 or 48, low and high numerosity condition respectively. While in the equality (same/different) and reproduction task, test duration estimates were found to be independent by the test numerosity (squares and up triangles), in both discrimination tasks perceived duration and numerosity covaried to each other with more numerous stimuli perceived to last longer and vice versa (circles and down triangles).

**B. Responses precision in the four experiments.** We indexed the precision of participants responses in the discrimination and equality task via the standard deviation of the response distributions. On average, SD values were quite similar for both tasks, those in which perceived numerosity interfered with duration estimates (time discrimination, Exp 1) as well as those in which no signature of interference was observed (equality task, Exp 2).

## 2.4 Discussions

In the current study, we measured duration perception of visual dot arrays. By manipulating the task-irrelevant numerosity of visual dots during a duration discrimination task, we tested whether numerosity affects time perception. The numerosity-time interaction was measured with several different tasks and judgment procedures while using the same stimuli and tasks matched for difficulty. Across four experiments, duration perception was measured against discrimination, equality judgments, and reproduction tasks. The results revealed a surprisingly task-specific interaction, with only discrimination tasks inducing a bias in temporal duration judgements as a function of stimuli numerosity, with more numerous stimuli being perceived as lasting longer. While behavioral magnitude interactions have been classically interpreted as a key proof for the existence of a generalized magnitude system, the current results cast doubt on such an interpretation, highlighting the need to carefully control for task-related factors (such as susceptibility to decisional biases) before drawing general conclusions. It is worth mentioning that this is not the first study highlighting a similar, controversial issue. Xuan et al. (2007) asked participants to judge which of two visual squares lasted longer (discrimination task). The results showed that relatively bigger squares were perceived as lasting longer compared to smaller squares, an effect also found by leveraging on a duration reproduction paradigm (Rammsayer & Verner, 2015). However, Yates et al. (2012) raised the question of whether bigger squares were genuinely perceived or merely judged as lasting longer. To this aim, Yates et al. (2012) measured the effect of size on time perception by employing two different tasks. The rationale was that if size genuinely affects time perception, the interference between these two dimensions, indexed in terms of bias in duration judgements, should occur independently of the task. The results obtained with a discrimination task similar to that used by Xuan et al. (2007) replicated the main effect, with bigger squares being judged as lasting longer. Crucially, when the effect was measured via a same-different task, the results showed an opposite timing bias, with larger stimuli perceived to last shorter. The authors concluded that task-dependent decisional biases play a key role in generating cross-dimensional interactions in magnitude judgements. This implies the need for careful experimental monitoring of how decisional factors can influence the results of investigations focused on cross-dimensional magnitude processing and the interpretation of the same results.

Before the present study, whether the perception of size and duration is the only cross-dimensional interplay to show a task-dependent selectivity or whether it generalizes to other domains was an unanswered question. Two previous studies that employed a discrimination task where participants had to judge which stimulus lasted longer reported a significant interaction between number and time magnitudes (Javadi & Aichelburg, 2012; Xuan et al., 2007). The method used in those studies is equivalent to the one employed here in Experiments 1 and 4, which, notably, were the only two experiments in which we found a significant influence of numerosity on time. Importantly, some previous studies failed to detect a significant interaction between the perception of numerosity and time durations (Cappelletti et al., 2009; Chang et al., 2011; Lu et al., 2009). However, it is worth noting that these studies used Arabic digits rather than visual numerosity stimuli. Recent fMRI investigations have demonstrated that the neural correlates of numerosity discrimination of symbolic and non-symbolic number stimuli activate networks of brain areas that are not entirely overlapping (Holloway et al., 2010). This result suggests that the interaction between numerosity and duration might be selective for the type of numerosity format considered in a study.

Why, in our study, was a significant interaction between numerosity and duration only found in the discrimination task (Experiment 1 and 4)? One possible explanation is that discrimination judgments are more difficult compared to other tasks, and this, in turn, would make discrimination judgments more prone to the influence of the irrelevant numerosity magnitude. Nonetheless, in our study, no significant difference in sensory precision was found between the discrimination (Experiment 1) and the same/different equality task (Experiment 2). This result rules out the possibility that the numerosity/time interaction that we have found in Experiment 1 and 4 can be accounted for by higher task difficulty.

Another possibility is that the bias induced by numerosity on duration perception occurs at the decisional level. The most striking difference between discrimination and the other tasks used in our study is that discrimination is the only forced-choice paradigm. In these tasks, the criterion is completely eliminated whilst it plays a critical role in the “non-forced choice” tasks in which participants are free to set a threshold to make their decisions. Being pressed to make a decision might have induced the observers to use all available information, even if this was task-irrelevant, thus triggering the interaction between time and numerosity. Although fascinating, this hypothesis cannot be tested with the present data thus, future studies have to tackle this issue directly.

In their original paper, Yates et al. (2012) aimed at determining whether larger stimuli are judged to last longer because size affects perceived duration or because size biases decisions about duration. Here we wish to develop this suggestion and propose that our data shows that response codes used for judging the numerosity magnitude also bias decisions on the magnitude in the time-duration domain. Yates et al. (2012) noted that in magnitude-interaction paradigms, decision effects could be guided by "strong conceptual and linguistic similarities between magnitude across different dimensions". Here we argue that when a participant is asked to use contrasting and dichotomic decision codes like "more or less", "longer or shorter" or "smaller or larger", a shared magnitude representation across different dimensions is triggered because these very codes can be used to express and communicate magnitude across different dimensions. This, in turn, would activate a semantic representation of magnitude that is superordinate to these different dimensions. In contrast, "qualitative" response codes like "same or different" are not directly or exclusively related to the concept of magnitude, thus, might not activate a semantic representation of magnitude that is superordinated to space, number and time.

To summarize, our results suggest that the functional interaction among magnitudes from the different domains of space, number and time might not be guided by a bottom-up sensory mechanism or by a shared bottom-up coding of magnitude. Rather, the results of our experiments suggest that high-level and top-down processes involved in decision-making and guided using "magnitude-related" response codes play a relevant role in generating interactions and interferences during the coding of magnitude in space, number and time domains (see: Pinto et al., 2019, 2021). To disentangle between the "bottom-up" vs "top-down" origin of interference effects among these domains, future studies should be designed to include more than a single perceptual task.

To conclude, while a task-dependent interaction between numerosity and time does not rule out, "per se", the possibility of the existence of a system dedicated to the coding of magnitude across these dimensions, it is also true that evidence for interference effects in the perception of different perceptual dimensions does not straightforwardly imply that these interferences originate from an automatic, bottom-up and shared common mechanism that codes magnitude across these dimensions.

# Chapter 3

# Motor Adaptation Distorts Visual Space

# 3. Motor Adaptation Distorts Visual Space

## 3.1 Introduction

Encoding the position of visual objects in the external world is an essential requirement for navigating and interacting with the environment. A fundamental organizing principle of the visual system is retinotopy: signals from different parts of the visual field activate different portions of the retina and this spatially organized activity is preserved along the visual processing hierarchy. This organization of the spatial maps allows the visual system to precisely reconstruct an internal representation of the spatial layout of the external environment, resulting in an extremely accurate ability to perceive objects' spatial positions. Despite such a well-organized representation, the construction of spatial maps poses several challenges to the visual system in terms of stability, given the continuously changing visual inputs yielded by eye and head movements. Moreover, despite very accurate performances in spatial judgments tasks, the neural representation of space seems to be not completely hard-wired as it is susceptible to strong distortions induced by contextual information. One of the most common techniques for investigating how sensory processes are prone to contextual information is sensory adaptation, a form of short-term plasticity induced by a sustained exposure to a particular stimulus, such as a steadily drifting pattern (Clifford et al., 2007; Mollon, 1974; Thompson & Burr, 2009; Webster, 2011). Adaptation is a very generalized property of perceptual systems applying to most of visual and non-visual features; thus, adaptation paradigms have proven to be fundamental psychophysical tools for studying several perceptual properties, including spatial coding. For example, the perceived position of a visual object can be markedly distorted as a consequence of motion adaptation, an effect known as positional motion after-effect (PMAE) (McKeefry et al., 2006; Nishida & Johnston, 1999; Snowden, 1998; Turi & Burr, 2012; Whitney & Cavanagh, 2003).

Recently, Hisakata et al. (2016) reported a new visual adaptation effect, able to distort space representation. In their work, the authors demonstrated that, after a few seconds of exposure (adaptation) to a dense dot-array, the perceived distance between two successively presented dots was robustly compressed. This result is of particular interest as it elegantly reveals that the human visual system exploits an adaptable metric to implement the internal representation of space. However, despite being valuable, Hisakata's work was confined within the visual system whilst, in everyday life, we continuously and actively interact with a multisensory environment, which raises the question whether this flexible visual spatial map might be linked to the motor system. To answer this question, we took advantage of a new technique (named motor adaptation) that has been previously proved to be able to distort two different visual dimensions, perceived numerosity and duration (Anobile, Arrighi, et al., 2016; Anobile, Domenici, et al., 2020). The technique consisted of a short motor adaptation phase in which subjects were required to produce a series of mid-air tapping movements performed around a specific location with no concurrent visual, haptic or auditory feedbacks. Results indicate that, because of motor adaptation, visual arrays or sequences of flashes were perceived as containing fewer elements/events than they actually did. Similarly, motor adaptation was found to distort the perceived duration of a moving grating, thus expanding the interaction between the perceptual and the motor system in the processing of perceived time. Interestingly, all aforesaid motor adaptation effects were spatially selective and only distorted the representation of stimuli presented within ≈10° around the tapping region, suggesting that motor adaptation effects occur at the sensory rather than cognitive representations of such magnitudes. Given that motor adaptation has been proved to be a sensitive and effective tool to unveil visuo-motor interactions, the aim of the current work is to exploit such a technique to test whether the representation of visual space is also linked with the motor system. The hypothesis is straightforward: if the visual spatial map interacts with the motor system, the motor adaptation should be able to affect visual spatial processing. Contrarily, if visual perception of spatial distances only relies on visual information, no effect of motor adaptation should be detected.

## 3.2 Methods

### 3.2.1 Participants

A total of 21 adults (all naïve, except one of the authors) all with normal or corrected-to-normal vision (mean age= 24.85, 17 right-handed, 4 left-handed) participated in the motor adaptation experiment. A subset of 9 of them also participated in the visual adaptation experiment. All participants gave written informed consent. The experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale – Azienda Ospedaliero-Universitaria Meyer – Firenze FI).

### 3.2.2 Apparatus

Stimuli were created with Psychophysics toolbox for Matlab (Brainard, 1997a; Kleiner, Brainard, Pelli, Ingling, Murray, et al., 2007; Pelli, 1997a) and displayed on a 60Hz – 23'' LCD monitor (Acer S23IHL) placed horizontally at a viewing distance of 57 cm. When required, hand movements were monitored by an infrared motion sensor device (Leap motion controller – https://www.leapmotion.com/) running at 60Hz. Subjects were tested in a quiet and dark room, to minimize visual and auditory feedback.

### 3.2.3 Stimuli and procedure

Visual perception of spatial distance was psychophysically measured with a discrimination task (2AFC). In all experiments, the stimuli for the discrimination task consisted in briefly and simultaneously presented pairs of black dots (duration 100ms, size 10 pixels diameter) centered 10° left and right relatively from a central fixation point (the same used by Hisakata et al. (2016)). The dot distance of the reference stimulus was kept constant across trials to 4° while the test stimulus varied trial by trial. The value of the test stimulus was decided with the method of the constant stimuli by randomly selecting, trial-by-trial, a value between 3° to 5° by steps of 0.33° (3°, 3.33°, 3.66°, 4°, 4.33°, 4.66°, 5°) roughly presenting each value an equal amount of time.

The orientation of two dot pairs was the same on a given trial but randomized (0°-360°, steps of 1°) across trials. In the motor adaptation experiment, the test stimulus was always presented on the dominant-hand side. In the visual adaptation experiment, within each trial session the positions of test and reference were kept constant (i.e. right and left respectively) but in half of the sessions the positions of test and reference were reversed. In all cases, the test was presented in the same location where the adapter had previously been displayed. Participants were asked to indicate which one of the two dot pairs appeared to be shorter and to guess if unsure. For the motor adaptation experiment, participants provided their responses verbally (left-right) and an experimenter (blind to the stimuli) recorded them by a key press. Participants generally completed each experiment on a separate day. The adaptation conditions were always performed after the baseline (to prevent artifacts due to possible relatively long-term adaptation effects). All trials of a given condition (e.g. adaptation or no adaptation) were blocked together.

### 3.2.4 Motor adaptation

As in Anobile et al. (Anobile, Arrighi, et al., 2016; Anobile, Domenici, et al., 2020), in the motor adaptation phase, subjects were asked to tap as fast as possible behind the screen with their hand floating between the monitor and the desk (without touching any surface). Participants tapped with their dominant hand for 6 seconds on each trial. The tapping movements were an “up-down” movement of one finger, with the hand concealed by the monitor itself. Tapping movements were monitored by a Leap motion controller (Fig. 11B). All trials in which the subject’s hand was not correctly positioned were automatically aborted. Similarly to Anobile et al. (2016; 2020), the tapping rate averaged across subjects was around 6 Hz (5.89 Hz , SD= 0.68, min = 4.91, max= 7.53). During the adaptation phase, only the central fixation point was presented on the screen and a change of its color signaled the subjects to stop tapping. Then, after 500 ms the visual dot stimuli were presented and participants provided their response. Each participant completed 190 trials (100 for the baseline and 90 for the adaptation condition respectively) divided into 5 separate blocks. Each test value was presented roughly equally, 7 and 6 times in the baseline and adaptation conditions respectively.

### 3.2.5 Visual Adaptation

This was a replication of the Hisakata et al. (2016) experiment (Fig. 11A). In the adaptation condition, the test phase was preceded by 60 seconds of visual adaptation (with a 5 seconds top-up at the beginning of the remaining trials). The adapter consisted of a square texture (15°x15°) containing 100 black dots (10 pixels in diameter). The position of each dot was defined with a random horizontal and vertical displacement (up to +/- 30 arcmin) and was updated every 300 ms. Each participant completed 300 trials (100 for the baseline and 200 for the adaptation condition respectively) divided into 10 separate blocks. Each test value was presented roughly equally, 7 and 14 times in the baseline and adaptation conditions respectively.

### 3.2.6 Statistical analysis

The proportion of trials where the reference appeared "shorter" than the test was plotted against the test dot pair distance and fitted with cumulative Gaussian error functions. The 50% point of the error functions estimates the point of subjective equality (PSE). The spatial delta between dots needed to move from 50% to 75% of correct responses was defined as JND (just notable difference) which was normalized by PSE gave Weber Fraction, an index of sensory precision.

Total adaptation magnitude was measured as the difference between the PSEs measured in the adaption and baseline condition. The effects induced by visual and motor adaptation were analyzed by frequentist and Bayesians ANOVAs. Effect size was reporter as $\eta^2$ and significance by p-values and Bayes Factor. Bayes factor is the ratio of the likelihood probabilities of the two models H1/H0, where H1 is the likelihood of a difference between PSEs calculated in the baseline and in the adaptation condition, and H0 the likelihood that the difference does not exist. BF were calculated by JASP (Version 0.8.6) software and reported by transforming the $BF_{10}$ (as provided by the software) into the Log10 of $BF_{10}$ (LBF). By convention, a LBF > 0.5 it is considered substantial evidence in favor of the existence of the effect, and LBF < −0.5 substantial evidence in favor of it not existing.

In order to quantitatively compare the magnitude of adaptation effect between the visual and motor adaptation, given the different sample size and the statistically different amount of variance (Levene's test p= 0.01), we applied an assumption free bootstrap test. On each of 10,000 iterations and separately for the visual and the motor conditions, we randomly resampled (with reemission) the adaptation effects (differences between PSEs), computed the average effects and then counted the proportion of time the motor condition provided higher values compared to the visual condition (the p value).

Data were analyzed with JASP Software (Version 0.8.6) and Matlab (R2017b).

## 3.3 Results

We measured whether and to what extent perceived distance between dot-pairs changed after visual or motor adaptation. In the baseline condition, subjects were asked to indicate which one of two distances demarked by a pair of visual inputs was shorter. In the visual adaptation condition, the discrimination task was preceded by a sustained exposure to a dense dot-texture (see Fig 11A). In the motor adaptation condition, the presentation of the visual stimuli was proceeded by 6 seconds of fast mid-air tapping not involving any visual, auditory or tactile stimulation (see Fig. 11B).

Figure 11C and D show sample psychometric functions for a single representative subject. In the baseline condition, the PSEs were around 4° (the actual dot distance of the fixed reference stimulus). After both motor and visual adaptation, the PSEs shifted rightwards relative to the baseline, indicating a compression of perceived distance for the adapted visual markers.

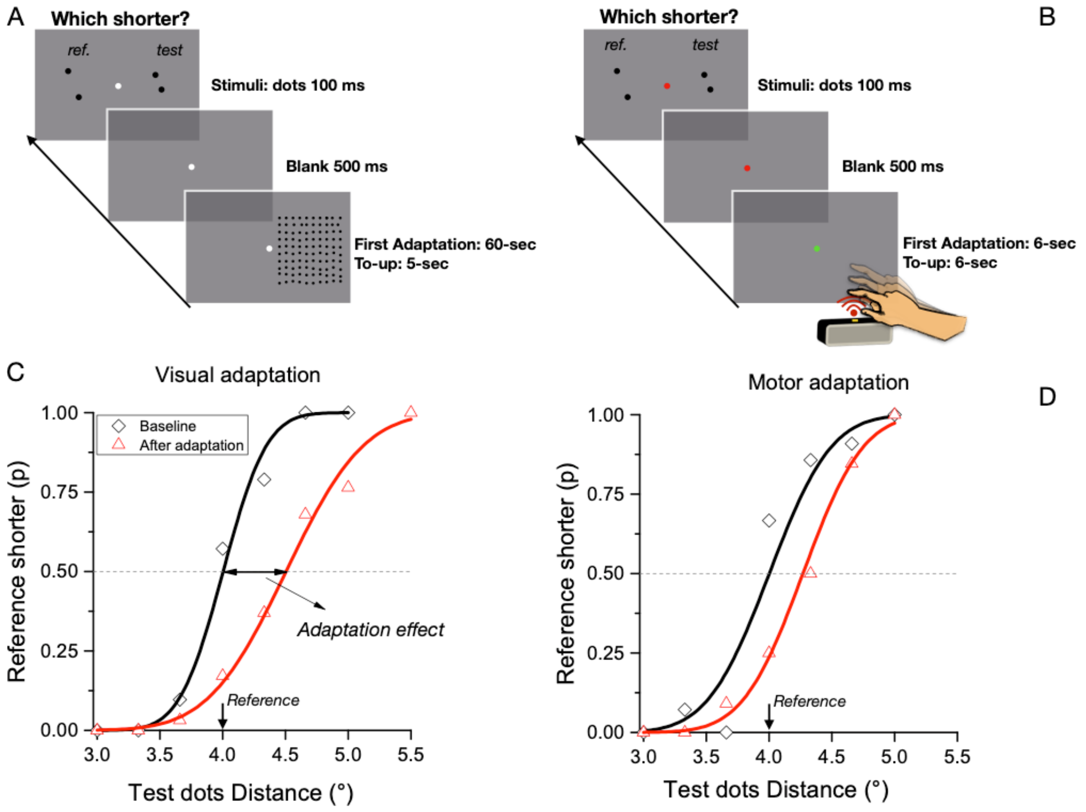

**Figure 11. Experiments Paradigm and Aggregate Subjects**

**A. Visual adaptation paradigm.** During the adaptation phase participants kept their eyes on a fixed point while they adapted to a peripheral dot-texture. Then the screen reverted to blank for 500 ms and two simultaneous dot-pairs (one on the left and the other on the right) appeared for 100 ms. Participants indicated which pair was shorter.

**B. Motor adaptation paradigm.** Stimuli were identical to the visual version of the experiment with the exception of the adaptation phase. Here participants performed a series of fast mid-air tapping movements behind the screen with their hand floating above an infrared motion-tracking device. After six seconds of motor-adaptation and a 500 ms of blank screen (fixation point only) the stimuli were presented, and participants indicated which pair was shorter.

**C & D. Sample psychometric functions for one representative observer.** The probability of judging the reference as shorter than the test was plotted against the dot separation of the test stimulus (variable). Black curves and datapoints indicate the baseline condition, whilst in red data and fitting curves for the adaptation condition (C, visual; D, motor). The rightward shift of the red curves (indicating the adaptation condition) reflects a perceived compression of the dot distance in the adapted test stimulus.

Perceived dots distance in the baseline and adaptation conditions were separately measured for each participant. Fig. 12A shows single subject data in terms of PSEs obtained in the adaptation conditions as a function of baseline PSEs for visual (open squares) and motor (filled circle) adaptation. Data falling above the equality line indicate a compression of visual space after adaptation. Despite a large inter-subject variability, 16 out of 21 participants (76%) experienced a compression of the spatial separation of the test stimulus (displayed around the tapping region) because of motor adaptation. As expected, the effect achieved in the pure visual condition was even more robust, with all participants showing a perceived compression of the adapted stimulus, a result in line with Hisakata et al. (2016).

To statistically test for the significance of the after-effects, we ran two separate ANOVAs, one for the motor and one for the visual adaptation condition. PSEs were entered in one-way ANOVAs with conditions (2 levels, baseline and adaptation) as factors. For both motor and visual adaptation conditions, the analysis revealed a significant main effect of condition ($F(1,20)=6.044$, $p=0.023$, $\eta^2=0.168$, LBF=0.42; $F(1,8)=32.481$, $p<0.001$, $\eta^2=1.056$, LBF= 2.89, for motor and visual adaptation respectively), indicating that both adaptation methods induced a significant change in the visual stimuli perceived position.

Figure 12B and C show adaptation effects averaged across subjects. The effect was indexed as the difference between PSEs obtained in the baseline and adaptation conditions. The overall effect induced by motor adaptation was 0.13° consisting of a change of the perceived spatial interval of about 3%. The effect induced by visual adaptation was about 12%, corresponding to an average PSE shift of 0.47°, a result in line with that reported by Hisakata et al. (2016) and statistically stronger compared to that provided by the motor adaptation ($p< 0.001$).

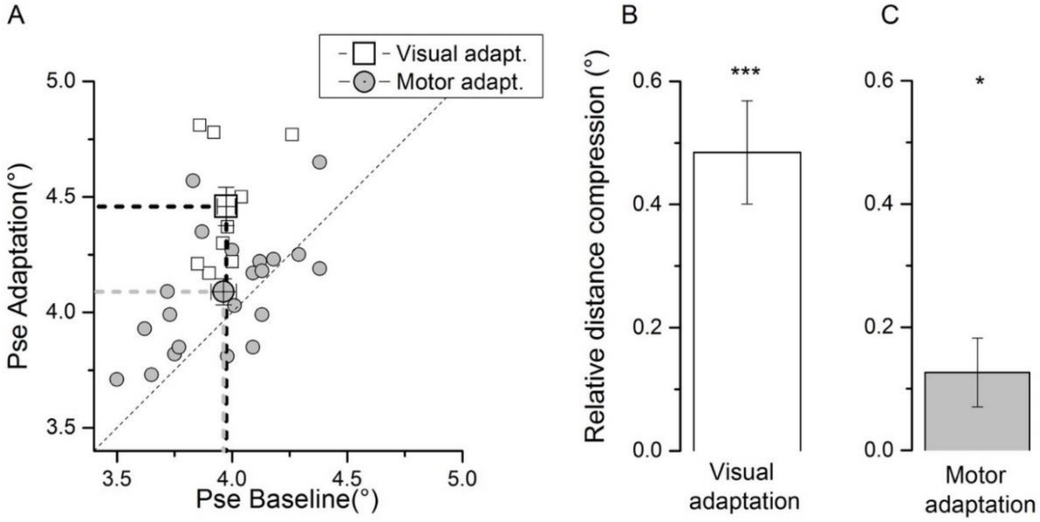

**Figure 12. Visual and motor adaptation effects on visual space**

**A.** Perceived dot-pair distance of the test stimulus to match the reference (PSEs) in the adaptation condition against those achieved in the baseline (no adaptation) condition. Open squares indicate pure visual condition whilst greys circles refer to motor adaptation. Small symbols indicate single subject data, big symbols indicate averages across participants. Data falling above the equality line indicates a perceptual compression of visual space after adaptation.

**B.&C.** Adaptation effect induced by visual (B) and motor (C) adaptation averaged across subjects.

* p<0.05, **p<0.01, *** p<0.001. Error bars reports ±1 s.e.m.

Finally, we looked at discrimination thresholds. In the motor experiment, the averaged baseline Weber fraction was 0.12 (SD=0.04), slightly decreasing after adaptation (M=0.10 SD=0.04, F(1,20)=3.309, p=0.084, $\eta^2$=0.004, LBF=0.15). Also in the pure visual experiment, the Weber fractions obtained in the baseline and adaptation conditions were similar (baseline 0.11, (SD=0.032), adaptation was 0.096 (SD=0.021) despite the fact that the difference turned out to be statistically significant F(1,8)=8.177, p=0.02, $\eta^2$=0.001, LBF=0.436). These results clearly indicate that the main effect of motor adaptation on stimuli perceived position mainly occurs for judgement accuracy, along with a tendency to reduce spatial discrimination thresholds.

### 3.4 Discussion

In this study, we reported that a period of fast mid-air tapping (not involving any visual, tactile and auditory stimulations) is able to decrease the apparent distance between dot pairs subsequently presented around the tapping region. Replicating previous findings (Hisakata et al., 2016), we also found that the same compression is induced by adapting to a dense visual dot-array. These results suggest that the visual and the motor system interact in order to compute the distance between visual objects.

In their original paper Hisakata et al. (2016) found that the effect of adaptation on space peaked when the average dot separation in the adapter matched that of the test stimulus, with the effect saturating for shorter separations. This result suggested that the adapting feature was the objects' separation, an index of density. Counterintuitively, adapting to the same dot array reduced the perceived density of a similar dot ensemble, making the elements appear sparser (Hisakata et al., 2016). Similarly, adaptation to a relatively high numerous dot array has been previously demonstrated to reduce apparent numerosity (Burr & Ross, 2008). Together, these results suggest an inverse link between perceived density, numerosity and spatial extent, with results differing when adapting with an array of dots and testing with a similar array of dots with lower density or testing with a single pair of dots. Interestingly, motor adaptation provides a similar pattern of results. Whilst being able to reduce the apparent numerosity of dot arrays (Anobile, Arrighi, et al., 2016), theoretically making the apparent stimulus sparser, it also compresses the perceived spatial separation of a dot pair (theoretically making the stimulus appear denser). This striking parallelism seems to suggest similar mechanisms for the visual and the motor adaptation effects. However, it is worth noting that, although both kind of adaptations yielded a compression of visual space revealing a visuo-motor interaction, the magnitudes of the effects were very different. While visual adaptation provided a perceived compression of about 12%, that induced by motor adaptation was much smaller, on average 3%. This difference could be partially induced by methodological differences (as the shorter initial motor adaptation phase compared to the visual condition) but it is also compatible with the idea that the two adaptations tap on different mechanisms. Interestingly, we recently found that motor adaptation provided stronger after-effects than visual adaptation when subjects were asked to estimate stimuli duration or numerosity of sequentially presented items (temporal numerosity). On the contrary, in case participants had to estimate the numerosity of objects scattered over a region of space (spatial numerosity) or discriminate between the speed of moving gratings, visual adaptation outperformed motor adaptation in producing perceptual distortions (Anobile, Domenici, et al., 2020). Notably, judgements on spatial numerosity or stimuli speed share a significant amount of spatial information (as the discrimination of spatial separation tested here), suggesting that the processing of visual spatial information is more easily distorted by visual than motor adaptation. One possibility to account for a such difference, it is in terms of "compatibility" of the adaptor and test stimuli. Primarily temporal and sequential routine like motor adaptation might affect to a larger extent sequential/temporal stimuli whilst visual adaptation with a prominent spatial component would be more efficient to distort the processing of spatial/numerical information.

What is the visual spatial mechanism that is distorted by motor adaptation? In the visual domain, it has been suggested that the discrimination of visual spatial intervals can be achieved by the use of pairs of coincidence detectors receiving inputs from separated and spatially localized regions of the visual space (Morgan & Regan, 1987). A distributed mechanism characterized by a population of such coincidence detectors, preferring different separations, could thus sustain distance perception (Kohly & Regan, 2000; Morgan & Regan, 1987). Though it is conceivable that visual adaptation aftereffects arise by a perturbation of the activity of such mechanisms, how motor adaptation might interact with such a mechanism is still unknown. A speculative hypothesis is that the output of the visual coincidence detectors is somehow normalized by the previous overall motor activity but, clearly, future studies are needed to test this idea.

That visual perception of magnitudes is linked with the motor systems is highly consistent with the influential ATOM (A theory of magnitude) theory according to which space, time and number are processed by a common parietal system (Bueti & Walsh, 2009; Walsh, 2003).

Crucially, the key idea of this theory is that action would be the linking factor across the different perceptual magnitudes, meaning that space, quantity and time would be combined by a common metric for action: an “action-based magnitude system”. The current results, together with previous reports, clearly demonstrate that a sustained activity of the motor system can distort all these magnitudes, suggesting a strong link between the visual and the motor system in magnitude encoding. In line with this, it has been reported that duration, numerosity and space are also similarly affected by saccadic eye movements (Burr, Ross, et al., 2011). Even if saccades are quite different from tapping movements, they also strongly engage parietal areas, suggesting that the interaction between the motor and the visual system might not be effector dependent (i.e. upper limbs) but generalizes to the programing and execution of very different motor routines. The close link between action and perception in the parietal cortex is well documented by both clinical and neuroimaging data: it is known from lesions studies that a wide range of sensorimotor functions can be selectively affected in patients with parietal lobe damage, including motor planning and execution (Freund, 2001).

In conclusion, with the current set of behavioural data, we cannot definitively explain why motor adaptation shapes visual perception of distances, as we cannot definitively conclude that the visual and motor adaptation are mediated by the same neural mechanisms. However, in light of the present data, we find it reasonable to frame the results within the well-established ATOM theory (Walsh, 2003) by suggesting that the mechanism linking motor adaptation to visual perception of space is a shared parietal metric for magnitude perception. Even if still speculative, the after-effects induced by motor adaptation would reflect a cross-modal calibration of this shared metric. As the visual environment continuously changes as a function of contextual effects, the adaptive nature of such a flexible mechanism could reside in linking goal-directed actions within the visual environment. It seems plausible to think that the functional role of the visual-motor adaptation is to maximize the efficiency of the motor interaction with the environment, by a continuous cross-calibration mechanism.

# Chapter 4

# Visual Duration but not Numerosity is Distorted while Running

# 4. Visual Duration but not Numerosity is Distorted while Running

## 4.1 Introduction

One of the core missions for perceptual systems is to provide the brain with reliable information about the environment to enable efficient interaction with nearby objects via goal-directed actions. Sensory estimates need to be accurate and precise in many dimensions as objects (and events) are internally represented within a multidimensional space encompassing many properties, including spatial position, time of occurrence, and numerosity. As these variables often correlate with each other (for example, it takes more time to walk a longer distance or to pick up more cherries from a table), it has been proposed that there exists within the parietal lobe of the human brain a shared magnitude system to process information about space, time, and quantity via a single mechanism. This idea, known as "A theory of Magnitude-ATOM", has been extensively tested by measuring the extent to which the processing of information in one of the ATOM dimension distorts estimates in another (Walsh, 2003). For example, several studies have reported that large visual stimuli are perceived to last longer than smaller ones presented for the same physical duration (Xuan et al., 2007). Duration estimates are also significantly affected by stimuli numerosity: numerous stimuli are perceived to last longer than less numerous ones (Dormal et al., 2006).

A shared mechanism processing quantitative information in multiple dimensions may be beneficial in providing a unique interface between the perceptual and the motor systems, sub-serving the transfer of sensory information between them. In line with this idea, voluntary movements performed during the presentation of visual stimuli can affect perceived duration. For example, at the time of saccades, duration is considerably com-pressed, by about 50% (Morrone et al., 2005). Similar (but weaker) compression also occurs when task-unrelated hand movements, either a series of discrete temporal patterns or continuous actions, are made during the presentation of visual stimuli (Ayhan & Ozbagci, 2020; Yokosaka et al., 2015). Action does not always cause compression: a saccadic movement to a clock's second hand can induce the illusion of temporal expansion, sometimes referred to as "saccadic chronostasis" (Yarrow et al., 2001).

Recently, a new motor-induced temporal illusion has been reported, where repetitive hand-tapping can distort the perceived duration of stimuli subsequently presented around the tapping area (Anobile, Domenici, et al., 2020). The perceived duration of visual stimuli is significantly compressed (by about 30%) after fast tapping and expanded after slow tapping. Motor adaptation of this type does not only distort perceived time but also perceived numerosity (Anobile, Arrighi, et al., 2016) and spatial distance (Petrizzo et al., 2020). However, motor adaptation does not affect the perception of stimulus speed, suggesting that the motor system might selectively interact with the processing of parietal information, without affecting that of earlier levels of visual processing.

A recent study from Lambourne et al. investigated the role of physical exercise on a temporal comparison task and found that visual stimuli presented during sustained aerobic exercise executed with the lower limbs (cycling) induced an expansion of perceived duration of about 15% (Lambourne, 2012). However, the study did not address whether these effects were selective only for temporal estimates or whether they generalize to other quantitative dimensions, as would be suggested by the ATOM Theory. A second question is whether sensory distortions are induced only during the execution of actions or whether the distortion persists after completion of motor activity, indicating a relatively long-term recalibration of the sensory system after physical activity. If the effect induced by self-motion were to disappear immediately after the end of the physical activity, it would indicate that the distortion of perceived duration is related to the movement itself and not to the other physiological variables that are changed during the activity and take time to revert to baseline levels. While both hand-tapping and cycling (or running) can be categorized as “self-motion”, they are very different in terms of effectors (upper or lower limbs) and frequency, and while hand-tapping could more closely resemble the action of counting items scattered on a surface, cycling is a non-goal-directed action. If a different influence of action on numerosity depending on the type of motion was to be found, it would suggest a selective interaction between action and numerosity, with types of motion more closely related to counting being more prone to distortion of numerosity.

In our new paradigm, the participants made a temporal or numerosity comparison (separate sessions) in three different conditions: at rest, during sustained physical exercise (running on a treadmill), or immediately after the exercise. In line with previous reports, perceived duration was expanded during the motor routines; however, estimates of numerosity were almost completely unaffected. Furthermore, time judgements were not distorted for stimuli presented soon after the end of the physical activity, although several physiological variables, such as heart rate, remained altered relative to the baseline, suggesting that distortions of time occur only during the execution of actions, with rapid re-calibration after the activity is completed.

## 4.2 Materials and Methods

### 4.2.1. Participants

A total of fifteen participants took part in the study (8 females, 7 males, mean age = 27.3, SD = 6.4; 11 were naïve to the purpose of the study, and 4 were authors). All participants had normal or corrected-to-normal visual acuity and provided written informed consent and a medical certificate for non-competitive physical activity. Each experiment was conducted on a different day, with the order of experiments pseudo-randomized across the participants. The duration of each experimental session was around 2 h per participant. The research was approved by the local ethics committee (“Commissione per l’Etica della Ricerca”, University of Florence, 7 July 2020, n. 111).

### 4.2.2 Apparatus

The experiments were conducted in a dimly lit, low-noise room with participants standing or running on a treadmill (JK Fitness Supercompact 48) at approximately 90 cm from the monitor (Telefunken Smart TV 43′’). Heart rate was measured with a Garmin Forerunner 55 smartwatch paired with an HRM-Dual Heartrate strap. The setup allows continuous monitoring of the participants’ heart rate (temporal resolution: 1 Hz) via Bluetooth. Stimuli were generated and presented with PsychToolbox3 (Brainard, 1997a; Kleiner, Brainard, Pelli, Ingling, Murray, et al., 2007; Pelli, 1997a) routines in Matlab 2016b (The Mathworks, Inc., Natick, Massachusetts, http://mathworks.com).

### 4.2.3. Duration Perception while Running

The task was similar to that used by Lambourne et al. (2012) (Fig. 13A). In each trial, the participants were presented with a central visual stimulus (24 cm × 24 cm blue square, approximately 15° at the viewing distance of 90 cm). The participants judged the stimuli as the "same" or "different" compared with a previously memorized stimulus lasting 600 ms (reference). The nine test stimulus durations were logarithmically spaced around the reference: 284, 342, 413, 498, 600, 723, 872, 1052, and 1268 ms.

An experimental block comprised seven steps (Fig. 13A). The first was a training session, where the reference stimulus was presented 5 times sequentially with no response required (encoding phase). Then, all the test durations were presented once in random order, and for each of them, the participants reported whether they had the same or a different duration from the reference. During this phase, response feedback was provided (correct or incorrect, signaled by a change in color of a central fixation point). When the participant reached 80% correct responses, the training stopped, otherwise another block of nine trials started. After training, the encoding phase started. In this phase, the participants were first presented with the reference stimulus 5 times (as at the beginning of the training); then, a first decoding phase started (baseline T1) after three minutes of rest from the encoding. The decoding phase consisted of 66 test trials, where each test of a different duration from the standard was presented 6 times, and the standard duration was presented 18 times. In each trial, participants reported whether each stimulus had the same or a different duration relative to the reference.

After the baseline T1, there was a new encoding phase, followed immediately by the running phase, lasting 3 min. During running, the treadmill speed was continuously adjusted by the experimenter to keep the participant's heart rate around 80% of the maximum heart rate for his/her age, according to the formula: 208 − 0.7*(participant's age) (Tanaka et al., 2001a). At the end of the first three minutes of running, when the target heart rate was reached and maintained, the participants started a second decoding phase (identical to the first) while they kept running. During the running phase, the speed was constantly monitored and regulated to maintain heartbeat as close as possible to the target. The test phase lasted about 5 min, with the total running time of the block lasting 8 min. Once the participants had stopped running, and the heartbeat reverted to the baseline level (±10 bpm), a new encoding phase started, followed by a second baseline (T2) measurement. After a short break (about 10 min), the whole procedure (apart from the training) was repeated in the same temporal order. At the end of the experimental session, each participant had completed 2 blocks per condition, for a total of 132 trials for each block (396 in total).

### 4.2.4. Duration Perception after Running

As for the previously described experiment, in each trial the participants were asked to judge whether a stimulus had the same or a different duration of the memorized reference (600 ms), with identical stimuli to those described above (Fig. 13B). As before, a block started with training followed by a decoding phase, a rest phase (this time lasting 8 min, to set the same interval between the decoding and the encoding phase as in the experimental phase), and a baseline (T1). After the baseline, a new encoding phase was performed before starting the running phase. During the first three minutes of running, the speed was manipulated to make the participant's heartbeat reach the target value (as in Exp 1). Once the target heartbeat had been reached, the participants kept running for an additional 5 min without being presented with any stimulus. During the running, the speed was adjusted to keep the heartbeat near the target value. After 8 min of activity, the treadmill was stopped, and the participants immediately started the test phase (test after run). In this experiment, we did not test the baseline at T2. After the running phase, the participants were allowed to take a break and rest, and after making sure that the heartbeat had returned to baseline levels (±10 bpm), the whole procedure was repeated, apart from the training.

### 4.2.5. Numerosity Perception while Running

This experiment was procedurally identical to the measurements of duration during running (see Fig. 13A), but in this case, the stimuli were circular arrays of black and white dots presented in the center of the screen. Each array had a diameter of 47 cm (about 29° at the average viewing distance of 90 cm), and each dot had a diameter of

1.5 cm (0.95°). In each trial, a single array was presented for 200 ms (to avoid serial counting). The reference numerosity was 24 dots, while the test numerosities were logarithmically spaced around the standard: 11, 14, 17, 20, 24, 29, 35, 42, or 51 dots.

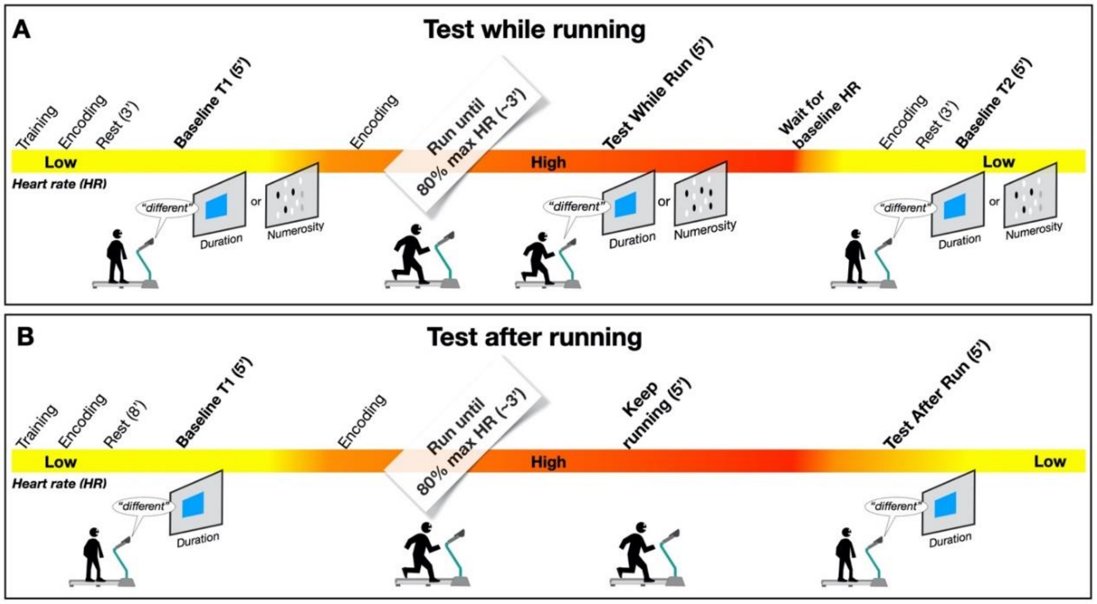

**Figure 13. Experimental procedure.**
**A.** Paradigm used to measure duration and numerosity perception while running. After a short training session, participants were presented with the reference stimulus (encoding phase: 600 ms or 24 dots) 5 times. After a rest period of 3 min, they were presented with a sequence of test stimuli to categorize as same or different, compared to the reference (baseline T1). After the task, the encoding was repeated, followed by the running phase. During the first three minutes of running, no stimuli were presented; then, the same different task (duration or numerosity) was performed, this time while participants kept running. After this test phase, participants were allowed to rest until the heart rate returned to the baseline level. At this point, a second baseline (T2) was measured. After a short break, the whole procedure was repeated.
**B.** Paradigm used to measure duration perception after running. This was similar to that described above (A) except the rest period before baseline measurement (T1) was 8 min instead of 3 min, and the test measurements were made after the participant stopped running while the heartrate reverted to baseline.

### 4.2.6. Running Variables and Heartbeat Parameters

Table 1 reports the descriptive statistics of heart rate, running speed, and total number of steps for each experiment. In the numerosity-while-running experiment, the heartrate of one participant was not collected due to technical failure. The heart rate and running speed were calculated excluding the first 3 min of warm up (the period in which the target heartrate was gradually reached, see Fig. 14). The number of steps refers to the whole running period (3 min warm up plus 5 min of running). Baseline heartrates were obtained by averaging all heartrates at resting state across the three experiments.

**Table 1. Descriptive statistics of running parameters.**

| Condition | Average HR B/m | Average Speed Km/h | Average Steps | Steps per Second Hz |
|---|---|---|---|---|
| Baseline (no run) | 87.06 ± 2.1 | -- | -- | -- |
| Duration while running | 159.6 ± 0.67 | 7.87 ± 0.66 | 1185.5 ± 20.8 | 2.47 |
| Duration after run | 160.4 ± 1.1 | 7.61 ± 0.62 | 1206.6 ± 24.67 | 2.51 |
| Numerosity while running | 158.1 ± 0.31 | 7.65 ± 0.63 | 1217.3 ± 27.8 | 2.53 |

Figure 14 illustrates the average heart rate across the session, with the temporal landmarks showing when the test stimuli were presented. As specified above, the target heartrate was defined as 80% of maximal heart rate, given the chronological age (Tanaka et al., 2001a). The average target heart rate was 150.9 ± 1.0 bpm. Figure 14 shows that for all the three experiments, the heart rate steadily increased during the first 3 min of warm up and then remained constant around the target value for the next 5 min of running.

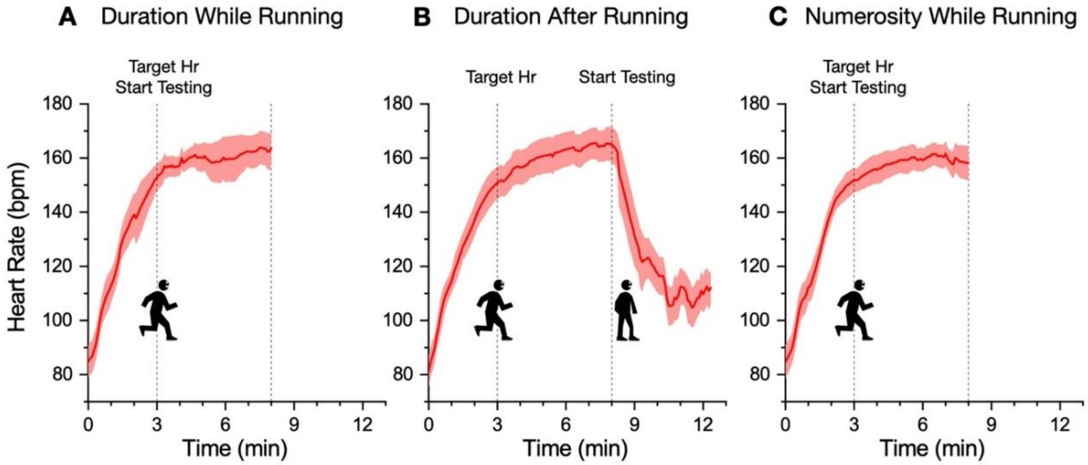

**Figure 14. Heartrate parameters.**
Average heart rate with ±95% C.I. as a function of time after running onset. In all the experiments (A, B, C), the heart rate gradually reaches the target value (see methods) within 3 min, then remains stable around that value for the subsequent 5 min of running.

### 4.2.7. Data Analysis

Perceptual accuracy (bias) was measured by plotting the proportion of trials in which the test was judged to be the same as the reference, as a function of the test stimulus magnitudes, plotted on a logarithmic axis (examples in Fig. 15). These distributions were fitted with Gaussian functions, and the peak of the fitted functions was taken as the “point of subjective equality” (PSE), where the test perceptually matched the reference. This point is the value that the test stimulus had to assume for the subject to have the highest probability to answer “same”. A peak value lower than the physical reference corresponds to the test stimulus being overestimated and vice versa. We describe under- or over-estimations as proportional shifts, defined as the difference between the PSE and the physical value of the reference, normalized by the reference value.

$$\text{Bias} = \left(\frac{\text{Reference} - \text{PSE}}{\text{Reference}}\right) * 100\% \qquad \text{Eq. 1}$$

We defined perceptual precision as Weber fractions (Wfs), the ratio of the just-noticeable difference (given by the width of the Gaussian fitting function) to the PSE. In practice, the Wfs were computed as the antilog of the standard deviations of the Gaussian log fits minus one.

The data were analyzed with repeated measure ANOVAs, t-tests, Pearson correlations, and bootstrap t-tests (Efron & Tibshirani, 1994). Whenever the sphericity assumption was violated, the Greenhouse–Geisser correction was applied. The standard statistics were complemented with the estimation of Bayes Factors (Rouder et al., 2009), which quantify the evidence for or against the null hypothesis as the ratio of the likelihoods for the experimental and the null hypothesis. We express it as the base10 logarithm of the ratio (Log10Bf10), where negative logarithms indicate that the null hypothesis is likely to be true, positive that it is false. By convention, absolute Log10 Bayes Factors greater than 0.5 are considered substantial evidence for the alternate or null hypothesis, and absolute log factors greater than 1 are strong evidence. All statistical analyses were performed with MatLab 2016b (The Mathworks, Inc., http://mathworks.com) and Jasp Software (version 0.14.1).

## 4.3. Results

### 4.3.1 Aggregate Data

As detailed in the methods section, the participants compared a previously viewed reference stimulus lasting 600 ms with a series of test stimuli and judged them as the same or different. In separate sessions, they made similar judgments about the numerosity of the stimuli compared with a 24-dot standard. Figure 15 shows the results of the aggregate data summed over all the participants, as the proportion of “same” responses as a function of test duration or numerosity. The peak of the Gaussian fits describing the distributions reflects the point of subjective equality of test and reference (PSE). A leftward shift of the curve peak compared to the reference value indicates an overestimation of the duration or numerosity of the test stimuli. For all the Gaussian fits on the aggregate subject, an R2 higher than 0.97 was achieved.

Figure 15A refers to duration estimates while running. On inspection, it is evident that, compared to the baseline performance before (T1) and after (T2), the visual durations were substantially overestimated during the running phase. While running, a stimulus lasting 513 ms was perceptually judged as equivalent to the 600 ms reference, an overestimation of about 15%. In the two baseline conditions, the peaks were both near the physical refer-ence duration (baseline T1: 608 ms, baseline T2: 588 ms). However, duration perception remained almost veridical when the stimuli were presented soon after the running phase, although heartrate was still elevated well above resting levels (Figure 15B, Test: 556 ms, baseline T1: 572 ms).

Figure 15C reports judgments of numerosity while running compared with the reference of 24 dots. Unlike the duration perception, the numerosity estimations measured while running were almost identical to the baseline conditions (Test: 24.2 dots, Baseline T1: 24.5 dots, Baseline T2: 25.0 dots).

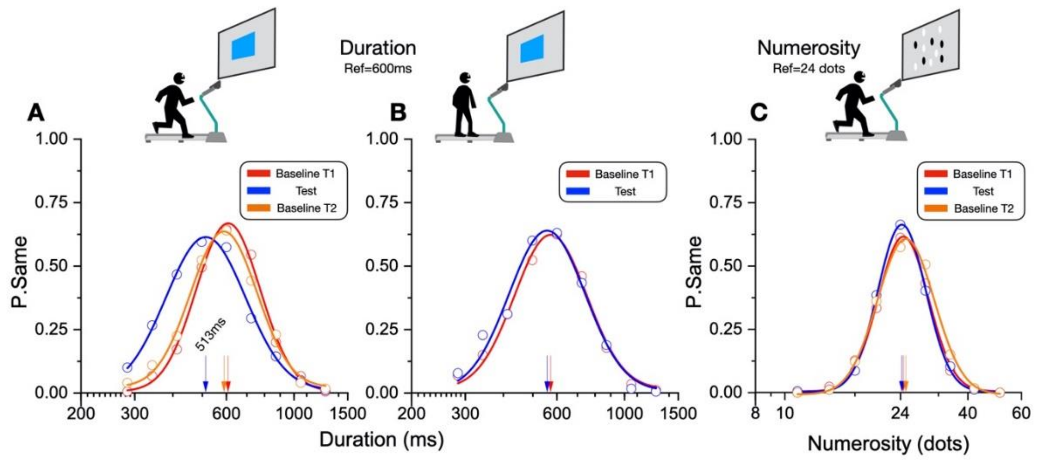

**Figure 15. Results on aggregate data for the duration (A,B) and numerosity (C) tasks.** Test stimuli magnitudes were plotted against the proportion of "same" responses and fitted with Gaussian functions. The peaks of the fits (arrows) correspond to the PSE (600 ms or 24 dots). A leftward shift (relatively lower peaks values) corresponds to an overestimation of the duration or numerosity of the test stimuli.

We quantified the significance of the biases of the aggregate data by the bootstrap test. On each repetition (10,000 iterations), and separately for each condition, the data were sampled with the replacement (as many independent samples as the full dataset) and fit with a Gaussian distribution, whose peak yielded an estimate of the PSE. The statistical difference was assessed by comparing the distribution peaks along the bootstrap iterations by Z-test, with the Z-score given by the distance between the distribution means di-vided by the estimate of the average standard error, given by the square root of the sum of the variances across the bootstraps (Efron & Tibshirani, 1994). Figure 16 shows the distributions of the peak boot-straps for each condition. The average peak for the duration perception while running (Fig. 16A, blue distribution) was 513.2 ± 6.7 ms, clearly different from the baseline meas-ured before (T1: 607.9 ± 7.0 ms, $Z = 9.7$, $p < 0.0001$) and after running (T2: 588.4 ms ±7.6 ms, $Z = 7.42$, $p < 0.0001$). The two baseline conditions were similar to each other ($Z = 1.14$, $p = 0.25$). These results confirm that the overestimation of visual duration while running was significantly different from the baseline.

The bootstrap results for the duration estimates after running (Fig. 16B) almost overlap those of the baseline and were clearly not statistically different (T1: 571.5 ± 7.7 ms, Test 556.3 ± 7.26 ms, $Z = 1.8$, $p = 0.07$). For numerosity (Fig. 16C), the distributions for the test and the baseline conditions show little to no difference. The two baseline conditions were almost overlapped (T1: 24.5 ± 0.27 dots, T2: 25 ± 0.28 dots, $Z = 1.36$, $p = 0.17$). The PSE for numerosity while running was slightly lower than the second baseline measured soon after the running phase (Test: 24.2 ± 0.24 dots, T2: 25 ± 0.28 dots, $Z = 2$, $p = 0.045 > \alpha = 0.017$, Bonferroni corrected for three comparisons). Overall, these results confirm that the running activity distorted duration perception, while numerosity was unaffected.

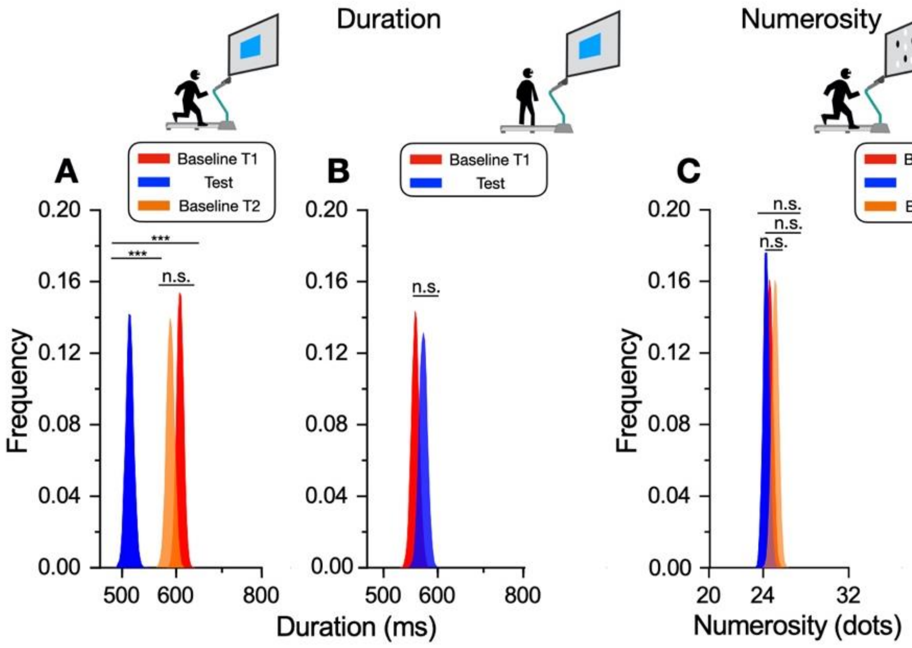

**Figure 16. Bootstrap Z-test on aggregate data.**
Distributions of fitted peaks for the duration (A,B) and numerosity (C) tasks. Overlapped distributions indicate no difference between conditions. p-values represent Z-test significance level: *** $p < 0.01 > \alpha = 0.017$, Bonferroni corrected for three comparisons.

### 4.3.2 Individual Data

We also analyzed the data separately for each participant and tested the differences with standard between-participant statistical tests. Using a similar technique to that used for the aggregate data, we fitted each participant's data with Gaussian functions and estimated the individual PSEs from the peaks in the individual curves. Figure 17 plots, for each participant, the PSE during (or after) running against that of the first baseline.

The points falling below the equality line mean that the PSEs during or after running were lower than the baseline, hence an overestimation. For the duration judgments during running, every single participant falls below the equality line, showing an overestimation of duration. The averages are shown by the arrows and are very similar to the estimates of the aggregate data (overestimation of ~20%). Obviously, this was statistically significant (t(14) = 7.27, *p* < 0.001, Cohen's d = 1.73, Log10Bf10 = 3.7). The biases in the duration perception after the running phase were scattered much closer to the equality line, with a weak tendency to fall below. However, the effect did not reach significance (t(14)=1.98, *p* = 0.07, Cohen's d = 0.54, Log10Bf10 = 0.09). For the numerosity task, there was clearly no tendency for underestimation (or overestimation), with most of the participants scattered around the equality line (t(14) = 0.21, *p* = 0.84, Cohen's d = −0.019, Log10Bf10 = −0.57). Figure 17D summarizes the individual data, showing the percent biases for the three conditions: averages as bar graphs and individual data as dots. Quite clearly, the only significant effect was duration while running, agreeing with the aggregate data.

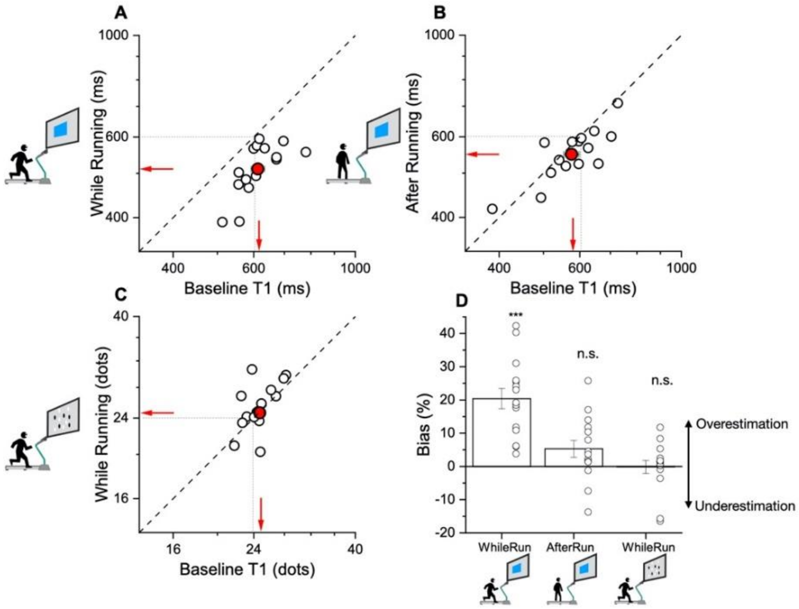

**Figure 17. Individual data and perceptual biases magnitudes.**
Scatter plots showing PSE (log units) separately calculated for each participant (open symbols). Filled symbols refer to group averages. Symbols falling below the equality line (dashed line) reflect lower PSEs in the running condition, hence an overestimation of duration or numerosity. (A) Duration PSEs during running against first baseline (T1). (B) Duration PSEs after running against first baseline (T1). (C) Numerosity PSEs during running against first baseline (T1). (D) Bar plot showing estimation biases relative to the baseline condition (T1), normalized by the reference stimulus (600 ms or 24 dots). Bars

represent the three experiments: duration while running, duration after running, and numerosity while running, respectively. Bars are between participant's average, error bars are ±1 SEM. Individual data are represented by symbols. *** $p < 0.001$ n.s. not significant.

While not reaching statistical significance, there was a slight systematic tendency for overestimation of duration after running. One possible explanation is that underestima-tion occurred reliably soon after the cessation of running but faded quickly. To test this possibility, we separated the baseline and test data (aggregated across the participants) into early and late trials, with a median split of the interval after the running was stopped. The results in Figure 18 show a similar null effect for both halves, suggesting that even in the very first trials after running, the effect was already absent (first half: T1 541 ms ± 9.59 ms, test 528.5 ms ± 9.65 ms, Z = 0.9, p = 0.36; second half: T1 604.1 ms ± 11.39, test 585 ms ± 10.22, Z = 1.3, p = 0.19).

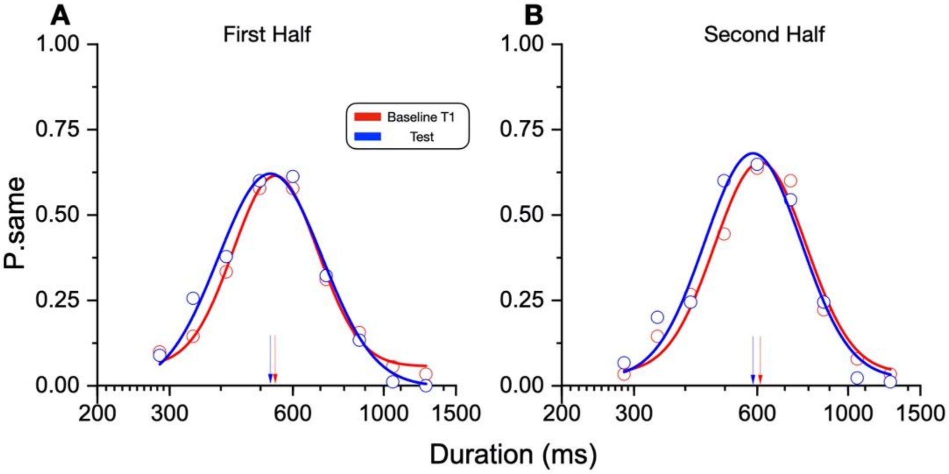

**Figure 18. Duration perception after running.**
As in Fig. 15B, stimuli durations were plotted against the proportion of "same" responses and fitted with Gaussian functions with the peak of the fits (arrows) corresponding to the test duration matched with the reference (600 ms). Blue curves report the aggregate data before running (baseline T1), the red curves the data collected after the running phase. To test whether the effect was detectable in the very first trials after the run phase, the analyses were performed on two sub-set of the data: the first (A) and second half (B).

### 4.3.3 Sensory precision

In order to assess the overall task complexity and difficulty, we analyzed the precision of the participants' responses, expressed as Weber fractions. Figure 19 shows the

Weber fractions (derived from the width of the fitted functions) separately for each participant. ANOVAs and t-tests confirmed that there were no significant differences in the Wfs between the conditions within each experiment (duration while running: F(1.3,18.5) = 2.95, p = 0.09; duration after running: t(14) = −0.686, p = 0.5; and numerosity: F(2,28) = 0.11, p = 0.9). As precision was unaffected by running, we averaged over the baseline and active condition separately for the three experiments. The Weber fractions were clearly higher for the duration conditions than for the numerosity (F(2,28) = 32.39, p < 0.001). Post hoc tests revealed similar and not statistically different levels of precision between the “while” and “after” running conditions (t = −0.969, p = 0.34), suggesting that this was not the reason for the difference in the results for these two conditions. On the other hand, both duration experiments statistically differed from the numerosity task (both p-values < 0.001).

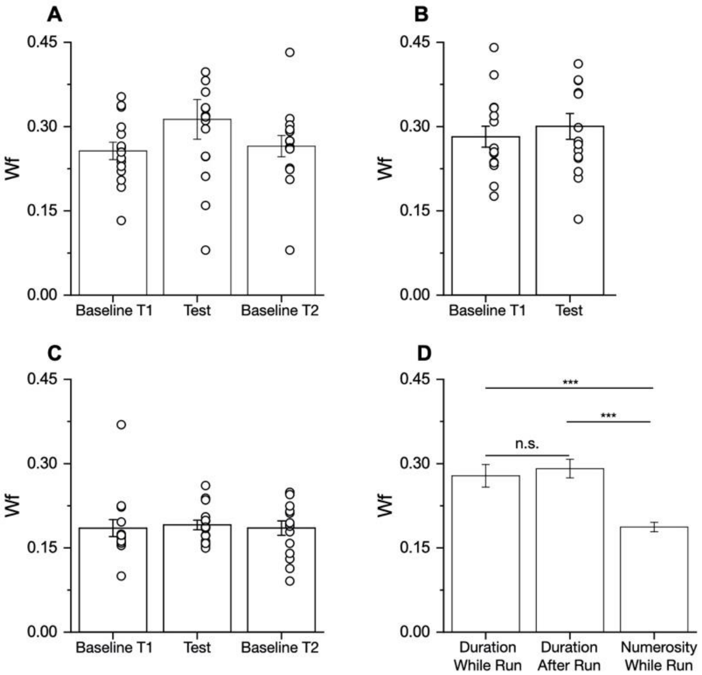

**Figure 19. Sensory precision.**
Bar plot showing estimation precision (Wfs) for duration (A,B) and numerosity (C) tasks. Bars show average, error bars are ± 1 SEM, and circles are individual data. (D) Average Wfs for the duration and numerosity conditions.

Finally, as much of the evidence suggests common mechanisms for numerosity and duration perception, we looked at the between-task correlations. We computed summary precision indexes separately for numerosity and duration by averaging all the standard deviations across conditions for the two tasks. In line with the involvement of a common mechanism in numerosity and duration perception, the results (Fig. 20) showed positive and statistically significant correlations between the precision levels (r = 0.58, p = 0.02).

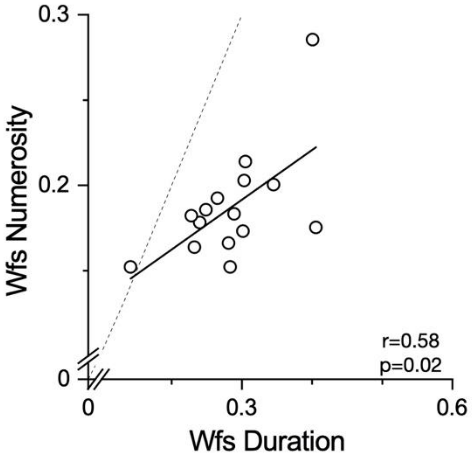

**Figure 20. Correlation between numerosity and duration Wfs.**
Scatter plot of individual Wfs as averaged across conditions for duration and numerosity.

## 4.4. Discussion

The main result of this study shows that while motor activity can significantly distort the perception of time, it leaves numerosity perception unaffected. The participants com-pared the duration or numerosity of a test stimulus while running, or having just run, with a standard encoded at rest. The first experiment measuring duration estimation during running supported the previous findings (Lambourne, 2012), reporting a systematical overestimation of perceived duration while running. The second experiment, however, showed that the duration measurements made soon after stopping running are veridical, showing that this effect is intrinsically related to the movement itself rather than to other physio-logical parameters altered by physical activity (such as heart rate). In the final experiment, we showed that the numerosity estimation was unaffected by running.

These findings suggest a magnitude-selective interaction between action and perception that involves only the perceived duration. However, one of the most prominent theories on the perception of magnitude posits that the human brain encodes space, time, and number via a shared mechanism (Walsh, 2003), opening the possibility that the effect of motor activity on the perception of time might also generalize to other magnitudes. Indeed, it has recently been reported that a repetitive motor routine executed with the upper limbs (hand tapping) distorts both perceived duration (Anobile, Domenici, et al., 2020) and numerosity (Anobile, Arrighi, et al., 2016). Moreover, motor activity related to eye movements has been reported to significantly distort numerosity (Anobile et al., 2021; Binda et al., 2011).

How can the discrepancy between the present and the previous studies be reconciled? One possibility regards the spatial congruency between the position where the visual stimuli were displayed and the area where the motor activity was directed. The perceived numerosity during saccadic eye movements was distorted only for stimuli dis-played between the saccadic starting and ending point, embracing a distance of roughly 20° (Binda et al., 2011). Similarly, hand tapping distorted the perceived numerosity of stimuli presented around the tapping area, with effects that rapidly faded off with the increase in the spatial offset relative to the tapping location and completely vanished for distances higher than 15° (Anobile, Domenici, et al., 2020).

Another possible explanation for the null effect found for numerosity may be the different sensory precision for the two magnitudes. The Weber fractions for the numerosity perception were lower than those for the duration perception. It is possible that the noisier system for duration perception is more prone to distortion by contextual variables, such as running. However, we found no difference in the Weber fractions between the duration judgements during and after running, making it unlikely that this is the general explanation for all lack of effects. A last methodological difference worth discussion is the presentation modality of the stimuli. As the dots in the numerosity task were all presented simultaneously, this might have required a lower involvement of the working memory com-pared to the duration stimuli. However, as other interactions between self-motion and numerosity were reported for both the sequential and the simultaneous (Anobile, Arrighi, et al., 2016) numerosities, this difference alone is unlikely to have cancelled out an effect of running on numerosity perception.

Interestingly, in many of the previous studies the participants underestimated perceived duration as a consequence of action. In contrast, the participants in the present study showed a tendency to overestimate the durations of visual stimuli presented during the running phase relative to those with the same physical duration perceived at rest. A possible reconciliation of these discrepancies may be the difference in methodologies. In all the previous experiments, the participants were required to compare two intervals presented one after the other or to immediately reproduce a temporal interval that had been just observed. In the paradigm of the present study, the intervals presented during the running phase were compared with the reference encoded before the onset of physical activity. This resulted in a delay between the encoding (at rest) and the test phase (during running) of at least 3 min, a much longer time for which sensory information had to be stored in the short-term working memory.

A second methodological difference regards the duration and the intensity of the motor activity. While many studies on eye and hand movements use transient motor routines in the sub-second or supra second regime, here participants were engaged in a strenuous physical activity lasting several minutes. Indeed, a previous report in which participants were required to estimate the duration of visual stimuli during a sustained cycling routine lasting several minutes revealed that the duration estimates during physical exercise were robustly lengthened (Lambourne, 2012). Typically, these time-dilation phenomena are accounted for by alterations in the rate of the internal pacemaker: physical activity could accelerate the clock rate, and this, in turn, would induce a perceived dilation of stimulus duration. To reconcile all these results, we might speculate that transient motor activities (such as saccadic eye movements or hand movements) momentarily slow down the rate of the pacemaker, resulting in a compression of perceived time. On the other hand, sustained physical activity may induce an acceleration of the internal clock, yielding the opposite phenomenon of time dilation.

An alternative explanation might be that time processing in different conditions involves several, independent temporal mechanisms in the brain. This idea of multiple clocks in the brain has been demonstrated within the visual domain. A grating drifting at high speed presented in a given location of the visual field strongly compresses the perceived duration of the stimuli subsequently displayed around that area, without affecting those displayed in other locations (Burr, Cicchini, et al., 2011; Johnston et al., 2006). This finding supports the idea of multiple time mechanisms, each responsible for time processing in a well-defined portion of the visual field. Despite previous reports supporting the idea that motor routines can affect time perception, it remains an open question whether such an interaction is prompted by the execution of the movements themselves or by the alteration of other physiological variables that are perturbated during action.

Past reports have proposed that heart rate might be directly related to the internal clock rate; so, an acceleration of heartrate would also speed up the internal clock, leading to an overestimation of perceived time (Jamin et al., 2004). To address this possibility, we measured whether time perception was affected not only during the running phase but also immediately after the end of the physical activity. The results indicate that no distortion occurred after completion of the motor routine, even though heartrate had not returned to the baseline level. Even when we took into consideration only the trials immediately after the physical activity, no significant perceived time dilation was observed. This result clearly questions the causal role of heartrate variations in distortions in perceived time and is in line with a previous study reporting significant time dilations when arousal increased but heart rate remained constant, or even decreased (Schwarz et al., 2013). Can the present results be accounted for by variations of the arousal level induced by motor activity? The lack of temporal distortions when duration estimates were made at the end of the physical activity also questions the arousal hypothesis, given that arousal levels have been reported to be still significantly altered at the end of a 10 min running exercise (Niedermeier et al., 2020) in a similar activity to the present study.

Taken together, the results of the present study reinforce previous studies showing that time perception is affected by running, but a similar running regime does not affect numerosity perception. However, a comparison between these findings with those in the literature revealed that this relationship is modulated by movement parameters, such as movement speed, type of effector, spatial proximity between stimuli, and movement location, as well as the time of stimuli presentation relative to the phases of the motor routine (Tomassini et al., 2018). Future studies should directly investigate each of these issues to provide a full com-prehension of the mechanisms and the nature of the interaction between the motor and the sensory systems.

The effect of long-term physical training on time perception should also be investigated. For instance, there have been anecdotical reports from tennis and baseball players that time slows down just before hitting the ball (Murphy & White, 1995). This suggests that the target of goal-directed actions can benefit from specialized processing of their temporal features, which might be aimed at maximizing motor performance and be induced by the extreme long-term training characterizing elite athletes. However, while the benefit of time dilation for goal-directed action is evident, the same does not hold for target-free rhythmic actions, such as running. This may suggest that while the observed behavioral effect is the same, it might be caused by different mechanisms. During sustained physical exercise, the fatigue accumulated by the participant may cause an overestimation of perceived time, as has al-so been reported to occur during sustained rowing exercise (Vercruyssen et al., 1989). In the light of this, future studies could investigate the precision and accuracy of temporal perception in elite athletes, such as those engaged in long-distance races (marathons) or hurdling, combining the running routine with a goal-directed, repetitive, transient action aimed at jumping over the obstacles.

# Chapter 5

# Similar Effect of Running on Visual and Auditory Time Perception in the Ranges of Milliseconds and Seconds

# 5. Similar Effect of Running on Visual and Auditory Time Perception in the Ranges of Milliseconds and Seconds

## 5.1 Introduction

Perceived duration reflects the subjective experience of the passage of time. Perceiving time is a pervasive activity, applying to most of everyday tasks, spanning over very different time scales (from milliseconds to several days) and involving all sensory modalities. Duration of sensory events can be passively perceived, however most of the interactions we have with the environment are not passive but characterized by active motor interactions. Within this dynamic context it is of critical importance to keep an accurate temporal synchronization between motor routines and the processing of sensory signals. Vincent Walsh (2003) suggested the idea of an integrated system dedicated to the perception of time, space and quantity (likely to be located in the parietal lobe) aimed to make efficient the interactions between the motor and the perceptual system. In line with this idea, of an intimate bi-directional link between signal encoding and the motor planning and execution, several studies reported temporal distortions while performing voluntary hands/arms actions as well as during whole-body movements.

For example, Ayhan et al. (2020) asked participants to reproduce the duration of a previously seen moving visual stimuli (dot arrays lasting from 0 to 1.5 s). In an "active" visuo-motor condition, in each trial the duration of the to-be-reproduced stimulus was generated by the participants via a key press. In a "passive" condition, the same durations exploited in the active phase were used to define the duration of the visual stimuli that participants had to reproduce. The results demonstrate that perceived duration of self-generated intervals was compressed, compared to passive viewing. Similarly, Yokosaka et al. (2015) found that during fast circular hand movements, visual duration was compressed, relatively to a resting condition. Evidence that perceived time can be expanded via self-produced motor routines have also been collected. Tomassini et al. (2018) found that perceived duration of visual stimuli was expanded when these were presented in the middle of two consecutive finger taps, while duration was compressed for stimuli displayed near tap onsets, to reveal a dynamic coupling between action and perception. Anobile et al. (2020) showed that visual time can be distorted by a motor routine  even when this has already ceased. In this experiment, participants performed mid-air tapping movements for a few seconds, either slowly or quickly (tested in separated sessions). Soon after the end of the motor phase they were asked to judge the relative duration of two drifting gratings, one spatially coincident with the tapped region and the other in a neutral location in the opposite visual field. The results revealed that after fast tapping perceived duration was compressed around the tapping region while slow tapping induced a perceived expansion of time.

While all aforesaid studies entail hands and/or arms actions, also lower limb and whole-body movements have been reported to shape time perception. Lambourne et al. (2012) investigated the role of cycling on duration estimates. Participants were asked, while cycling or resting, to compare in a same/different task the duration of visual stimuli (lasting from 0.14 to 1.27 s) to a previously learned duration (generalization task). The results showed that, while cycling, perceived duration was expanded of about 15%, relatively to time estimates made at rest. With a time reproduction task, Tonelli et al. (2022) replicated and expanded these results by showing that time distortions were still evident approximately 15-20 minutes after the end of physical activity. Furthermore, despite time distortions occurred for all the tested durations, they were stronger for stimuli within the milliseconds range (0.2-0.8 ms) compared to longer stimuli (1.6, 3.2 secs). This long-lasting effect has been interpreted as the consequence of a dopaminergic or GABAergic modulation induced by physical activity and the stronger effect for the milliseconds range as the consequence of a relatively higher involvement of motor control on this temporal range. Finally, in this study it was demonstrated that perceptual distortions induced by cycling did not generalize to all visual tasks as visual spatial estimates (distance between two stimuli) remained veridical to ruling out the possibility of role of generalize, a-specific factors.

The perceived dilation of time for visual stimuli in the milliseconds range induced by cycling has been recently generalized to another motor activity: treadmill running. By leveraging on the same methodology as Lambourne et al. (2012) it was shown that also running provided a robust expansion of visual time in the millisecond range with running alike cycling  that selectively affected time perception by leaving unaffected non-temporal features such as numerosity (Petrizzo et al., 2022). However not all temporal distortions induced by running resemble those yielded by cycling. For example, while cycling distort time perception for a long period after the end of the physical activity the expansion of perceived time induced by running completely vanished immediately after the end of the exercise. Indeed, the recalibration of the temporal mechanisms following the end of the exercise was so rapid that even in the first trials after the running phase, when for example heart rate and other physiological variables were still well above the baseline level, time estimates returned to be veridical.

Beyond the milliseconds vs seconds categorization, another common distinction in the timing literature is related to sensory modalities. It is now well established that while vision dominates space perception over audition (Alais & Burr, 2004), audition largely dominates vision for time perception. For example, with an audio-visual temporal bisection task Burr et. al. (2009) demonstrated that visual timing can be “captured” by auditory stimuli, dragging visual time towards the auditory time to induce a “temporal ventriloquist” effect. The dominance of audition over vision on time perception has been related to the common finding that time sensory thresholds are much lower for auditory compared to visual stimuli, making auditory timing more reliable, at least in the millisecond range (for a review see: Rammsayer, 2014). Clinical evidence also sustains this dissociation. For example, Tinelli et al. (2015) showed that auditory but not visual time sensory discrimination thresholds (in the millisecond range) are impaired in preterm children, a finding difficult to reconcile with the existence of single a-modal system. Importantly for the aim of the current study, the dominance of audition over vision is not constant across temporal ranges. The auditory modality has been shown to dominate sensory precision (lower thresholds) over the visual modality predominantly for stimuli within the millisecond range while similar thresholds have been reported for longer durations above the second (Rammsayer, 2014; Rammsayer et al., 2015). Overall, the current literature seems to suggest a (probably smooth) transition from a sensory specific timing mechanism to a more generalized system, as a function of stimuli duration.

Despite the timing literature suggests different mechanisms for vision and audition, to the best of our knowledge only one study investigated the influence of physical activity on auditory time perception (Kroger-Costa et al., 2013). Interestingly, the reported results the effect of running on sounds in the range of milliseconds to be task dependent: subjective time was found to be expanded when perceived time was measured with a discrimination task while none distortion was found when time was measured via a generalization task.

To summarize, the literature is consistently pointing toward a robust link between motor activity and time perception. However, a full comprehension of the nature of this interaction as well as the involved brain mechanism is far to be achieved. Most of the previous studies have just measured the effect of motor activity in either a range (milliseconds) or the other (seconds). More there exists a huge variability in the methods used to measure time performance (e.g. discrimination, reproduction, generalization) as well as in the kind of motor activity investigated (e.g. running or cycling) in particular about the exercise intensity level (moderate or vigorous). Finally, most of the previous studies mainly cope with visual stimuli to leave the effect of physical exercise on audition almost completely neglected. The aim of the current study was to fill in all these gaps. By leveraging on a single and already validated paradigm (Petrizzo et al., 2022) it was aimed to investigate the role of vigorous running on visual as well auditory stimuli whose duration fall in both, the sub-second and seconds range.

## 5.2 Methods

### 5.2.1. Power analysis

To estimate the sample size, we used as references the results obtained by (Kroger-Costa et al., 2013; Lambourne, 2012; Petrizzo et al., 2022). Alike the current study, these studies employed a time generalization task to measure perceived durations during physical exercise and at rest. Specifically, Petrizzo et al. (2022) and Kroeger-Costa et al. (2013) measured running-induced temporal biases for durations in the millisecond range (standard 600 ms) for visual and auditory stimuli. Lambourne et al. (2012) instead measured cycling-induced biases for visual durations in the millisecond range (standards 300 and 600 ms). From these studies, we extracted and averaged Cohen's d values for stats contrasting the results obtained at rest and during physical exercise. The between studies average Cohen's d value was 0.88. Using software G*power (Faul et al., 2007b), we then calculated the sample required for a (two-tailed) t-test against measuring the difference between two dependent means (physical exercise Vs resting), considering a significance level of $\alpha = 0.05$ and power of $(1-\beta) = 0.95$. We found that a sample size of 19 participants would be needed.

### 5.2.2. Participants

A total of 33 participants with normal or corrected-to-normal vision and no auditory impairments participated in the study (4 authors, 29 naïve, 13 females, mean age 26.4±4.96). Eighteen participants performed both the visual and auditory tasks, ten performed only the visual task, five only the auditory task. In sum, the visual task was completed by 29 participants while the auditory task was completed by 23 participants. Independently by the sensory modality, all participants performed the task for both temporal ranges (milliseconds and seconds). Participants' sports habits were investigated by asking whether they practiced any sport and, if so, how many times per week over the past six months. Five participants reported no sporting activity. The others reported exercising two to three times a week with an average frequency of two/three days for one/two hours each time. The activities performed were heterogeneous: artistic gymnastics, weightlifting, tennis, dance, volleyball, boxing, running, ultimate frisbee, martial arts.

All participants provided written informed consent and a medical certificate for non-competitive physical activity. Each experimental condition lasted about 2h per participant. The research was approved by the local ethics committee (*"Commissione per l'Etica della Ricerca"*, University of Florence, 7 July 202, n.111).

### 5.2.3. Apparatus and Stimuli

For each condition, participants were standing or running on a treadmill (JK Fitness Top Performa 186), in a dimly lit and quiet room at approximately 90 cm from a monitor (Telefunken Smart TV 43´´). Auditory stimuli were delivered by Bluetooth high quality headphones (Sony WF-SP800N). Heart rate was continuously monitored via a Bluetooth connection via a Garmin Forerunner 55 smartwatch paired with an HRM-Dual Heartrate strap. Following our previous experiment (Petrizzo et al., 2022) in the visual version of the experiment, intervals were marked by the on and offset of a centrally displayed blue square (subtending an area of approximately 15°X15° at the viewing distance of 90 cm). In the auditory version of the experiment stimuli consisted of pure tones with a frequency of 1000 kHz and an intensity of 75dB measured at the sound source. In all experiment participants judged the duration of the test stimuli against a reference of either 0.4 s (sub-second range) or 2 s (seconds range) tested in separated sessions. The test durations were logarithmically spaced around the standards, with a constant difference between successive durations of approximately 25%. In details, in the milliseconds range, test durations were: 0.2, 0.252, 0.318, 0.4, 0.504, 0.634 and 0.798 s while for the seconds range were: 1.002, 1.262, 1.589, 2, 2.518, 3.170 and 3.990 s. Stimuli were generated and presented with PsychToolbox 3 routines in Matlab 2016b (Brainard, 1997a; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997a).

### 5.2.4. Procedure

Time perception was measured with a time generalization same-different task. A schematic representation of the procedure is depicted in Fig. 21 The milliseconds and seconds range as well as the visual and auditory modality were tested in separate sessions. Each experiment included an initial training session. This session started with an “encoding phase” in which the reference stimulus was repeated sequentially five times with no response required. Then in a block of seven trials, all possible durations of the test stimuli were randomly presented with participants required to judge the interval to be the same or different compared to the previously learned standard. In this phase response feedback was provided by a colour change of the central fixation point (green for correct responses, red for mistakes). Every seven trials, the percentage of correct responses was calculated, and the training continued (in blocks of seven trials) until the percentage of 85% of correct responses was achieved. After the training, a new encoding phase started with the reference stimulus presented five times followed by a resting of 3 minutes. At the end of the resting phase participant started the baseline condition. This consisted of 54 test trials, with each test duration presented 6 times, and the standard duration 18 times. As for the training, participants had to report whether test duration was the "same" or "different" from the reference duration. Baseline was followed by another encoding phase, at the end of which the participant started the running phase. During the first 3 minutes of running no stimuli were presented and the treadmill speed was adjusted to make participants reach a pre-defined heart rate corresponding to the 80% of the maximum heart rate for his/her age following the formula: 208 – (0.7 * age; see Tanaka et al., 2001). To reach and maintain the heart rate at the target value, the treadmill speed was continuously adjusted by the experimenter and all participants succeeded to reach the target heart rate within 3 minutes. After this preparation phase, the timing task was repeated while running. This second test phase lasted about 4 minutes for the milliseconds range and about 5 minutes for seconds range, with the total running time of the block lasting 7 and 8 minutes respectively. During the decoding phase, the treadmill speed was adjusted, if necessary, to keep participants heart rate around the target (80% of the maximum heart rate).

After the testing phase, the participants were allowed to take a break and rest, and when the heartbeat had returned to baseline levels (±10 bpm) the whole procedure (apart from the training) was repeated in the same temporal order. At the end of the experimental session, each participant had completed two blocks per condition, for a total of 108 trials.

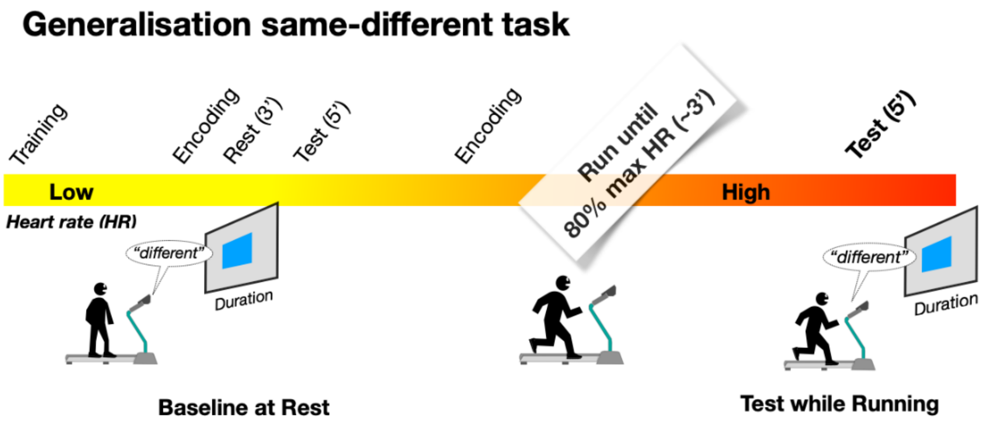

**Figure 21. Schematic representation of the paradigm.**
After a training session, participants were presented with the reference stimulus five times (Encoding phase). After three minutes of rest, the baseline was measured, at rest (see methods for details). Then, after a second encoding phase, participants started running. After three minutes of running the timing task was repeated, this time while participants were running at 80% of their maximal heart rate.

### 5.2.5 Running Variables and Heartbeat Parameters

Heart rate and running speed were calculated during runner since the target heart rate had been reached, while the number of steps refers to the whole running period. The baseline heart rate was obtained with a 1-minute recording at rest. This measurement was repeated each time before the test session. In two auditory running conditions (one relative to the sub-second and one for the supra-second range) the heart rate of one participant was not collected due to technical failure that also occurred for two participants in the auditory baseline condition (second range). Running speed and steps number of one participant were not collected in the auditory-milliseconds-while-running and in the auditory-seconds-while-running conditions. Figure 22 reports the between participants average heart rate for the visual and auditory tasks in both interval ranges, milliseconds, and seconds. Heart rate increased during the first 3’ and remained constant until the end of running phase. Descriptive statistics are reported in Table 2.

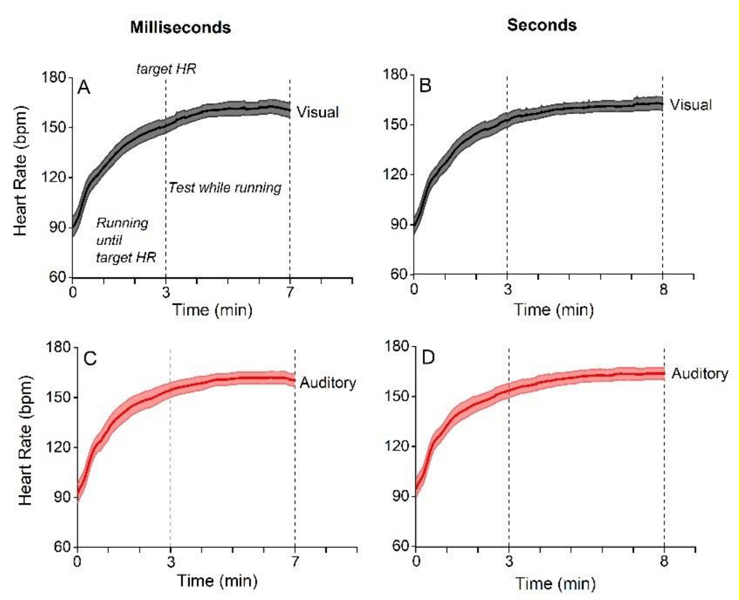

**Figure 22. Heart rate parameters**

Temporal trajectories of heart rate for visual (grey) and auditory (red) experiments for stimuli in the ranges of milliseconds (panels on the left) and seconds (on the right). In all experiments (A-D), the heart rate gradually reaches the target value (see methods) within three minutes and remained stable for the subsequent four/five minutes of running (testing phase). Lines reports between participants average, the shaded areas report 95% CI.

**Table 2. Running Parameters**

| Condition | Heart rate (Bpm) | Running speed (Km/h) | Steps per seconds (Hz) |
|---|---|---|---|
| Visual | | | |
| Milliseconds Baseline | 89±0.17 | n.a. | n.a. |
| Milliseconds While running | 159.65±0.19 | 9.9±0.22 | 3.69 |
| Seconds Baseline | 89.35±0.05 | n.a. | n.a. |
| Seconds While running | 159±0.15 | 9.5±0.19 | 3.92 |
| Auditory | | | |
| Milliseconds Baseline | 92.9±0.06 | n.a. | n.a. |
| Milliseconds While running | 160±0.14 | 9.7±0.31 | 3.4 |
| Seconds Baseline | 92.6±0.08 | n.a. | n.a. |
| Seconds While running | 161±0.17 | 8±1.99 | 3.68 |

Bpm= beats per minute; Km/h= kilometres per hour

Numbers reports between participants average, ± 1 s.e.m.
n.a.= not available

### 5.2.6 Data analysis

The proportion of “same” responses were plotted as a function of test duration and fitted with a Gaussian function. The peak of the fits describing the data distributions reflects the point of subjective equality of test and reference (PSE): the duration of the test stimulus being perceived to be the same as the reference stimulus. From the best gaussian fit we also retrieved a measure of sensory precision indexed by Weber Fraction (Eq. 2). The magnitude of the temporal distortions induced by running was measured as the standardized difference between the PSEs measured at rest and while running (Eq. 3). Similarly, as an index of heart rate (HR) acceleration we measured the difference between HR measured at rest and while running. As described in the dedicated section, the database was unbalanced with only a proportion of the sample who performed both the visual and acoustic task. For this reason, to statistically quantify the effects on accuracy and precision the raw PSEs or WFs were analysed with a linear mixed model ANOVA. PSEs or WFs were entered ad depend variable, modality (visual and auditory), duration range (milliseconds, seconds) and motor condition (resting and running) were entered as fixed effects. Participants were entered as a random effect. For all conditions PSEs and Wfs were normally distributed (Shapiro-Wilk, all $p>0.05$).

Complementing the frequentist ANOVA we also run a series of Bayesian t-tests (two-tailed) contrasting the normalized effect against zero (no effect) or between temporal regimes. As not all participants completed the visual and auditory tasks but all of them completed, for a given sensory modality, the tasks with short and longer durations, we did not compare the normalized effects between visual and auditory modalities (information however provided by the ANOVA). Bayesian statistic was also reported for correlations (Pearson’s r, two-tailed) between the normalized effects across conditions as well as between normalized effects and HR acceleration. For the same reason described above we only performed correlations within modalities and not between modalities. For these statistics we measured Bayes Factors, the ratio of the likelihood of the alternative to the null hypothesis and reported them as base 10 logarithms (LBF) (Jarosz & Wiley, 2014; Jeffreys & Jeffreys, 1998; Lavine & Schervish, 1999). By convention (Jarosz & Wiley, 2014) LBF from 0 to 0.47 is considered weak evidence for the alternative hypothesis, LBF > 0.47 is considered substantial evidence in favour of the alternative hypothesis and LBF < −0.47 substantial evidence for the null hypothesis. Absolute values greater than 1 are considered strong evidence, and greater than 2 definitive. Data were analysed by JASP (Version 0.16.3) and Matlab software. Matlab was used to fit the timing task data with Gaussian functions to estimate PSEs and Wfs. JASP was used for all the other statistical tests.

$$Wf = 10^{\sigma} - 1 \qquad \text{Eq. 2}$$

Where σ reflect the standard deviation of the gaussian fit (on a log range) describing the proportion of “same” responses against test stimulus duration.

$$Normalized\ effect = \frac{PSE\ (running) - PSE\ (rest)}{PSE\ (running) + PSE\ (rest)} \qquad \text{Eq. 3}$$

Where PSE running and PSE rest reflect the Point of Subjective Equality measured in the running or baseline (resting) condition respectively.

## 5.3 Results

### 5.3.1 Perceived duration: Aggregate data

As described in the methods section, participants were asked to compare the duration of a series of visual or auditory stimuli to the duration of a previously visual or auditory reference stimulus (different sensory modalities investigated in separated sessions). Depending on the condition the reference could last 0.4 s (“milliseconds range”) or 2 s (“seconds range”) with test stimuli ranging from 0.2 to 0.8 s or from 1 to 4 s respectively. All the conditions were tested in separate blocks with participants resting or running on a treadmill.

Figure 23 shows the results for the aggregate data. Panels A and B show the results obtained in the visual modality, for short and longer stimuli respectively while panels C and D show the results for auditory stimuli. On visual inspection, it is evident that all the curves obtained while running were shifted leftward relatively to those measured while resting, indicating that duration was overestimated while running. In the resting conditions the peaks were all near to the physical reference duration (milliseconds range: 0.4 s and 0.38 s for vision and audition; seconds range: 1.9 s and 2 s for vision and audition). In the milliseconds range, while running, for both vision and audition a stimulus lasting 0.36 s was perceptually judged as equivalent to the 0.4 s reference, an overestimation of about 9%. Similar effects emerged in the seconds range. While running, both a visual and an auditory stimulus lasting 1.9 s were perceptually judged as equivalent to the 2 s reference, an overestimation of about 5%.

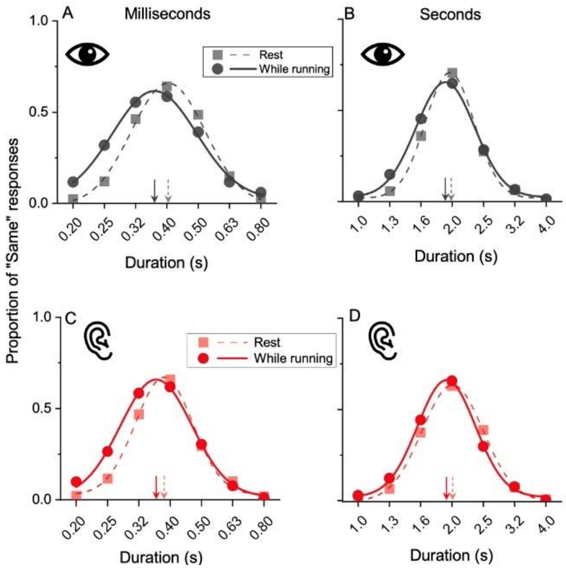

**Figure 23. Aggregate Data**
Results on aggregate data for visual (A, B) and auditory (C, D) stimuli belonging to the subsecond (reference 400 ms: A, C) and second range (reference 2 s: B, D) obtained while resting (squares, dashed lines) or while running (circles, continuous lines). Test stimuli durations were plotted against the proportion of "same" responses and fitted with Gaussian functions. The peaks of the fits (arrows) correspond to the PSEs. A relative leftward shift corresponds to a duration overestimation of the test stimuli.

### 5.3.2 Perceived duration: group analyses and individual data

With the same fitting procedure used for the aggregate data, we also analyzed the data separately for each participant and condition. For all the Gaussian fits on the individual data, an $R^2$ higher than 0.7 was achieved (see table 2 for $R^2$ descriptive statistics). Figure 24 shows the between participants PSEs average for stimuli in the milliseconds (A) and seconds (B) range for visual and auditory stimuli. The results mirrored those obtained with aggregate data with almost veridical duration perception while resting (values around the reference line) and a clear duration overestimation (lower PSEs values) while running. A visual inspection confirms a similar pattern of results across sensory modalities and stimuli durations range (see Table 3 for PSEs descriptive statistics).

A linear mixed ANOVA, together with an obvious effect of duration range (F(1,169.56)= 6061, p<0.001) indicating that PSEs scales with stimuli duration, revealed a main effect of motor condition, confirming lower PSEs values (duration overestimation) while running compared to resting (F(1,169.56)= 9.87, p=0.002). Crucially all the interactions were not statistically significant (see table.4) indicating a similar effect of running on PSEs across sensory modalities and stimuli duration range.

**Table 3. Descriptive statistics (Gaussian fit $R^{2)}$**

| | | **Milliseconds** | | | |
|---|---|---|---|---|---|
| | | N | mean | SD | min |
| Visual | Rest | 29 | 0.95 | 0.055 | 0.74 |
| | Run | 29 | 0.93 | 0.07 | 0.73 |
| Auditory | Rest | 23 | 0.97 | 0.03 | 0.85 |
| | Run | 23 | 0.95 | 0.06 | 0.7 |
| | | **Seconds** | | | |
| | | N | mean | SD | min |
| Visual | Rest | 29 | 0.96 | 0.04 | 0.83 |
| | Run | 29 | 0.96 | 0.04 | 0.82 |
| Auditory | Rest | 23 | 0.97 | 0.03 | 0.88 |
| | Run | 23 | 0.95 | 0.06 | 0.72 |

N= number of observations; Mean = between participant's average; SD= standard deviation; Min= minimum

**Table 4. Descriptive Statistics (PSEs)**

**Milliseconds**

| | | N | mean | St.err | SD | min | max |
|---|---|---|---|---|---|---|---|
| Visual | Rest | 29 | 0.405 | 0.008 | 0.044 | 0.31 | 0.5 |
| | Run | 29 | 0.366 | 0.01 | 0.059 | 0.26 | 0.48 |
| Auditory | Rest | 23 | 0.388 | 0.01 | 0.047 | 0.3 | 0.5 |
| | Run | 23 | 0.363 | 0.012 | 0.056 | 0.25 | 0.47 |

**Seconds**

| | | N | mean | St.err | SD | min | max |
|---|---|---|---|---|---|---|---|
| Visual | Rest | 29 | 1.99 | 0.033 | 0.176 | 1.73 | 2.35 |
| | Run | 29 | 1.9 | 0.04 | 0.228 | 1.46 | 2.5 |
| Auditory | Rest | 23 | 2.04 | 0.058 | 0.279 | 1.66 | 2.84 |
| | Run | 23 | 1.93 | 0.048 | 0.231 | 1.47 | 2.32 |

PSEs= Point of Subjective Equality; N= number of observations; Mean = between participant’s average; St.err= standard error of the mean; SD= standard deviation; Min= minimum; Max= maximum

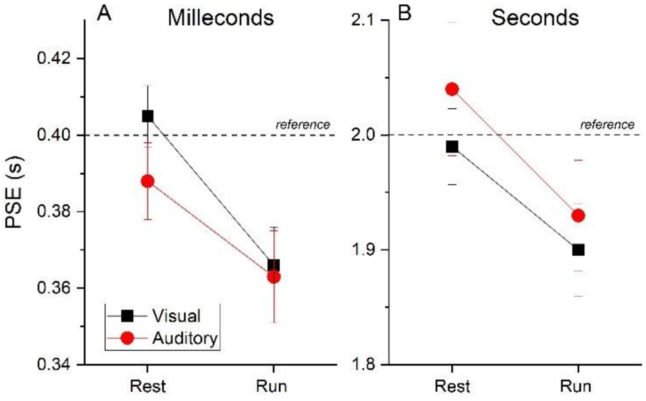

**Figure 24. PSEs Averages across subjects**
Between subjects PSEs average for visual (black squares and lines) and auditory (red circles and lines) stimuli belonging to the milliseconds (A) and seconds (B) ranges divided by motor condition (resting and running). Dashed lines reports reference duration. Relatively lower values reflect duration overestimation of the test stimuli. Error bars are ±1SEM.

**Table 5. Mixed ANOVA on PSEs, Summary Table**

| Parameter | df | F | p |
|---|---|---|---|
| Modality | 1, 197.95 | 0.234 | 0.629 |
| Range | 1, 169.56 | 6061.650 | < 0.001 |
| Motor | 1, 169.56 | 9.879 | 0.002 |
| Modality*Range | 1, 169.56 | 1.631 | 0.203 |
| Modality*Motor | 1, 169.56 | 0.006 | 0.940 |

| | | | |
|---|---|---|---|
| Range*Motor | 1, 169.56 | 2.532 | 0.113 |
| Modality*Range*Motor | 1, 169.56 | 0.188 | 0.665 |

PSEs= Point of Subjective Equality

To better visualize the effects induced by running we calculated, separately for each participant, a standardized index of the effect’s magnitude (see Eq. 3). Figure 25 A shows the results obtained within the seconds range against those found in the milliseconds range, for auditory (red) and visual (black) stimuli. Despite a large interindividual variability, most of the data points falls in the positive quadrant, confirming a temporal overestimation induced by the running phase. The data points for visual and auditory stimuli were largely overlapped, confirming similar effects across sensory modalities. The average effects, together with associated 95% CI (shaded area) are depicted in Figure 25 B.

Complementing the frequentist linear mixed ANOVA we also run a series of Bayesian t-tests contrasting the normalized effects against zero (no effect). For visual stimuli in the seconds range, the results provided substantial (LBF= 0.65) evidence if favor of H1. For visual stimuli in the milliseconds range the evidence for H1 was decisive (LBF= 3.89). Regarding auditory stimuli the results revealed substantial evidence for H1 in case of short durations (LBF= 0.89) and weaker (LBF= 0.35) evidence for H1 in case of longer durations.

As described in the methods, not all the participants performed both the acoustic and the visual tasks. However, within the two modalities, all participants performed the tasks for both stimuli in the milliseconds and seconds ranges. To further characterize the effects across temporal regimes, we compared and correlated the effects between the milliseconds and seconds ranges, separately for visual and auditory stimuli. For auditory stimuli the results suggested substantial evidence in favor of H0 (no difference, LBF= –0.56). For visual stimuli the results suggested weak evidence for H1 (LBF= 0.31). To investigate the links between the effects, we thus run two correlations, one for the visual and one for auditory stimuli, contrasting the effects measured for short (milliseconds) and longer (seconds) stimuli. If the effects for the two temporal regimes originates from a unique mechanism dedicated for both, we expect positive correlations. Contrarily to the prediction, the results showed no evidence for correlations, for both visual (r= –0.078, LBF= –0.6) and auditory (r= 0.37, LBF= 0.03) stimuli (Figure 25A).

Overall, these series of Bayesian checks on the normalized effects, confirmed the results provided by the frequentist linear mixed model suggesting an effect of running similarly affecting short and longer durations within visual and auditory modalities.

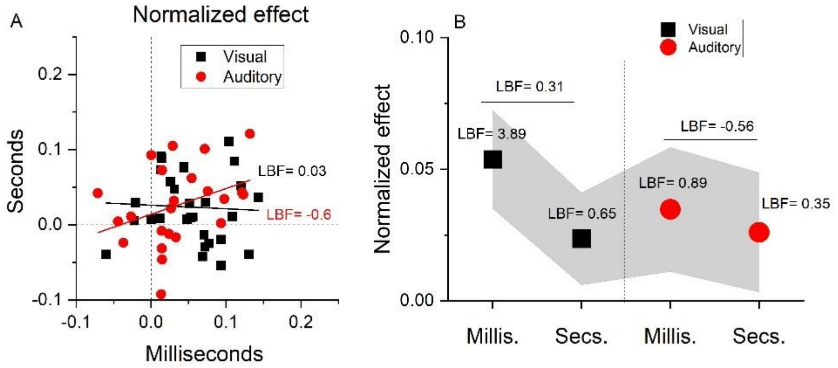

**Figure 25. Effects**

**A.** Single subjects' data reporting the running effect measured in the seconds range against that measured in the milliseconds range divided by stimuli sensory modality (auditory: red circles, visual: black squares). Positive values indicate a temporal overestimation. Continuous lines report best linear fits.

**B.** Between participants average effect as a function of experimental conditions (Vis.: visual, Aud.: auditory, Ms: milleconds range, Secs: seconds range). Shaded area report 95% CI.

### 5.3.3 Correlations with heart rate

As previous results obtained with both running (Petrizzo et al., 2022) and cycling (Tonelli et al., 2022) procedures suggested an independence between timing biases and heart rate acceleration induced by exercise, we also run a series of correlations between the perceptual biases induced by the running phase and heart rate modulations. As an index of heart rate modulation induced by the running phase we calculated, separately for each participant and condition, the difference between the heart rate measured at rest (see methods) and the average heart rate measured while running (without considering the first three minutes needed to reach the HR threshold, see methods). The average heart rate modulation for the visual conditions were: 71 and 71.4 beats per minute for stimuli in the milliseconds and seconds range respectively. The average heart rate modulation for the auditory conditions were: 62.2 per minute for both temporal ranges. Importantly for the correlational analysis, across all the conditions, there was a substantial interindividual variability with heart rate modulation varying between a minimum of around 50 to a maximum of 88 beats per minute (descriptive statistics are reported in table 5). The results showed substantial evidence for no correlations between heart rate modulation and effect's magnitude for all the four conditions (all p> 0.46, max LBF= –0.49, see Figure 26 and table 7).

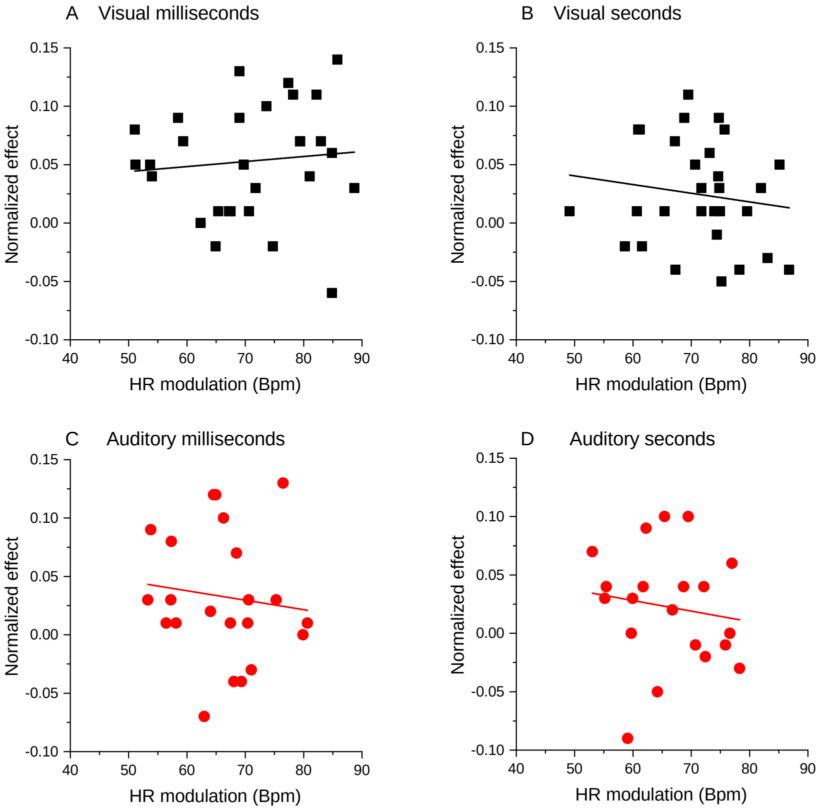

**Figure 26. Correlations between the normalized running effect on time perception and the heart rate increase induced by running, relatively to a resting state.**

**Table 6. Heart rate modulation descriptive statistics**

| Condition | Mean | SD | Min | Max |
|---|---|---|---|---|
| Visual Seconds | 71.4 | 8.55 | 49 | 86 |

| | | | | |
|---|---|---|---|---|
| Visual Milliseconds | 70.9 | 11 | 51 | 88 |
| Auditory Seconds | 66.2 | 7.8 | 53 | 78.2 |
| Auditory Milliseconds | 66.2 | 7.9 | 53 | 80 |

Mean = between participant's average; SD= standard deviation; Min= minimum; Max= maximum; Numbers reports beats per minute

**Table 7. Correlations between the effect's magnitude and hr modulation**

| Condition | Pearson's r | p | LBF |
|---|---|---|---|
| Visual Seconds | –0.14 | 0.469 | –0.53 |
| Visual Milliseconds | 0.097 | 0.615 | –0.58 |
| Auditory Seconds | –0.14 | 0.55 | –0.49 |
| Auditory Milliseconds | –0.116 | 0.61 | –0.52 |

Heart rate modulation = (Heart rate measured while running – Heart rate measured at rest); LBF= base ten log Bayesian Factor

### 5.3.4 Sensory precision

To assess whether running yielded distortion on the precision of sensory estimates across sensory modalities and duration ranges, we analyzed Weber Fractions (Wf, see Table 8 for descriptive statistics). Figure 27 shows between subject's average Wf measured while resting and while running. On inspection it is evident that Wf in the milliseconds range were higher (lower precision) compared to those measured in the seconds range, regardless of the sensory modality. Collapsing together visual and auditory data, Wf were on average 0.27 and 0.2 for the milliseconds and seconds ranges respectively. Another result emerging the data reported in Figure 27 is that in the two temporal ranges Wf varies differently between sensory modalities. In the milliseconds range, Wfs for the auditory modality were lower than that obtained in the visual modality while for longer durations (seconds range), visual and auditory Wfs were rather identical. This latter result was independent from the motor condition to hold true when time perception was measured while resting as well as during running. Finally, for both vision and audition and for both temporal ranges, Wf were higher while running compared to the resting condition (Wf = 0.26 and 0.21 for the running and resting conditions respectively).

A linear mixed ANOVA (Table 9) provided a statistically significant effect of range (F(1,196.97)= 50.93, p< 0.001) confirming higher precision at rest compared to during running as well as a statistically significant effect of modality (F(1,196.97)= 4.877, p= 0.02) indicating higher precision for auditory stimuli. Crucially, the modality*range interaction was also statistically significant (F(1,196.97)= 10.24, p= 0.002) confirming lower precision in the visual modality, but only in the milliseconds range. All the other interactions were not statistically significant confirming that visual and auditory Wfs varied similarly across motor conditions (modality*motor = F(1,196.97)= 0.43, p= 0.51), the effect of running was similar across temporal ranges (range*motor= F(1,196.97)= 1.48, p= 0.22) and that the effect of running on precision was similar across temporal ranges and sensory modalities (modality*range*motor= F(1,196.97)= 0.49, p= 0.48).

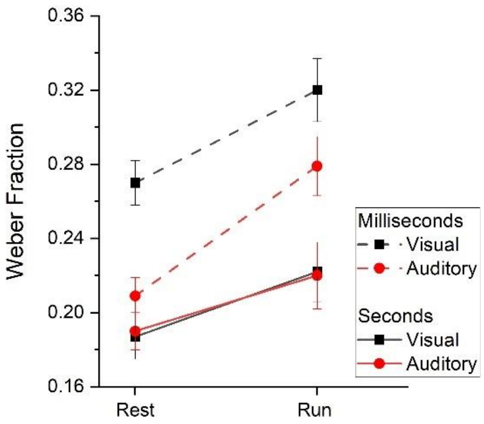

**Figure 27. Sensory Precision**

Between subjects' average Weber Fraction measured at rest and while running divided by duration range (subsecond: dashed lines, second: continuous lines) and stimuli sensory modality (vision: black squares and lines, audition: red circles and lines). Error bars are ±1SEM.

**Table 8. Descriptive Statistics (Weber Fraction)**

**Milliseconds**

| | | N | Mean | St.err | SD | min | max |
|---|---|---|---|---|---|---|---|
| Visual | Rest | 29 | 0.276 | 0.012 | 0.065 | 0.15 | 0.4 |
| | Run | 29 | 0.32 | 0.017 | 0.093 | 0.17 | 0.54 |
| Auditory | Rest | 23 | 0.209 | 0.01 | 0.047 | 0.14 | 0.29 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Run | 23 | 0.279 | 0.016 | 0.076 | 0.17 | 0.41 |
| | | | **Seconds** | | | | |
| | | N | mean | St.err | SD | min | max |
| Visual | Rest | 29 | 0.187 | 0.012 | 0.065 | 0.08 | 0.33 |
| | Run | 29 | 0.222 | 0.016 | 0.088 | 0.09 | 0.42 |
| Auditory | Rest | 23 | 0.19 | 0.01 | 0.05 | 0.1 | 0.29 |
| | Run | 23 | 0.22 | 0.018 | 0.085 | 0.08 | 0.4 |

N= number of observations; Mean = between participant's average; St.err= standard error of the mean; SD= standard deviation; Min= minimum; Max= maximum

**Table 9. Mixed ANOVA Summary Table (Weber Fraction)**

**Summary Table (Weber Fraction)**

| **Parameter** | **df** | **F** | **p** |
|---|---|---|---|
| Modality | 1, 196.97 | 4.877 | 0.028 |
| Range | 1, 166.26 | 50.931 | <0 .001 |
| Motor | 1, 166.26 | 25.990 | < 0.001 |
| Modality*Range | 1, 166.26 | 10.241 | 0.002 |
| Modality*Motor | 1, 166.26 | 0.439 | 0.509 |
| Range*Motor | 1, 166.26 | 1.481 | 0.225 |
| Modality*Range*Motor | 1, 166.26 | 0.494 | 0.483 |

## 5.4 Discussion

In the current study we measured the effect of running on time perception for short (milliseconds) and longer (seconds) durations for both visual and auditory stimuli. The results obtained with a standard generalization task (Lambourne, 2012; Petrizzo et al., 2022) confirmed previous studies showing that subjective time for visual short durations is expanded during a vigorous running phase. The results then expanded the previous findings by showing that the perceived time expansion also occurs for longer durations (in the seconds range) and regardless from stimuli sensory modality (visual or auditory).

It is worth to be mentioned that the current results on perceptual biases were partially different from those obtained in the only available study investigating the effect of physical exercise on auditory time perception. As mentioned in the introduction, Kroeger-Costa (2013) measured auditory time perception in the range of milliseconds

(300-700 ms) during running, compared to a resting condition. Time perception was measured with a discrimination task in which participants were asked to classify durations as “long” or “short” in terms of their relative similarity to two previously learned anchors setting the minimum and the maximum of the stimuli range, as well as by a generalization task, like that used here. The results obtained with the discrimination task showed a significant time overestimation induced by running, like the current results. However, at odds with the present study, the generalization task did not provide any significant effects. While these results might indicate that a discrimination task could be more sensitive to measure timing biases during physical exercise, the deviation from our results might also stem from a combination of methodological differences. The first is related to the lower sample size recruited in the mentioned study (10 participants), compared to the current experiment (23 participants for the auditory task). In line with this possibility, while the effect for auditory stimuli in the subsecond range found here was on average reasonably robust, there was also a considerable inter-individual variability (see Fig. 25A). A sample of 10 participants, given the level of variability, might have not been sufficient to reveal any significant effect in the Kroger-Costa study (2013). A second difference regards the running procedure. In Kroger-Costa study the physical effort was not equalized between participants and a fixed treadmill speed equal to 7.2Km/h was used for all participants. Here we equalized the physical effort across participants by defining for each participant a given heart rate value that was reached by dynamically adjusting the treadmill speed (80% of the maximal, see methods) during the running phase. This procedure resulted in an average running speed of about 10 km/h, which was considerably higher compared to 7.2. Overall, the fixed treadmill speed procedure used by (Kroger-Costa et al., 2013) could have made the physical activity effort not sufficiently strong (at least for some participants) to elicit a measurable effect on time perception, washing out the average effect. This partial discrepancy between studies calls for further investigations on the role of the aforesaid methodological differences. It is of interest to compare the present data also with the study by Tonelli et al (Tonelli et al., 2022) investigating the effect of moderate cycling on visual time perception. The results, obtained with a reproduction paradigm, showed that while temporal distortions were qualitatively present across all the tested durations, they were statistically different from zero just in the milliseconds range (200–800 ms vs 1.6–3.2 secs). In the current experiment, replicating previous evidence (Sayalı, Uslu, et al., 2018) we instead found that the effect for visual stimuli in the seconds range was clearly above zero (LBF= 0.65). Moreover, the ANOVA showed no interactions between motor conditions (rest, run) and stimuli regimes (milliseconds, seconds), confirming similar effects for short and longer durations. However, it should also be noted that the Bayesian analysis directly contrasting the visual effects between regimes, returned an LBF of 0.31 that, by convention, indicates a weak and non-decisive result, to leave open the possibility for smaller time distortions in the seconds regime. Anyway, partial discrepancies amongst the two studies might also suggest that different types of physical exercise and different experimental procedures to measure time perception (reproduction vs generalization tasks) are likely to yield different effects, probably tapping on different time mechanisms. Indeed, compared to cycling, running is a more complex motor routine, involving all the four limbs and requiring a higher level of proprioception and balance. Moreover, during running the continuous up and down movement of the head might triggers a series of complex vestibulo-ocular movements to stabilize the eye relatively to the external world (Purves et al., 2001) movements that are significantly mitigated during cycling. These and probably other factors might had contributed to the differences observed in the effects of running and cycling on time perception including the fact that while the effect of cycling has been reported to last several minutes after the end of the exercise (Tonelli et al., 2022), the effect of running on time perception seems to fade out immediately after the running period (Petrizzo et al., 2022). With the current results, we cannot determine which factors underlie these differences, but these certainly highlight the need for studies directly comparing the effects yielded by different physical exercises on time perception.

Together with a rather a-specific effect of running on time, we also collected clear evidence for partially separate systems involved in the encoding of short/long durations and between stimuli modality (vision vs audition). Replicating previous findings (Hayashi et al., 2014), for both visual and auditory stimuli, sensory precision levels were higher for stimuli in the seconds range compared to stimuli belonging to the milliseconds range. Furthermore, as found by Rammsayer et al. (2015), the results obtained here showed higher sensory precision for auditory stimuli but only for short durations, in the milliseconds range. Overall, the results on sensory precision are difficult to be explained by a single mechanism encoding time across temporal ranges and sensory modalities and are in line with the previously suggested possibility of a smooth transition from an a-specific timing mechanism encoding short durations (independent by sensory modalities), to a more sensory dependent mechanism encoding longer stimuli (Rammsayer et al., 2015). Moreover, within both sensory modalities, the effects of running for stimuli in the milliseconds and seconds ranges were weakly or not at all correlated between each other, again in line with the idea of partially separate mechanisms for short and longer durations.

It should be noted that these replications are important sanity checks for the current study, ensuring that with this paradigm and stimuli we were able to stimulate the milliseconds and seconds ranges. Despite this, the temporal biases induced by running were qualitatively and quantitatively similar across conditions, indicating that these temporal mechanisms – whether separated or not – nevertheless make use of shared resources linked to the motor system.

Which factor (or factors) underlies the observed effects on time estimates? One possibility we can easily exclude is that sensory precision level was driving the effects. Indeed, running similarly affected the milliseconds and seconds ranges despite they had clearly different precision levels. Moreover, in the milliseconds range, while the effects were similar for vision and audition, the sensory precision level was much higher for auditory stimuli. The independence between sensory precision and timing contextual effects was not granted. Indeed, has been previously showed that auditory time perception, compared to visual, is much less susceptible to contextual factors such as the well-known central tendency effect (a general perceptual phenomenon dragging the current perception towards the average if the tested range (Cicchini et al., 2012). The robustness of the acoustic timing system to this contextual effect has been linked to its higher sensory precision, compared to the visual modality. Another factor we can reasonably exclude is heart rate modulation. The results, confirming previous evidence (Petrizzo et al., 2022; Tonelli et al., 2022) demonstrated that the heart rate acceleration from the resting state to the maximal effort during running was not predictive of the effect magnitude, across all the experimental conditions. Heart rate level has been long considered a reliable indicator of arousal (Thayer, 1970) both of which might influence the speed of the internal clock. That arousal might be not the driving factor, it is in line with previous results showing that while time perception is distorted during physical exercise, estimates for other visual properties such as numerosity and spatial separation remain veridical (Petrizzo et al., 2022; Tonelli et al., 2022). A generalized effect induced by arousal would have been probably resulted in a generalized distortion of multiple visual features. Moreover, with the very same methods used here, we recently found that the effect of running on time perception vanished soon after the running phase while heart rate and thus likely arousal were still well above the baseline level (Petrizzo et al., 2022). This last result makes also unlikely explanations based on changes in the release of hormones or neurotransmitters, as these also take time to fully reuptake. It has been previously suggested that physical exercise might change time perception through a generic deprivation of the cognitive resources that are allocable to the timing task (Behm & Carter, 2020). According to this idea, running would act as a distractor task, dragging attention and cognitive resources away from the timing task thus modifying temporal encoding and hampering accuracy and precision. In line with this hypothesis, the current results showed that sensory precision worsens during running, compared to the resting state. Although it could be argued that running represents a rather automatized motor routine, this might not be true in our case where running was performed on a treadmill, a condition not entirely familiar for most participants. In should be noted that this (probably simplistic) explanation is in line with the lifespan of the effect induced by running. As soon as the run ends and thus attentional resources are released, the distortion on time perception vanished (Petrizzo et al., 2022). The idea of a generic attentional deprivation induced by running could also explain why the effect generalizes to stimuli of different durations and sensory modalities. This explanation might appear at odds with the fact that running does not interfere with visual number perception, however, there is much evidence suggesting that numerosity perception is fairly attentional free (Anobile et al., 2012; Anobile, Tomaiuolo, et al., 2020; Burr et al., 2010). Obviously, all these hypotheses are at present are speculations and would need future ad-hoc experiments to be tested.

# Chapter 6

# Time and Numerosity Estimation in Peripersonal and Extrapersonal Space

# 6. Time and Numerosity Estimation in Peripersonal and Extrapersonal space

## 6.1 Introduction

A precise and reliable representation of space is crucial to efficiently interact with objects in the environment. For instance, to successfully detect, reach and grasp objects located close to us, a detailed internal representation of the objects' position relative to the observer is needed. The space around us can be divided into two categories: peri-personal (PPS) and extra-personal (EPS) space, depending on the relative distance between the agent's body and the object of interest. The border between these two categories has been defined as the space within or outside our arms' reach (Rizzolatti et al., 1981) or the possible operational space of behavioral relevance achievable through tool use (Anelli et al., 2015; for a review see: Hunley & Lourenco, 2018; Longo & Lourenco, 2006).

Previous studies have shown that spatial attention can be differently distributed when individuals operate within versus beyond PPS. For example, when asked to bisect a horizontal line, neurologically healthy individuals tend to provide leftward biased responses, a phenomenon called pseudo-neglect, and thought to show a default leftward bias in spatial attention (McCourt & Jewell, 1999). Interestingly, this attentional bias attenuates progressively with distance: when asked to perform the bisection task in EPS, subjects' responses shift rightward not leftward (Longo & Lourenco, 2010; McCourt & Garlinghouse, 2000). The difference between PPS and EPS has been found to influence attention in the physical space as well as the mental representation of numbers as shown by the reduction of the leftward biases in EPS space in a mental number line bisection task involving digits (Longo & Lourenco, 2010).

The existence of multiple representations of space has also been suggested by neuroimaging studies showing that areas of the dorsal and the ventral stream were differentially recruited when stimuli were presented in either PPS or EPS (Fink et al., 2000; Weiss, 2000). A stronger activity in occipito-parietal regions was observed when line bisection tasks were performed in PPS compared to EPS, while the opposite contrast induced a higher activation in occipito-temporal regions (Weiss, 2000). The existence of a different neural substrate supporting the representations of PPS and EPS is further suggested by reports of a double dissociation in neglect patients, with some of them showing selective attentional deficits in PPS and others showing it only in EPS (Aimola et al., 2012; Butler et al., 2004; Cowey et al., 1994). In healthy individuals the double dissociation observed in neglect patients has been simulated by interfering with the activity of the dorsal or ventral areas via rTMS stimulation (Bjoertomt, 2002; Bjoertomt et al., 2009; Fierro et al., 2000). These results suggest a possible segregation of the cortical areas recruited when visual stimuli are processed at different distances from the observer: while perceiving stimuli in PPS potentially involves dorsal visuomotor areas, the processing of stimuli in EPS would mostly require the activation of visuo-perceptual ventral regions.

The representation of spatial information might not only be modulated by space-related characteristics of the objects but also by their temporal properties and numerosity. According to the ATOM theory, space, time and number are part of a generalized magnitude system and are processed by common neural resources(Bueti & Walsh, 2009; Walsh, 2003). Several behavioral studies showing interactions across the different magnitudes strongly support this idea of a shared representation. Duration discrimination judgements, for instance, can be influenced by the stimulus numerosity (Xuan et al., 2007), spatial position (Vicario et al., 2008) and items size (Xuan et al., 2007). Similarly, perception of non-symbolic numerosity is prone to the SNARC effect, resulting in faster reaction times to smaller numbers when responding using the left hand and vice versa, an effect suggesting an internal representation of numerosity along a spatial configuration from left to right (Dehaene et al., 1993; Nemeh et al., 2018). Numerosity perception is also influenced by other spatial non-numerical magnitudes such as total area, convex-hull, density and contour length as shown by both estimation and discrimination tasks (Dakin et al., 2011; DeWind et al., 2015; Gebuis & Reynvoet, 2012; Hurewitz et al., 2006; Nys & Content, 2012; Szucs et al., 2013) especially when these non-numerical dimensions are more salient than the numerical information.

It is worth noting that while most of the studies mentioned above reported cross dimensional interactions in PPS, it is still an open question whether these also occur in

EPS. Indeed, while a shared representation of magnitudes might be useful in PPS to optimize motor routines towards objects we want to interact with, the same might not hold when these are placed out of reach. Recent reports support the idea of a different processing for spatio-temporal (motion) or temporal (duration) information when stimuli are presented in PPS or EPS (Anelli et al., 2015; Vagnoni et al., 2012). It has been reported that looming threatening stimuli were perceived as approaching more rapidly than non-threatening stimuli in PPS (Vagnoni et al., 2012). Furthermore, duration estimates were found to vary according to stimulus distance from the observer. When participants were asked to reproduce half of the duration of a visual stimulus (a duration bisection task) they showed a tendency to overestimate visual stimuli duration in the EPS whilst the opposite, underestimation, occurred for stimuli presented in the PPS (Anelli et al., 2015). The representation of Arabic numbers was also found to be affected by the position of the stimuli either in PPS or EPS: when subjects were asked to estimate the number in between two digits presented in PPS, they showed a leftward bias on their mental numberline that decreased with increasing distance between the subjects and the visual stimuli(Longo & Lourenco, 2010).

In the present study we investigated whether, similarly to duration, numerosity perception is also affected by the position of the stimuli in PPS or EPS. First, we aimed at replicating the effect of viewing distance on duration perception which has been previously reported by Anelli et al. (2015). Then we tested if and to what extent the same effect also applies to numerosity perception.

## 6.2 Methods

### 6.2.1 Subjects

To establish the sample size needed to achieve an effect size comparable (f=0.87) as computed from Anelli et al. (2015), we performed an a-priori power analysis. The power-analysis for a repeated-measures within factors ANOVA to evaluate the factor “stimulus distance” ($\alpha$=0.01) revealed that 10 participants were needed to reach a power (1-$\beta$) of 0.95.

A total of 25 adults (mean age=26.4±4.03 years old, 14 females), all with normal or corrected-to-normal vision, participated in the experiments. 21 subjects were included in the duration reproduction experiment and 22 subjects in the numerosity estimation experiment (19 subjects completed both experiments). All participants gave written informed consent. The experimental procedures were approved by the local ethics committee (Comitato Etico Pediatrico Regionale – Azienda Ospedaliero-Universitaria Meyer – Firenze FI).

### 6.2.2 Stimuli and apparatus

Stimuli were created with Psychophysics toolbox for Matlab (Brainard, 1997b; Kleiner, Brainard, Pelli, Ingling, & Murray, 2007; Pelli, 1997b) and displayed on a 75 Hz – 22'' LCD monitor (ASUS VW225) with a resolution of 1680x1050 pixels (px). Subjects were tested in a quiet dark room, to minimize visual and auditory feedback.

### 6.2.3 General procedures

We measured subjects' accuracy and precision in a duration reproduction and numerosity estimation task via a bisection paradigm. For the duration reproduction task, we replicated Anelli et al.'s (2015) paradigm: participants were asked to press the spacebar to reproduce half of the duration of a visual stimulus they were presented with. A similar paradigm was used in the numerosity task: participants were asked to verbally report half of the numerosity of the cloud of dots. In separate sessions, visual stimuli were presented in PPS or in EPS for both experiments. Subjects were allowed to take a brief break in between the two sessions. The order of sessions within each experiment was pseudo-randomized across all subjects, except for an additional control condition of the numerosity experiment that was always performed on a separate day for all subjects.

### 6.2.4 Duration Reproduction Task: Replication of Anelli et al. (2015)

Participants sat in front of the monitor, with their dominant hand on the spacebar. During the "duration encoding phase" a blue square was centrally presented on a black background for 1600, 1800, 2000, 2200 or 2400 ms. Subsequently, after an ISI of 500 ms, a red square appeared to prompt the duration reproduction phase in which participants had to press the spacebar to reproduce half of the duration of the blue square. The red square disappeared as the spacebar was released and, after a fixed interval of 2000 ms, the next trial started (Fig. 28A). No feedback was provided to the subjects about the accuracy of their responses. In separate sessions, duration reproduction was measured with stimuli displayed at two distances from the observer: 60 cm (PPS) or 120 cm (EPS). The physical size of the stimuli was also manipulated so that there were two classes of stimuli, “small” and “big”, subtending the same angular size for each viewing distance. When stimuli were presented at the nearest distance (PPS), the sizes of the small and big stimuli were 31 and 62 px respectively. When presented at the farthest distance (EPS) the sizes of the small and big stimuli were doubled relative to those presented in PPS: 62 and 124 px. As a result, small stimuli subtended 1° whilst big stimuli 2° (Fig. 28B) when displayed in PPS as well as in EPS. Within each session, defined by a given stimulus distance (PPS or EPS), stimuli of different sizes (small or big) were randomly presented, and participants completed a single block of 60 trials (12 trials for each duration).

### 6.2.5 Number Estimation task

Participants were briefly (250 ms) presented with a central cloud of 6, 8, 10, 12, 14, 16 or 18 black dots. Participants were asked to verbally report half of the numerosity of the cloud as fast as possible (Fig. 29C). An experimenter, blind to the stimuli, stopped the reaction time recording as soon as the answer was given by the subject and recorded the answer via a keypress. Subjects were informed about the range of numerosity tested, but they were not given any feedback about the accuracy of their estimates neither during nor at the end of the experiment. As for the duration experiment, the task was performed twice, once with the monitor placed in PPS and once in EPS (60 and 120 cm respectively).

Each dot in the cloud subtended 0.4° and the dots spatial configuration was designed to have them fall within a virtual circle of 6° diameter in both PPS and EPS conditions (i.e. the angular size of the stimuli was the same irrespective of stimuli distance). This implied that the diameter of individual dots was either 12 or 24 px and the size of the virtual circles was either 186 or 372 pixels for stimuli presented in PPS and EPS respectively (Figure 29D). For each spatial condition a total of 140 trials were tested divided into 5 blocks of 28 trials each, separated by breaks. This procedure ensured that each numerosity was tested 20 times at each distance.

An additional condition was devised to control for possible interactions between numerosity estimates and stimulus size (Dakin et al., 2011; DeWind et al., 2015; Gebuis & Reynvoet, 2012; Hurewitz et al., 2006; Nys & Content, 2012; Szucs et al., 2013) consisting of a numerosity estimation task performed with stimuli subtending 12° (372 pixels) with the diameter of individual dots equal to 0.8° (24 pixels) displayed in PPS. In this condition subjects collected 140 trials divided into 5 blocks.

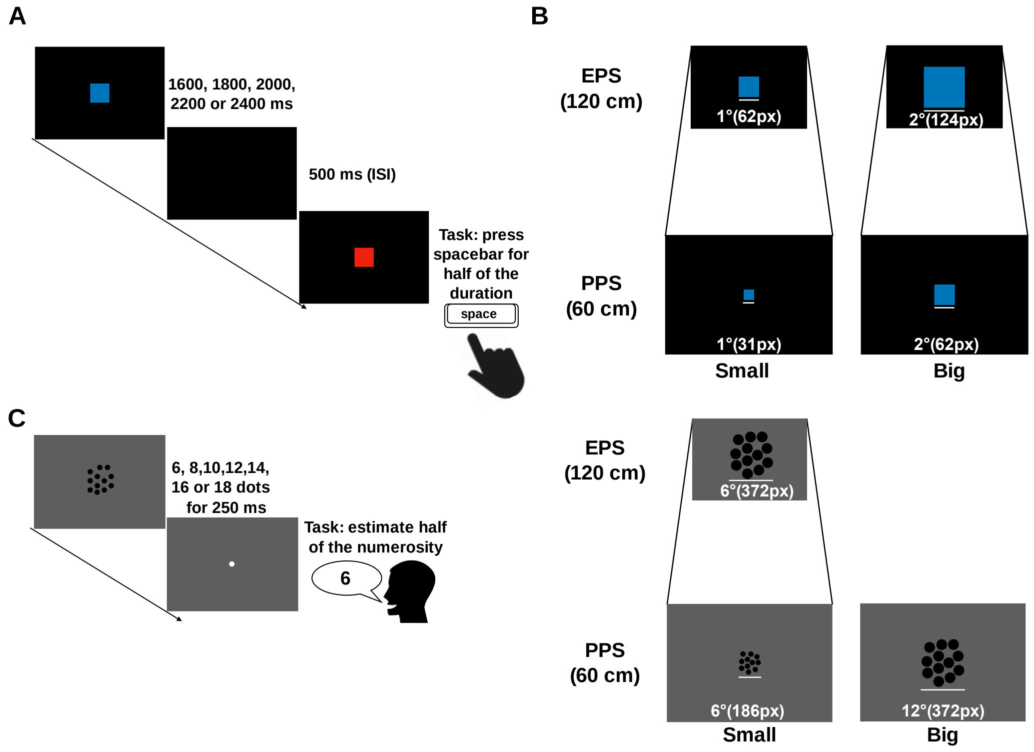

**Figure 28. Overview of the experimental design**

**A.** Duration Reproduction Task, replication of Anelli et al. (2015). Subjects were presented with a blue square lasting 1600, 1800, 2000, 2200 or 2400 ms. After a 500 ms ISI a red square appeared, and participants were asked to press the spacebar for half of the duration of the blue square. The red square disappeared when the spacebar was released and the next trial started.

**B.** Example of stimuli used in A. Stimuli could be either small (1°) or big (2°) and the screen was placed at either 60 cm (PPS) or 120 cm (EPS) from the subject. Stimuli presented in PPS were retinotopically matched to those presented in EPS (small/big stimuli subtended 1°/2° corresponding to a size of 31/62 and 62/124 px in PPS and EPS respectively).

**C.** Number Estimation Task. Subjects were briefly (250 ms) presented with a cloud of dots consisting in 6, 8, 10, 12, 14, 16 or 18 dots. Subsequently, a white dot appeared in the center of the screen and subjects were asked to verbally estimate half of the numerosity shown in the array. An experimenter (blind to the stimuli) stopped the registration time when the participant gave the number and recorded the answer via keypress.

**D.** Example of stimuli used in C. Stimuli could be either small (6°) or big (12°) and the screen was placed at either 60 cm (PPS) or 120 cm (EPS) from the subject. Small stimuli shown in PPS were retinotopically matched to the ones shown in EPS (6°) corresponding to 93 and 186 px respectively. In the control condition big stimuli were presented in PPS and subtended 12° (372 px).

### 6.2.6 Statistical Analysis

For each task (duration or numerosity) we measured the perceived magnitude and the precision of the responses separately for each participant. Perceived magnitude was indexed as the median of subjects' responses, while precision was indexed by Weber fractions, that is, the standard deviation on the response distribution for a given stimulus magnitude, normalized by the mean response for the same magnitude. In order to control for outliers, responses were also converted into Z scores and those lower or higher than 3 were excluded from the analysis (as a result less than 1% of all trials across all subjects and conditions for the numerosity task were discarded whilst no trials were discarded in the duration task). To assess whether, and to what extent, differences in stimulus size (a dimension that covaries with distance when the object angular size is kept fixed) play a role in duration and numerosity estimates, we compared the perceived magnitude for small stimuli in PPS (small PPS) with the perceived magnitude for big stimuli in PPS (big PPS) and with the small stimuli in EPS (small EPS). The difference in perceived magnitude was quantified using the following equation:

$$Difference = \left(\left(\frac{Perceived\ Magnitude_{BigPPS\ or\ SmallEPS}}{Perceived\ Magnitude_{SmallPPS}}\right) - 1\right) * 100 \qquad \text{Eq.4}$$

Statistical significance for differences in accuracy and precision of the achieved estimates in both PPS and EPS were analyzed by repeated measures ANOVAs (when Mauchly's Test of Sphericity was significant the Greenhouse-Geisser correction was applied), ANCOVAs and post-hoc paired t-tests. Statistical analyses were performed with SPSS Software (IBM Corp. Released 2019. IBM SPSS Statistics for Macintosh, Version 26.0. Armonk, NY: IBM Corp.) whilst the power analysis was performed using G*Power software (version 3.1.9.3 for Macintosh) (Faul et al., 2007a).

## 6.3 Results

### 6.3.1 Duration reproduction task: replication of Anelli's et al. (2015)

For the duration reproduction task we replicated the experiment previously performed by Anelli et al. (2015). Fig. 29A shows how duration estimation differs in PPS and EPS: on average, reproduced durations were significantly overestimated when stimuli were displayed in the EPS compared to the PPS by about 80ms (mean value ± S.E.M. for EPS: 1008±45ms and for PPS: 928±49), a result in line with Anelli et al. (2015). To assess whether this effect occurred for each of the tested stimulus durations, we plotted participants' responses as a function of the veridical duration for stimuli in PPS (red) and EPS (blue) for each tested duration (Fig. 29B). All tested durations were reproduced as longer when stimuli were displayed in EPS compared to PPS. To test for the statistical significance of these differences, subjects' reproduced durations were entered in a Two-Way Repeated Measures ANOVA with "stimulus distance" (2 levels: PPS or EPS) and "duration" (5 levels: 1600, 1800, 2000, 2200 or 2400ms) as factors. The ANOVA revealed a main effect of duration, meaning that the subjects correctly performed the task by varying their estimates of the different interval's length ($F(1.95,39.06)=49.8$, $\eta^2_p=0.71$, $p<0.001$), post-hoc analyses confirmed that all the durations estimated were indeed statistically different from each other (all p-values < 0.05). Importantly, the perceived duration was significantly overestimated for stimuli in PPS (1008±45ms) compared to stimuli in EPS (928±49) (significant main effect of the "stimulus distance" factor: ($F(1,20)=12.67$, $\eta^2_p=0.39$, $p=0.002$). The overestimation effect was comparable across all tested durations, as shown by the non-significant interaction between duration and space ($F(2.54,50.74)=0.94$, $\eta^2_p=0.05$, $p=0.42$).

To summarize, the duration estimation task succeeded in replicating the previous report by Anelli et al. (2015) and with a similar effect size ($\eta^2_p$=0.43 vs. $\eta^2_p$ =0.39) showing that duration of visual stimuli is perceived differently in PPS and EPS, with stimuli shown in EPS space being estimated as lasting longer compared to those presented in PPS.

### 6.3.2 Numerosity estimation task

Once the robustness of the paradigm used by Anelli et al. (2015) was confirmed for the investigation of visual duration perception in PPS and EPS, we applied a very similar paradigm to the perception of visual numerosity. Instead of reproducing half of the duration of a stimulus, in this task subjects were asked to verbally report half of the perceived numerosity of a quickly presented set of elements (preventing serial counting). As participants were informed about the tested numerical range, they could have anchored their response to the two extreme numerosity and this, in turn, could have provided edge effects. To control for this possibility, we discarded the two extreme numerosities (6 and 18 dots) from all the analyses (see Figure 29C). The results indicate that subjects showed a slight tendency to overestimate the numerosity of stimuli presented in EPS compared to PPS: averaged estimates pooled across all numerosities were equal to 6.03±0.10 and 5.77±0.12 (mean value ± S.E.M.) for stimuli presented in the EPS or PPS space respectively. Similarly to the duration experiment, we analyzed participants' responses as a function of the veridical numerosity in PPS and EPS separately for each tested numerosity. Numerosity estimates were entered in a Two-Way Repeated Measure ANOVA with "stimulus distance" (PPS or EPS) and numerosity (8, 10, 12, 14 or 16 dots) as factors. The main effect of numerosity was significant (F(2.25,47.29)=284.48, $\eta^2_p$=0.93, p<0.001) meaning that subjects correctly performed the task by modulating their estimates of the different numerosities, as confirmed by post-hoc tests (all p-values <0.05). Most importantly, there was an overall tendency to overestimate numerosity in EPS compared to PPS, as indicated by a significant main effect of the factor "stimulus distance" (F(1,21)=11.69, $\eta^2_p$=0.36, p=0.003). The interaction between numerosity and space was not statistically significant (F(3.03,63.54)=1.05, $\eta^2_p=0.05$, p=0.38), suggesting that perceptual biases were similar across numerosities.

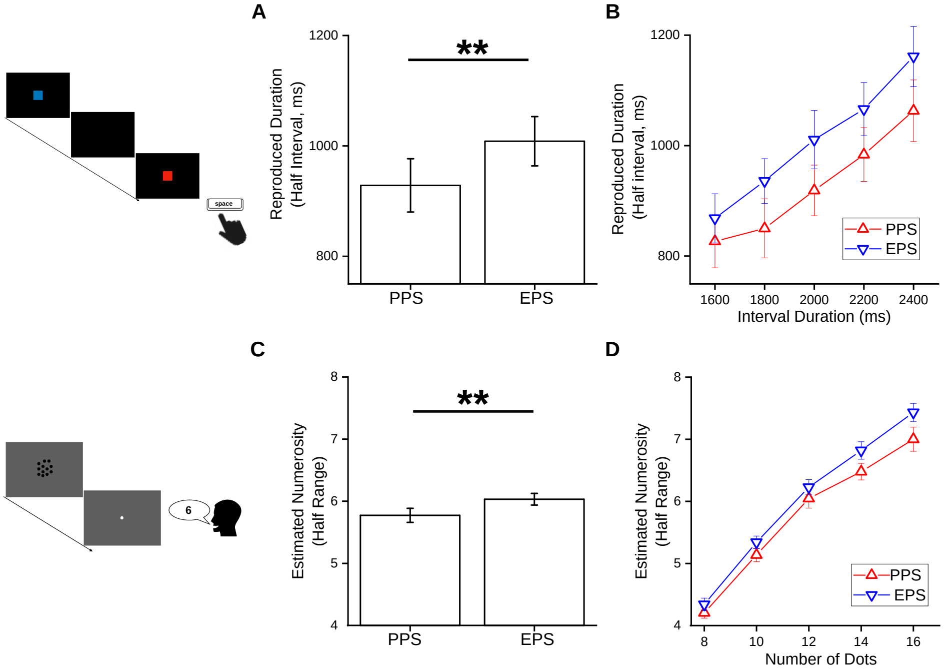

**Figure 29. Perceived duration and numerosity in peripersonal vs extrapersonal space**
**A.** Perceived duration in peri-personal vs extra-personal space. On average subjects significantly overestimated duration when stimuli were presented in EPS than PPS. Bars depict mean [M] ± 1 standard error of the mean [SEM]. **p<0.01.
**B.** Perceived duration plotted as a function of the veridical duration (y and x axis respectively) for stimuli presented in PPS (red) and EPS (blue). All tested durations were reproduced as lasting longer when stimuli were presented in EPS compared to PPS. Symbols represent average across subjects (N=21, data points show M±SEM). **p<0.01.
**C.** Perceived numerosity in PPS vs EPS space. Subjects significantly overestimated numerosity when stimuli were presented in EPS.
**D.** Perceived numerosity plotted as a function of the veridical numerosity (y and x axis respectively) for stimuli presented in PPS (red) and EPS (blue). All tested numerosities were estimated as more numerous when stimuli were presented in the EPS compared to PPS (N=22).

### 6.3.3 Influence of stimulus size on perceived duration and numerosity

In both experiments about perceived duration and numerosity, stimuli in the EPS were retinotopically matched to those presented in PPS. This means that while the stimuli were subtending the same angular size (at the level of the retina) they were physically different and potentially perceived to be so (larger stimuli in EPS). This is a realistic hypothesis because several depth cues were available to participants (e.g. the screen frame and the table edges). Moreover, previous studies have found interactions between size and both numerosity and temporal perception, with larger visual stimuli perceived as lasting longer (Rammsayer & Verner, 2014; Xuan et al., 2007) and being more numerous (Dakin et al., 2011; DeWind et al., 2015; Gebuis & Reynvoet, 2012; Hurewitz et al., 2006; Nys & Content, 2012; Szucs et al., 2013) compared to smaller stimuli. To rule out the possibility that the change in perceived duration and numerosity for stimuli presented in the EPS was driven by stimulus size and not by their distance, we compared subjects' responses to small stimuli in PPS and EPS (having the same angular size) with those obtained in a condition in which large stimuli were presented in PPS. If perceived magnitude is affected by stimulus distance regardless of stimulus size, we expected to find differences in subjects' responses for stimuli presented in PPS and EPS (small stimuli in PPS vs. small stimuli in EPS) but not when stimuli of different sizes were presented at the same distance (big stimuli in PPS vs. small stimuli in PPS). On the other hand, if stimulus size plays a role in defining perceived duration and numerosity, we should find a difference between estimating stimuli of different sizes presented at the same distance (big stimuli in PPS vs. small stimuli in PPS). First, we compared subjects' responses in the small stimuli condition in PPS and EPS (i.e. stimuli that were matched for angular size but differed in physical size), after covarying out the responses provided in the condition with big stimuli displayed in PPS (i.e. stimuli that had the same physical size of small stimuli in EPS). For the duration experiment, we performed an RM ANCOVA entering the perceived duration for the small stimuli in PPS and small stimuli in EPS conditions as dependent variables with "stimulus distance" (2 levels: PPS or EPS) and "duration" (5 levels: 1600, 1800, 2000, 2200 or 2400 ms) as factors and the perceived duration for the big stimuli in PPS condition as a covariate. The main effect of stimulus distance remained significant for duration estimates ($F(1,15)=8.93$, $\eta^2_p=0.37$, $p=0.009$), demonstrating that perceived duration was genuinely overestimated for stimuli presented in the EPS relative to those presented in the PPS, a result again in line with that found by Anelli et al. (2015). The same analysis was performed for perceived numerosity. In this case results showed that the difference in perceived numerosity for stimuli of the same angular size presented in PPS or EPS space (small stimuli in PPS and small stimuli in EPS) was not statistically significant (F(1,16)=1.32, $\eta^2_p$=0.08, p=0.27) when the difference in physical size was taken into account (responses for big stimuli in PPS stimuli used as covariate), suggesting that the size of the stimuli and not their distance in space accounted for the perceptual illusion reported in the numerosity estimation experiment.

The possible role of perceived size relative to stimulus distance was further investigated by comparing responses to big stimuli in PPS and to small stimuli in EPS (stimuli in both conditions have the same physical size) against the condition with small stimuli in PPS (stimuli used as baseline) that matched the former for stimulus distance and the latter for stimulus angular size. The difference was quantified by using the equation illustrated in the Statistical Analyses paragraph of the Methods section. Again, if responses were modulated by stimulus distance and not by stimulus physical size, the difference in subjects' responses was expected to be zero when comparing stimuli of different physical size shown at the same distance from the observer (small stimuli in PPS vs. big stimuli in PPS). On the other hand, a statistically significant difference in subject's responses had to be expected when comparing stimuli of the same angular size (even if different in physical size) shown at different distances (small stimuli in PPS vs. small stimuli in EPS). The results showing the effect of distance on perceived duration are reported in Fig. 30A, where we plotted the mean effect averaged across all durations/numerosities and across subjects. An almost null (0.11%±1.45) difference was obtained when comparing perceived duration for stimuli of different sizes presented at the same distance (small stimuli in PPS vs. big stimuli in PPS), which indicates that difference in physical size did not affect subjects' duration estimates. On the other hand, when comparing durations estimates of stimuli that differed for both, in physical size and distance (small stimuli in PPS vs. small stimuli in EPS) a mean difference of 9.99%±2.67 emerged and it was significantly larger (t(20)= –3.38, p=0.003) than the first one (small stimuli in PPS vs. big stimuli in PPS), suggesting that distortions in duration estimates were mostly triggered by stimulus distance from the observer.

Figure 30B shows the same analysis for the numerosity task. In this case, once normalized by the baseline (small stimuli in the PPS), perceived numerosity for stimuli of the same physical size presented in the PPS was 4.97% (±1.35) and 2.56% (±1.62) in the EPS with a not statistically significant difference (t(21)=1.74, p=0.1). These results suggest that perceived numerosity, at odds with duration, is primarily affected by stimulus perceived size with such an effect accounting for the overestimation of stimulus numerosity presented at far distance (EPS).

To summarize, these analyses revealed that presenting stimuli within or beyond PPS had different effects on duration and numerosity perception. While perceived duration was genuinely modulated by stimulus distance (independently of stimulus perceived size), difference in perceived numerosity for stimuli displayed at different distances appeared to be, to a large extent, induced by the difference in stimulus size.

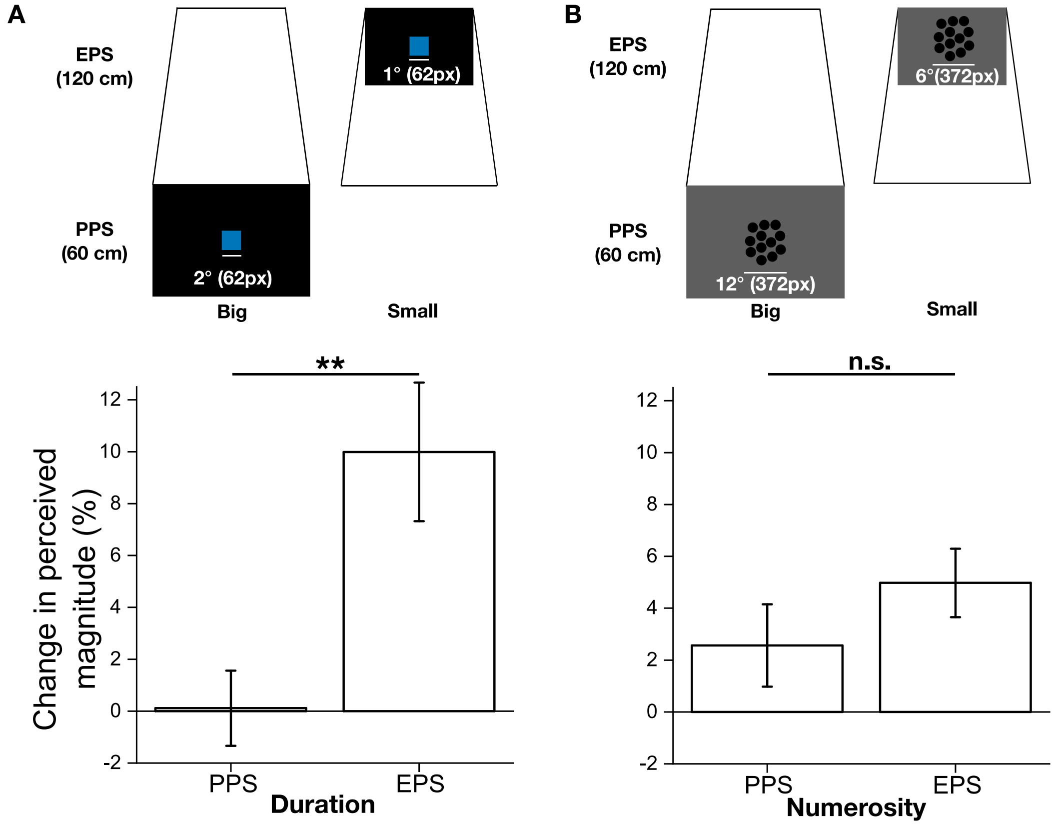

**Figure 30. Perceptual difference induced by stimulus physical size and distance on perceived duration and numerosity**

**A.** Changes in perceived duration for big (2°) stimuli presented in PPS and small (1°) stimuli presented in EPS relative to the baseline condition defined by small (1°) stimuli presented in the PPS. Perceived duration of the stimuli in PPS was the same despite stimuli differing in size. On the contrary, duration estimates were overestimated for stimuli presented in EPS compared to those presented PPS.

**B.** Changes in perceived numerosity for big (12°) stimuli presented in PPS and small (12°) stimuli presented in EPS relative to small (6°) stimuli presented in PPS. Regardless of distance from the observer, the numerosity of stimuli was always overestimated, suggesting that stimulus perceived size, not distance was the cause of the distortions in perceived numerosity.

In both panels, bars represent data averaged across subjects and error-bars indicate ±1SEM.

### 6.3.4 Sensory Precision

One main concern with perceptual biases is that they might derive from a decrease in the subject's precision or an increase in task difficulty, rather than from a real perceptual change induced by an environmental factor, such as the distance of the stimulus from the observer (Anobile et al., 2019; Castaldi et al., 2018). To rule out this possibility we analyzed Weber fractions for each subject as this measure is commonly used to assess subject's precision. The results indicate that Wfs were overall higher for the duration than numerosity experiment (0.20±0.01and 0.13±0.003 respectively). Importantly, Wfs were not statistically different between PPS and EPS neither in the duration task (mean value ± S.E.M. for small stimuli in PPS:0.22±0.02 ; small stimuli in EPS: 0.19±0.01, F(1,20)=3.11, p=0.09) nor in the numerosity task (mean value ± S.E.M. for small stimuli in PPS= 0.14±0.004, small stimuli in EPS: 0.13±0.005, F(1,21)=1.41, p=0.25) suggesting that changing the stimuli distance from the observer did not significantly affect their precision. In conclusion, the effect of stimulus distance on perceived duration and numerosity was unlikely to be driven by the subject's lower perceptual precision in performing both estimation tasks but, rather, by a perceptual change induced by stimuli being presented either in the PPS or EPS.

## 6.4 Discussion

It has been recently demonstrated that duration perception of visual stimuli differs when stimuli are presented in PPS or EPS (Anelli et al., 2015). In the current study we tested whether numerosity perception is also influenced by viewing distance. Specifically, we asked whether duration and numerosity judgments are prone to similar perceptual biases when stimuli are presented in PPS or EPS. We first replicated Anelli et al. (2015)'s results, showing that duration is overestimated in EPS compared to PPS. We then devised a similar procedure to test whether numerosity judgements were also biased by stimuli distance, with stimuli presented in EPS being overestimated compared to those presented in PPS. Crucially, while the overestimation found in the duration task was genuinely induced by the stimulus distance from the observer, in the numerosity task the effect was explained by stimulus perceived size rather than by the stimulus distance from the observer. The different effects on numerosity and duration judgements suggest that the perception of these magnitudes might rely on partially different mechanisms and highlight the importance of considering the action-space as a tool to investigate differences between magnitudes perception.

In line with the experiment by Anelli et al. (2015), we found that stimulus duration was significantly overestimated in EPS compared to PPS and that this effect was not mediated by stimulus size. The independence of duration judgments from stimulus size might seem in contrast with previous studies reporting interference effects across dimensions, e.g. larger stimuli were found to be judged as lasting longer using discrimination (Xuan et al., 2007) or full-length interval reproduction (Rammsayer & Verner, 2014) tasks. One possibility is that in the present study, the variability induced by having to reproduce only half of the presented duration might have washed out the bias induced by stimulus size. However, given that the studies reporting interference effects across dimensions used shorter stimulus duration (Rammsayer & Verner, 2014; Xuan et al., 2007), future experiments will be needed to achieve a definitive answer.

We then tested the effect of distance on numerosity perception. Mirroring what we found for duration judgments, numerosity was also overestimated when stimuli were shown in EPS compared to PPS, although to a much lesser extent (a difference of about a factor of 2). Importantly however, we demonstrated that in this case the overestimation was due to the interference between numerosity and stimulus perceived size rather than by viewing distance. In the current study, in order to match the angular size of the stimuli at different distances, stimuli shown in Extrapersonal space were physically larger compared to those shown in Peripersonal space. Even if stimuli were retinotopically matched, visual depth cues may have been used to cognitively infer the real size of the stimuli presented in EPS. Such cognitive strategy may have triggered overestimation of numerosity judgments due to differences in perceived stimulus size. This hypothesis was indeed confirmed: overestimation of numerosity occurred even when participants were tested with stimuli presented in PPS but larger in size. Varying stimulus size without changing the distance from the observer was sufficient to account for the overestimation effect observed when placing the (same) physically larger stimulus in EPS. This is in line with previous studies reporting interference effects between stimulus size and numerosity judgments (Dakin et al., 2011; DeWind et al., 2015; Gebuis & Reynvoet, 2012; Hurewitz et al., 2006; Nys & Content, 2012; Szucs et al., 2013).

Taken together, these results suggest that numerosity perception, at least in the numerical range tested in the current experiment, seems to be much less affected by stimulus distance which, on the other hand, genuinely affects duration estimates. Whether there is an effect of distance on numerosity ranges higher than those employed in the current experiment is currently unknown. A recent set of behavioral studies has demonstrated that at least three different systems support numerosity perception: the subitizing system for arrays of up to 4 items, the approximate number system (for numerosities higher than 4 and below the density range) and the texture/density system that kicks in for very high numerosities when segregation of the items becomes impossible (see: Anobile, Cicchini, et al., 2016b for a review). These three numerical regimes are governed by different psychophysical rules and rely to a different extent on attentional resources (Anobile, Tomaiuolo, et al., 2020; Castaldi et al., 2020; Pomè et al., 2019). In the current study the presented (8 to 16 items) and the estimated numerosities (i.e. the half of the displayed numerosities) were comprised within the approximate number range. Given that a signature of the approximate number system is to be characterized by constant Weber fractions, we expect the current results to hold also for slightly higher numerosities as long as they tap onto the same approximate number system. However, for even higher numerosities analyzed by the density system, the current results may not hold. Future studies should test whether the conclusion of the current study can be extended to a larger numerical range.

It can be objected that Weber fractions differed between tasks, potentially suggesting that the numerosity estimation task was slightly easier compared to the duration task. While we cannot formally rule out the possibility that the PPS/EPS effect was smaller in the numerosity task due to the lower difficulty of the numerosity compared to the duration estimation tasks, we think that this interpretation is unlikely. Indeed, within each task (numerosity and duration separately), the Weber fractions did not change between PPS and EPS, yet durations were overestimated in EPS while the same did not hold for numerosity when size was considered. Given that the Weber fractions were similar within each task and across spatial locations, the effect of stimulus distance on perceived duration and numerosity can hardly be explained by the subject's lower perceptual precision in performing the task in PPS compared to EPS. Thus, rather than depending on task difficulty, the perceptual change seems to be genuinely induced by stimuli being presented at two different locations in space. Nevertheless, future studies should replicate the current result after selecting stimuli that would match Weber fractions across both dimensions (numerosity and duration).

Numerical perception at different distances has been previously investigated by Longo and Lourenco (2010), however in this case a different task was used, involving symbolic rather than non-symbolic numerosities. The authors used a mental number line bisection task with symbolic numbers and found a leftward bias in PPS which tended to disappear when performed in EPS and concluded that numerical space is affected by the distance. Our results, suggesting that numerosity might not be affected by stimulus distance, seem in contradiction with this conclusion. However, beyond the major methodological differences between experiments (number bisection task with digits vs numerosity estimation), it is worth noting that the effect reported by Longo and Lourenco (2010) was most pronounced at larger distances in EPS compared to those tested in the current study and their effect was much weaker at 120 cm from the subject, which corresponds to the only distance tested here. Our results are thus in line with their observation at the same distance. Future studies should test whether increasing the viewing distance even more would result in overestimation of numerosity or whether distance has a different impact on non-symbolic and symbolic numbers.

To summarize, the current results suggest that duration and numerosity perception is differently modulated in PPS and EPS. The interaction between time, numerosity and space has been highlighted by several studies, suggesting a common encoding system shared between domains as proposed by the ATOM theory (Bueti & Walsh, 2009; Walsh, 2003; Walsh et al., 2013). For example, it has been demonstrated that adapting to duration alters numerosity discrimination judgements (Tsouli et al., 2019). Furthermore, more numerous stimuli are judged as lasting longer, compared to less numerous stimuli, and vice versa, stimuli presented for longer durations are perceived as being more numerous (Javadi & Aichelburg, 2012).

One of the key ideas of the ATOM theory is that the development of a common magnitude system may be shaped by actions. Space, time and numerosity are highly correlated in the environment and we learn this association through active interactions (Bueti & Walsh, 2009). Recent studies confirmed the idea that magnitudes perception is closely linked to the activity of the motor system (Anobile, Arrighi, et al., 2020; Anobile et al., 2019). A form of sensory adaption, called "motor adaptation", has been proven to be a useful tool to reveal visuomotor interactions (Anobile, Arrighi, et al., 2016; Maldonado Moscoso et al., 2020). When participants were asked to perform a series of finger tapping movements with their dominant hand in the same spatial location in which a visual test stimulus was subsequently presented, numerosity estimates of visual arrays or sequences of flashes and the speed of a moving grating were significantly over or underestimated depending on the tapping rate during the adaptation period (Anobile, Arrighi, et al., 2016; Anobile et al., 2019). These results suggest a common influence of the motor system on the perception of both numerosity and duration. However, it is important to note that these studies were performed with all stimuli displayed at a short distance from the observer, within the PPS. Future studies are needed to test whether the same interactions between the motor and the perceptual system also occur when stimuli are presented in the EPS, that is out of arm's reach.

Interestingly, the ATOM theory predicts that, given that the development of a magnitude system was meant to optimize action execution, our perception of magnitudes (and the interference effects among them) may vary depending on whether the stimuli are within or outside the 'action space' (Bueti & Walsh, 2009). The current study provides empirical evidence in support of this hypothesis: perceived duration and numerosity were both overestimated for stimuli presented out of the arm's reach (EPS). However, while distortions for perceived duration were genuinely yielded by viewing distance, those for numerosity were triggered by the interaction between stimulus size and numerosity and not by viewing distance, suggesting that this parameter may not equally affect information processing in the three dimensions of the ATOM: space, time and quantity.

Overall, the present findings suggest the existence of at least partially independent systems, one for PPS, which is the one relevant for the execution of motor actions, and the other for the EPS, in which a shared processing of time and numerosity may not be so useful, as an immediate interaction with far stimuli cannot be achieved. This view is in line with the recent "Action Field Theory of Peripersonal Space" by Bufacchi and Iannetti (2018). The authors suggested a functional definition of peri-personal space defined as the space of "relevance of potential actions that aims to either create or avoid contact between a stimulus and a body part" (Bufacchi & Iannetti, 2018). Our findings suggesting that numerosity and duration may be encoded by the same system in PPS to support action guidance, but not necessarily in EPS, where goal-directed actions on the objects cannot be executed, fit well with this idea.

In conclusion, our results point to a partial dissociation in the processing of numerosity and duration that seems to be affected differently by stimulus location in either PPS or EPS. However, if the proposed dissociation between the systems supporting numerosity and duration perception were to be confirmed, it would not necessarily provide evidence against the ATOM theory. Indeed, if the link between magnitudes develops through the motor system (Anobile, Arrighi, et al., 2020), space, time and number might share the same metrics only when presented in the space we can act on, while they might be encoded differently in the space where actions are not possible. More generally, this study suggests that investigating the perception of stimulus properties as a function of distance from the observer and, in particular, comparing magnitudes perception across locations where it is or is not possible to act (EPS Vs PPS) may be a useful tool to reveal how magnitudes are represented, as some characteristics of the related mechanisms may otherwise pass unnoticed when a single spatial plane is taken into consideration.

# Chapter 7

# Reshaping of Peripersonal Space in a Virtual Reality Environment

# 7. Reshaping of Peripersonal Space in a Virtual Reality Environment

## 7.1 Introduction

The space around us can be divided based on what lies within our reach or outside of it. This distinction is of primary importance for defining efficient motor plans that allow us to interact with the environment. The area surrounding our body, which is known as the *Peripersonal space* (PPS), was first described in monkeys, with the discovery of multi-modal neurons that only fire if a stimulus is placed near the body of the animal (Rizzolatti et al., 1981). These neurons are located in the ventral premotor cortex F4 (Gentilucci et al., 1988) and have receptive fields that surround the monkey's hand and move with it (Rizzolatti et al., 1981). Interestingly, the electrical stimulation of these neurons elicits defensive-like movements in monkeys, as if the animals are trying to protect the part of the body where the receptive fields of the stimulated neurons are located (Graziano et al., 2002). The PPS can thus be conceptualized as a system specifically dedicated to the perception of stimuli that are in the immediate surroundings of the body and that may indicate potential risk or interest. In line with that, it has been proposed that the activity of brain areas in which PPS neurons are located aims at maintaining a margin of safety around the body (Graziano & Cooke, 2006).

Neuropsychological studies with neglect patients provide evidence for the presence of a specific area in the human brain dedicated to the perception of stimuli in the PPS. Hemineglect, or simply neglect, is a condition resulting from brain damage that leads to the inability to attend to stimuli presented in the contralesional hemifield (Vallar, 1998). In some cases, neglect patients fail to report the presence of a stimulus presented in the controlesional side when a competing stimulus is simultaneously shown in the ipsilesional side, a phenomenon known as "extinction" (De Renzi, 1982). Ladavas et al. (1998) demonstrated that the extinction effect also occurs cross-modally: the reduction in sensitivity to a tactile stimulus triggered on the controlesional hand induced by an ipsilesional touch was rather identical to that yielded by a visual stimulus displayed around the ipsilesional hand, suggesting the existence of a cross-modal visuo-tactile extinction. However, this effect was significantly reduced when the visual stimulus was presented outside of the patient’s PPS, indicating that the deficit in the combination of visual and tactile information in neglect was more pronounced within the PPS. A dissociation between PPS and the Extrapersonal space (EPS) is also found in pseudo-neglect, an attentional deficit presented by neurologically healthy individuals. When asked to bisect a horizontal line, most people tend to provide leftward-biased responses (McCourt & Jewell, 1999). Interestingly, this attentional bias attenuates progressively with distance. When asked to perform the bisection task in EPS, individual responses shift rightward instead of leftward (Longo & Lourenco, 2010; McCourt & Garlinghouse, 2000).

While the general definition of the size of the PPS is straightforward, its precise measurement poses some challenges. In animal models, the border between PPS and EPS can be measured with accuracy using in-vivo single-cell recording (Rizzolatti et al., 1981). However, in humans a non-invasive behavioral approach has to be adopted. One of the most widely used methods to capture the boundary between PPS and EPS is the audio-tactile detection task pioneered by Canzonieri et al. (2012). In this task, participants are presented with a looming auditory stimulus that creates the illusion of an approaching sound source. Following a predetermined delay, a tactile stimulus is delivered to the hand as a vibration and participants are instructed to react to this as fast as possible, while ignoring the auditory stimulus. If the vibration is delivered when the sound is perceived as being in the PPS, participants are faster to react than when the sound is perceived as being in the EPS. Thus, the operational definition of PPS using this auditory-tactile detection task can be summarized as the maximum distance from the participant’s body at which the auditory stimulus can still facilitate the detection of the tactile stimulus. Notably, one of the characteristics of PPS neurons is that they are multimodal (Rizzolatti et al., 1981) and thus capable of firing for both visual and auditory impulses. This has opened up to the possibility of measuring detection facilitation within the PPS with visual instead of auditory stimuli.

However, PPS should not be considered as a static bubble that surrounds one's body. Not only the PPS has been reported to show different characteristics between healthy and clinical populations (Di Cosmo et al., 2018; Noel, Failla, et al., 2020), but it has also been shown to be malleable to environmental conditions. For instance, as the size of the PPS is robustly based on the extension of our reach, if our reach changes, the PPS gets modulated accordingly. Peripersonal neurons tuned to a specific area within the surrounding space have been shown to quickly reshape their receptive fields to accommodate changes in the extent of the reaching area. Indeed, when monkeys are trained to use a stick to retrieve food from a distance, the receptive field of PPS neurons becomes longer (Iriki et al., 1996). In humans, there have been reports of amputees (Canzoneri et al., 2013) and wheelchair users (Scandola et al., 2016) having a smaller PPS compared to controls, whereas blind cane users (Serino et al., 2007) and long-term computer mouse users (Bassolino et al., 2010) have a larger PPS when holding their cane or mouse respectively. Also elite athletes show a remapped PPS. For instance, experienced tennis players exhibit larger PPS when they hold their racket (Biggio et al., 2017), with a similar effect also being found in fencers holding their sword (Biggio et al., 2020).

While modulation resulting from long-term conditioning induces a stable and durable reshaping of the PPS, there have also been reports of PPS reshaping after a short training session. For instance, after performing a task in which participants use the tip of a cane to find objects scattered on the floor, an extension of the PPS was reported. This effect was similar to blind cane-users, however the remodulation in the healthy participants was transient (Serino et al., 2007). Indeed, when participants were retested the day after the training, the PPS extension had disappeared. This result supports the idea that the duration of the training is proportional to the stability of the remapping. Indeed, this brief extension of PPS as a result of a short tool-use training has been observed under several different conditions (Bassolino et al., 2010; Canzoneri et al., 2013; Holmes et al., 2004; Patané et al., 2016). An enlargement of the PPS has also been observed while walking on a treadmill (Noel, Bertoni, et al., 2020), suggesting that the illusion of moving forward, even when there is no overall displacement, increases the perception of what can be considered within reach. However, as the expansion of PPS has been achieved via quite different motor routines, it is not clear which aspect of the training triggers the reshaping. Is it the forward motion of a body part, the proprioceptive feedback of reaching with a tool, or the motion of the body induced by walking?

Virtual Reality (VR) set-ups offer an ideal environment to study which aspect of the training plays a key role in inducing the reshaping of the PPS as it allows to design ecologically-plausible looming visual stimuli. Indeed, previous reports suggest that PPS can successfully be investigated with VR (Buck et al., 2020; Lee et al., 2021; Serino et al., 2018). As it has been demonstrated for the audio-tactile task, if the vibration is delivered when the virtual visual stimulus is perceived as being close to the participants body, reaction times (RTs) to the vibration are significantly reduced, and in some cases almost halved (Buck et al., 2020).

However, some concerns have been presented on whether measuring the PPS in VR provides a true representation of the PPS in the real world. Specifically, Ferroni et al. (2022) asked participants to perform a short training in which they had to move small objects from point A to point B with a horizontal dragging motion, with both A and B being landing points placed in EPS. This task triggered an enlargement of the PPS when the task was performed in the real world. However, this was not the case when the same routine was executed in a VR environment. Even though this result seems to question the usefulness of VR environments to study modulations of the PPS, it is important to note that a large variability of the effectiveness of the motor training has also been reported for experiments carried out in real world, so a more systematic investigation is needed to reach a definitive conclusion.

In our study we attempted to induce a reshaping of PPS in a VR environment by carrying out four different types of training. The first group of participants (Experiment 1) was trained using the most widely used task to induce a reshaping of the PPS: pulling an object closer to one’s body with the use of a tool. In a different condition, the same participants were instead instructed to perform a similar motor routine but with the opposite goal: to push an object away from their bodies into the EPS. In Experiment 2 we aimed to determine whether crossing the PPS/EPS border, as in the push-pull conditions in Experiment 1, is essential for reshaping the PPS or whether any repetitive hand movement with a tool can induce such a reshaping. To this end, participants had to repeatedly hit a target in the EPS using a hammer. To further explore this issue, in a final condition, participants were required to interact with the target in the EPS without any direct “physical contact” as they were required to shoot the target with a toy-gun. The first assessment in validating the VR as a tool to investigate PPS would be to replicate the PPS expansion as a consequence of training that involved pulling movements, as this training is the one of the most widely used in previous literature. Then, in case the PPS malleability is bidirectional, we would expect to reduce the PPS space as a consequence of pushing. Finally, with the hammering and shooting conditions, we aimed to investigate whether crossing the PPS/EPS border (hammering) or direct physical contact with a target (shooting) during training is essential for modulating the size of the PPS.

## 7.2 Methods

### 7.2.1 Participants

A total of 46 participants took part to Experiment 1- Push & Pull (mean age: 21.43±3.85, 37 females, 1 author). 33 participants took part to Experiment 2 – Hammer & Gun (mean age:22.12±3.37, 24 females, 1 author). All participants had normal or corrected to normal vision and gave written informed consent. The study was approved by the Cyprus National Bioethics Committee (Protocol Number: EEBK EP 2018.01.138) and was in accordance with the ethical standards of the 1964 Declaration of Helsinki. Participants were also asked to abstain from caffeine for at least two hours prior to the experiment to control for possible effects induced by stimulants on RTs (Childs & de Wit, 2006). Due to technical failure of hardware, complete behavioral datasets from 5 participants were not collected and were thus excluded from further analyses, leaving a total of 42 participants for Experiment 1 and 32 participants for Experiment 2.

### 7.2.2 Apparatus

A total of 46 participants took part to Experiment 1- Push & Pull (mean age: 21.43±3.85, 37 females, 1 author). 33 participants took part to Experiment 2 – Hammer & Gun (mean age:22.12±3.37, 24 females, 1 author). All participants had normal or corrected to normal vision and gave written informed consent. The study was approved by the Cyprus National Bioethics Committee (Protocol Number: EEBK EP

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### 7.2.3 Measurements of PPS – Baseline Task

To measure the size of the PPS we used the visuo-tactile detection task first proposed by Serino (2018). The experiment took place in a neutral virtual room in which three blob avatars were positioned at a distance of 2.5 m away from the observer, either straight ahead (at 0°) or at an eccentricity of 30° to the left or to the right of the observer (Fig. 1A). The avatars remained still for the whole duration of the task apart from an idle animation: slight up-and-down bouncing on the spot and blinking of their only eye. Participants were instructed to stand still inside a small circle which ensured a fixed distance (2.5m) from the blob avatars, to fixate on the central blob avatar, and to pull the trigger on the controller each time they felt a vibration. On each trial, one of the avatars (the central avatar on 80% of the trials) launched a semi-transparent bubble with a diameter of 10cm that travelled horizontally at a constant speed of 75cm/s towards the participant. The vibration could be delivered when the bubble was at 2.25, 1.75, 1.25, 0.75 or 0.25 meters from the participant. In total we collected 20 repetitions for each distance in Experiment 1 and 15 repetitions for each distance in Experiment 2 for practical reasons. On top of that, 15 trials for each of the two control conditions were added: (1) tactile only, in which the vibration was delivered without a bubble being launched, and (2) the bubble travelled the whole distance with no vibration being delivered. The control conditions ensured that the appearance of the ball did not trigger a stereotypical response. This meant that on each PPS measurement the participant was presented with a total of 140 trials for Experiment 1 and 105 trials for Experiment 2 with a single block lasting approximately 10 minutes.

### 7.2.4 Experiment 1 – Push and Pull

**Pull Training**

The participant was positioned in the same non-descriptive white room used for the Baseline Task described above, with only one blob avatar placed at 2.5 m directly in front of them (Fig. 1B). The blob avatar did not move except for the idle animation. On each trial a small round marble appeared on the floor between the participant and the blob avatar at a maximum distance of 1.5 m and an eccentricity of 0°, 30° or 60° on the left or the right respectively, at one of five possible positions. Participants were instructed to use a shovel (1.45 m long) to pull the marble into a circle of 70 cm radius, with participants standing in its center. Once the marble had been successfully dragged into the circle, the next trial was initiated. Each participant completed a total of 200 trials, with 40 trials for each possible eccentricity. The whole block lasted approximately 10 minutes.

**Push Training**

The methods were identical to those for the Pull training, except that participants were instructed to perform a pushing routine. Specifically, on each trial they had to use the shovel to push the marble away from them into a circle of 70cm radius positioned around the blob avatar, instead of pulling it towards them as in the previous condition. This task used in Experiment 1 aimed at testing whether the direction of action while using a tool plays a role in reshaping the PPS (Fig. 1C).

### 7.2.5 Experiment 2 – Hammer & Gun

**Hammer Training**

In this condition participants were positioned in the same non-descriptive white room with a single blob avatar standing at 2.5 m and moving from left to right completing a semi-circular trajectory reaching a maximum of 30° of eccentricity on each side at a speed of 2.618 m/s (Fig. 1D). Participants were equipped with a hammer bridging the distance between their extended arm and the blob avatar and were instructed to hit the avatar on the head. Each successful hit was signaled by both a vibration of the controller and a back-and-forth rocking motion of the avatar (as if it was reacting to the hit). Furthermore, to make the task more engaging, a green life-bar representing the remaining energy left of the avatar was positioned above it. On each successful hit, the life-bar decreased, reaching 0 after 200 successful hits. Each participant performed three blocks of this training in succession, with a total duration of about 10 minutes (same as in previous trainings).

### Toy-Gun Training

Participants had to use a yellow toy-gun to hit the blob avatar that moved along the same trajectory described for the hammer training. Every time the trigger was pulled the controller vibrated and each successful hit was signaled by a back-and-forth movement of the blob avatar (similar to the hammer training). The bullet travelled towards the target at a speed of 2.618 m/s. The same life-bar used for the hammer training was used here as well. Each participant completed 3 blocks of 200 trials. (Fig.1E).

### 7.2.6 Procedure

Independently of the experiment and the order of conditions, the experimental session began with presenting participants with a 7-trial sample of the Baseline Task in order to familiarize them with the procedure.

Participants performed the Baseline Task to measure the extension of their PPS three times in each experiment: once without having performed any training (Baseline Condition) and once after each training session (Push Condition and Pull Condition for Experiment 1 or Hammer Condition and Gun Condition in Experiment 2). The order of conditions was counterbalanced across participants. Between each condition participants removed the VR headset and took a 15-minute break to ensure that any remaining effect induced by training wore off before beginning the next condition of the experiment.

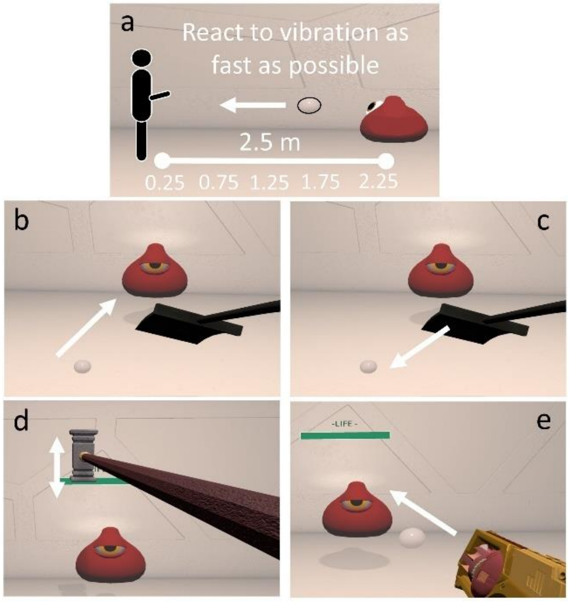

**Figure 31. Experimental paradigm.**
**A. Measuring of PPS.** Participants were instructed to react to a vibration delivered through the controller as fast as possible, while ignoring an approaching visual stimulus.
**B. Push Training:** participants used the shovel tool to push the marble towards the avatar.
**C. Pull Training:** participants used the same shovel tool was used to pull the marble towards their feet.
**D. Hammer Training:** participants used a hammer to hit the avatar using an up-and-down vertical motion. A Green Life Bar decreased at each successful hit.
**E. Toy-gun Training.** Participants used a gun to shoot the avatar, the same Life Bar used in the Hammer Training was used to signal the progression of the task.

### 7.2.7 Data Analysis

To measure the size of the PPS we pooled together trials from all participants in which the bubble was released by the central monster (80% of all trials) and analyzed them at the group level. During the data preprocessing all trials in which participants failed to pull the trigger or pulled the trigger before the vibration, were excluded. To further ensure that we only considered genuine responses to the tactile stimulus, we also excluded trials in which the RTs were unreasonably fast (<100 ms-possibly indicating a reaction to the release of the bubble and not the vibration) or slow (>1000 ms-possibly indicating lack of attention) or fell beyond 3 standard deviations from the average individual RTs for each possible distance. In practice, this led to the rejection of less than 1% of all trials.

There have been various reports in the literature showing that RTs in a visuo-tactile or audio-tactile detection task are expected to increase as a function of increasing irrelevant stimulus distance (Buck et al., 2020; Canzoneri et al., 2013; Lee et al., 2021;

Noel, Bertoni, et al., 2020; Serino et al., 2018). For this reason, in a preliminary analysis we plotted individual RTs against visual stimulus distance and fitted them with the linear function (Eq. 1):

$$y(x) = ax + b \qquad \text{Eq.1}$$

In order to make RTs easier to compare among conditions, average RTs at the group level were normalized between 0 and 1 (Eq.2)

$$z_i = \frac{(x_i - min(x))}{max(x) - min(x)} \qquad \text{Eq.2}$$

To compute the exact PPS border in each condition, average RTs at the group level were plotted against visual stimulus distance and fitted with a sigmoid function (Eq. 3) as suggested by Serino et al. (2018). Fitting parameters were set to anchor the sigmoid curve between 0 and 1, and x0 was restricted between 0.25 and 2.25 m.

$$y(x) = \frac{y_{min} + y_{max}e^{(x-xc)/b}}{1 + e^{(x-xc)/b}} \qquad \text{Eq.3}$$

Statistical significance was tested using the bootstrapping method (Efron & Tibshirani, 1994). On each repetition (12,000 iterations) and separately for each condition, the data were sampled with replacement (as many independent samples as the full dataset) and fit with the sigmoid function described above, whose peak yielded an estimate of the size of PPS. As an additional step to ensure that each tested distance was represented equally in the new re-sampled dataset, each tested distance was resampled an equal number of times, thus preventing a possible unbalanced dataset. For Experiment 1, each distance was resampled on average 532 times in each new dataset while in Experiment 2 each distance was resampled on average 323 times. PPS size distributions for each condition were tested for significance separately using a Bootstrap t-test (Efron & Tibshirani, 1994).

## 7.3 Results

### 7.3.1 Experiment 1

## Data Preprocessing

As there is an extensive literature showing that during a visuo-tactile or audio-tactile detection task participants RTs decrease as the irrelevant stimulus approaches (Buck et al., 2020; Canzoneri et al., 2013; Lee et al., 2021; Noel, Bertoni, et al., 2020; Serino et al., 2018), we looked for a decrease or increase in RTs in the Baseline condition as a function of visual stimulus distance at which a tactile vibration was delivered. For each participant, we measured the linear regression (Eq.1) and then correlated the variance explained by the linear model ($R^2$) with the slope of the fit (*b* in Eq.1). As expected, we found a strong correlation between the two (Pearson's r=0.95, p<0.001). Data in Fig.2 show that participants with the steepest slope, indicating a steeper increase in RTs as a function of visual stimulus distance, also had the highest goodness of fit. Furthermore, there is a clear cluster of participants who had both a very poor goodness of fit ($R^2$<0.1) and a very flat slope (*b*<0.1), suggesting that not only RTs did not increase but also did not follow a linear trend in general (Fig.32, datapoints within dotted rectangle). In other words, these participants showed no reduction in RTs as the incoming stimulus was approaching, but the variance of the whole dataset was poorly accounted for by a linear model indicating poor performance in general. For this reason, this cluster of 8 participants was excluded, leaving a dataset of 34 participants for further analyses.

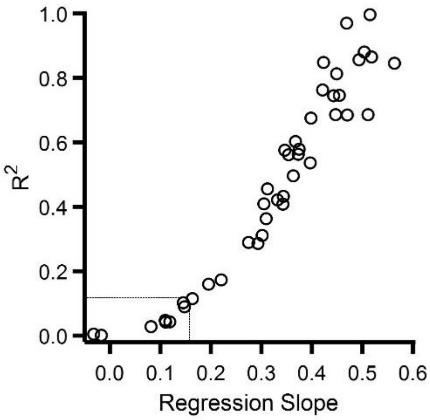

**Figure 32. Correlation between $R^2$ and linear fit slope for participant's RTs in the baseline condition of Experiment 1**

Individual average RTs as a function of visual stimulus distance were fit with a linear regression model. The goodness of fit and the slope predicted by the model for each participant were then correlated with each other. Participants with both the lowest goodness of fit and flattest slope (shown within the dotted rectangle at the bottom left of the graph) were excluded from further analyses.

## Size of PPS before and after training

Individual and average RTs for each visual stimulus distance are plotted in Fig.33 for the three conditions. In all three conditions, when the size of the PPS was measured using the Baseline Task there was a clear influence of stimulus distance on RTs, with longer distances triggering the slowest response. RTs, averaged across participants, ranged between 250 ms and 310 ms, in line with previous reports (Serino et al., 2018).

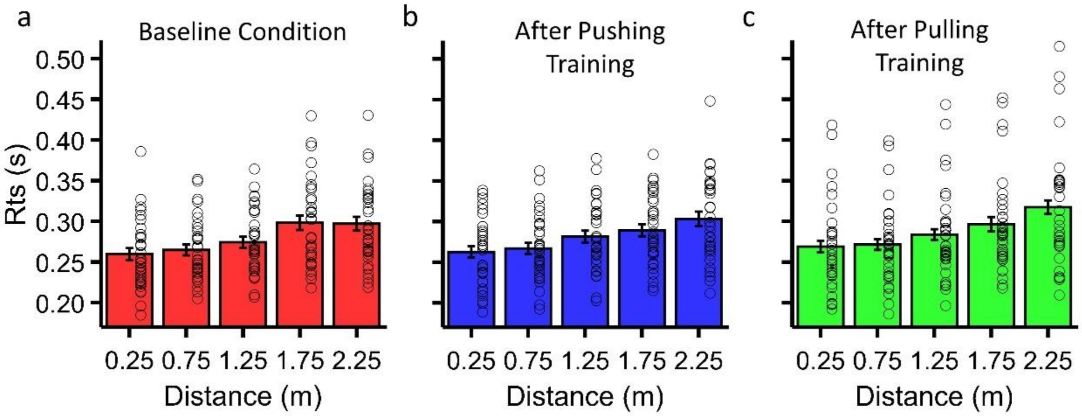

**Figure 33. Average Rt's as a function of visual stimulus distance in the three conditions.**
Hollow circles represent individual reaction times, vertical bars depict average reaction times ±S.E.M. In all three conditions there is an evident increase in RTs as the distance of the visual stimulus from the participant increases when the tactile vibration is delivered.

To test whether the PPS of participants had changed as a result of the training performed in the Push and Pull conditions, individuals RTs for the trials in which the ball was launched from the central monster (80% of all trials) were pooled together and analyzed at the group level. To make the three conditions easier to compare with each other, average RTs were normalized between 0-1 using Eq.2. To determine the exact border of the PPS in the three conditions average RTs were plotted as a function visual stimulus distance and fit with a sigmoid function (Eq.3). The point of maximum slope of the fit (x0) can be considered as the border of the PPS (Serino et al., 2018).

Aggregate sigmoid functions for the three separate conditions are plotted together in Fig. 34A. The PPS appears to be the smallest in the Baseline Condition (red curve) with a size of 1.28 m, while the PPS appears to get enlarged as a result of both the Pull (green curve) and the Push training (blue curve), yielding a PPS measuring 1.55 m and 1.46 m respectively. The size of the PPS in the Baseline condition is very similar (only a difference of 1 cm) to the one previously found by Buck et al. (2020) using the same paradigm in VR.

The significant difference between the aggregate data for each condition was quantified by the bootstrap sign test. On each one of the 12,000 iterations, separately for each condition, the data were sampled with the replacement (as many independent samples as the full dataset) and fit with a sigmoid function, to estimate the border of the PPS. For the Push condition (Fig. 34B) there was a slight trend of PPS enlargement after training, as shown by the peaks of the distribution that were rather spread apart. However, this trend did not reach statistical significance (p=0.12). For the Pull condition (Fig.4C), the same trend of a PPS enlargement after training was observed but this time modulation was quantitatively higher and was found to be statistically significant (p=0.04). These results suggest that, in line with several previous reports, the Pull Training yielded a significant enlargement of the PPS of almost 20% (0.22 m of difference between the two conditions). The Push training, despite including a motor routine in the opposite direction (from PPS to EPS), also showed a tendency to induce an enlargement of the PPS, suggesting that modulation of the PPS is not selective for the actions towards the participant’s body. However, as changes in PPS size in the push condition failed to reach statistical significance, it seems that motor routines in which elements within the PPS are moved further away to the EPS cannot change the size of PPS.

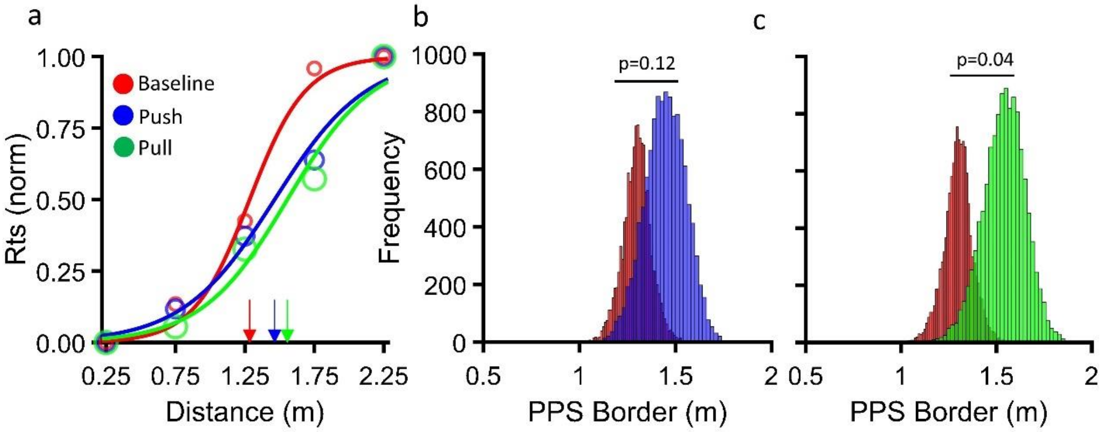

**Figure 34. Reaction times sigmoidal fit and bootstrapping.**
**A.** Average reaction times (normalized in a 0-1 range) are plotted against visual stimulus distance and fit with a sigmoid function. The point of maximum slope of the fit (x0) is considered the border between the PPS/EPS.
**B.** Bootstrap distributions for the Baseline and Push conditions. Each column represents how many times a certain value was obtained out of 12 000 iterations. The difference between the 2 distributions is then tested with a bootstrap t-test.
**C.** Bootstrap distributions for the Baseline and Pull conditions. In this case the difference between the two distributions is statistically significant.

### 7.3.2 Experiment 2

### Data Preprocessing

In the second experiment, we tested for the very first time the role of training motor routines that (a) did not involve a crossing of the PPS/EPS border or (b) did not include a direct, physical contact between the observer and the target in EPS. As a preliminary step, and similarly to Experiment 1, individual RTs were fitted with a linear function to test for linear increase as a function of visual-stimulus distance. Also in this case, we found a strong correlation between the variance explained by the linear model ($R^2$) and the Regression Slope (b in Eq. 1). The two values were strongly correlated with each other (Pearson's r=0.49, p=0.003) and again we found a small cluster of participants (within the dotted rectangle of Fig 35) who exhibited both a very low goodness of fit and a very flat slope. As these participants that provided noisy and stereotypical responses were excluded from the subsequent analyses, resulting in a total of 28 participants in the final dataset.

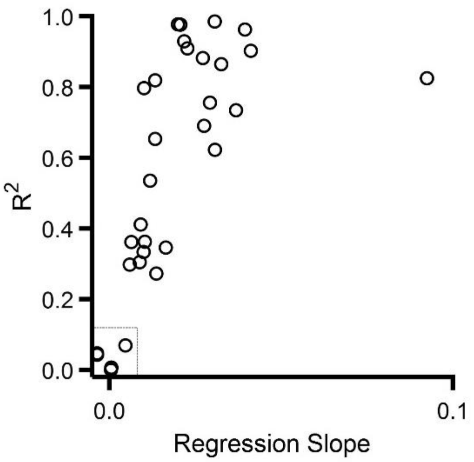

**Figure 35. Correlation between $R^2$ and the slope of the linear fit for participant's RTs in the baseline condition of Experiment 2.**
Individual average RTs as a function of visual stimulus distance were fitted with a linear regression model. The goodness of fit and the slope predicted by the model for each participant were then correlated with each other. Participants with both the lowest goodness of fit and flattest slope (dotted rectangle, bottom left) were excluded from further analyses.

### Size of PPS before and after training

Average RTs plotted as a function of distance in the three conditions are plotted as a function of visual stimulus distance in Fig.36. Experiment 2 confirms the validity of the Baseline Task as a tool to measure the border of PPS, given that RTs steadily increase as the distance of the approaching visual stimulus at which vibration is delivered increases. Furthermore, average RTs are in line with Experiment 1, ranging from 250 ms to 320 ms.

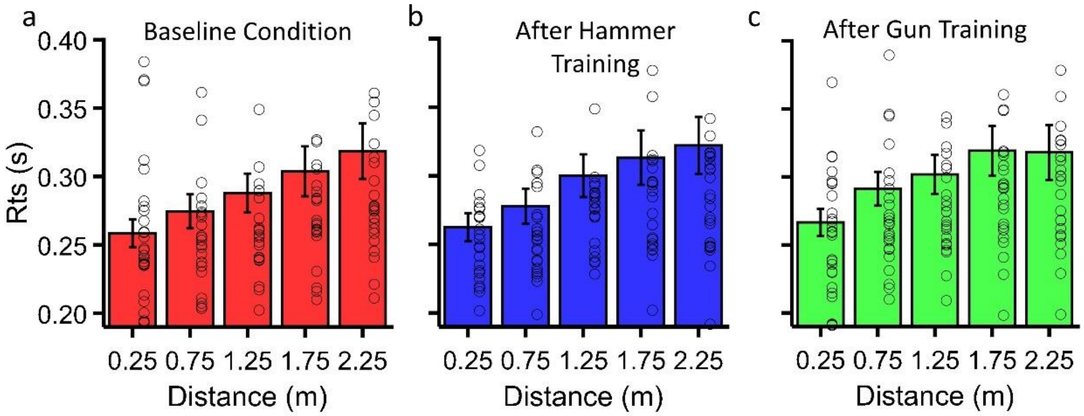

**Figure 36. Average RTs as a function of visual stimulus distance in the three conditions.** Hollow circles represent individual reaction times, bar depict average reaction times ±S.E.M.

To test whether the Hammer and Toy-Gun training had any influence on the size of the PPS, all trials in which the ball was launched from the central monster (80% of all trials) were pooled together and analyzed at a group level. First, average reaction times were normalized between 0-1 using Eq.2. Then, average RTs as a function of visual stimulus distance were fitted according to Eq. 3 (see Methods) and the point of maximum slope (x0) was taken as the border of PPS.

Sigmoid functions on aggregate data across participants for the three separate conditions are plotted in Fig.37A. As it is clear from inspection, the size of the PPS was the biggest in the Baseline Condition (red curve) with a size of 1.20 m. This result is very close to the size of PPS found in the Baseline Condition of Experiment 1 (1.28 m). Indeed, there was no statistically significant difference between the Baseline conditions of two experiments (p=0.74), as tested with the same bootstrapping procedure implemented in Experiment 1.

At odds with Experiment 1, the two trainings employed in Exp. 2 did not induce any significant changes of the size of PPS. Both conditions yielded a slight shrinkage of the

PPS, that was more pronounced in the Hammer condition (0.96 m) than in the Gun Condition (1.04 m) and in contrast with the enlargement reported for the pulling effect of Exp. 1. However, as already mentioned, neither the use of the hammer nor that of the toy-gun induced a significant change on the size of the PPS, suggesting that when the items we interact with do not cross the PPS/EPS border (hammer) or when no physical contact is established between objects in the PPS and EPS (toy-gun), no significant change in the PPS size occurs.

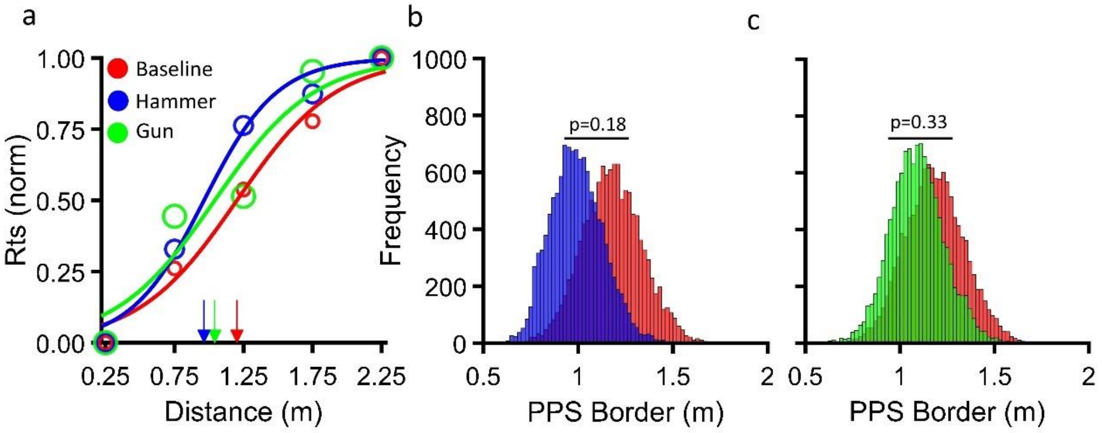

**Figure 37. Reaction times sigmoid fit and bootstrapping for Experiment 2.**
A. Normalized average RTs are plotted against approaching visual stimulus distance and fit with a sigmoid function. The point of maximum slope of the fit (x0) is defined as the border between the PPS/EPS.
B. Bootstrap distributions for the Baseline and Hammer conditions. Each column represents how many times a certain value was obtained out of 12 000 iterations. The difference between the 2 distributions is then tested with a bootstrap t-test.
C. Bootstrap distributions comparing the Baseline and Gun conditions.

### 7.4 Discussion

In this study we investigated the effects of a brief tool-use training on the extension of the PPS in a VR setting. Across two experiments, participants had their PPS measured before and after performing four different types of tool-training. The task we chose to measure the size PPS was the visuo-tactile detection task, which has been shown before to be a valid tool for determining the size of the PPS in humans (Serino et al., 2018). In the Baseline condition of both experiments we found that the extension of PPS before any training was 1.28 m and 1.20 m respectively. This result is reassuring in terms of validation of the visuo-tactile paradigm in VR as it almost perfectly replicates previous findings (Buck et al., 2020; Lee et al., 2021).

In Experiment 1, the size of PPS was measured after two kinds of training: the Pull training in which participants had to pull marbles from their EPS to their PPS and the Push training in which participants had to push marbles away from their PPS into their EPS. We found that the Pull training triggered a significant enlargement of the PPS of more than 20% after only 10 minutes of activity. This result is in line with previous reports that used a similar training motor routine in animal models (Iriki et al., 1996), brain-damaged patients (Bonifazi et al., 2007; Farnè & Làdavas, 2000; Maravita et al., 2002), and healthy controls (Anelli et al., 2015; Canzoneri et al., 2013). However, this is the first time in which an expansion of the PPS is achieved in VR via tool-use training, thus providing key evidence for the effectiveness of using VR environments to measure and modulate the PPS. Furthermore, even though the Push training in which the interaction with the objects was carried out in the opposite direction (from PPS to EPS), we found a trend for an expansion of the PPS (around 15%) but this effect was quantitatively less robust and failed to reach statistical significance. To further investigate how different motor routines during training can modulate the PPS size, in Experiment 2 we designed two new training actions. In one condition, participants had to use a hammer to hit a blob avatar that was moving sideways in the EPS, while in the other condition they had to use a toy-gun to shoot the avatar placed in the far space. Although we did observe a slight shrinkage of the PPS, none of the two types of training had any significant effect on the size of the PPS.

Considering the results of Experiment 1, one might speculate that the direction of motion during the training is crucial, with the Pull routine requiring to move objects from the EPS to the PPS being the only kind of motion capable of remapping PPS. Indeed, there have been previous reports of action specificity on the extension of the PPS suggesting that different action kinematics might yield different effects. For instance, Brozzoli et al. (2010) compared the effects of a grasping and a pointing action on visuo-tactile interactions. They found that during the approaching phase of the moment, the Grasping action led to a stronger cross-modal congruency effect compared to the pointing action, in which participants approached the target without touching it. Results from Experiment 2 seem to suggest that it might be also possible to induce a shrinkage of PPS, even though the kind of training we leveraged on (hammering and shooting), failed to induce a significant change in PPS. A reduction of the PPS size might be related to the need to become more conservative in terms of defensive behavior. As participants were asked to use weapons to hit the blob avatar, this might have triggered the implicit belief of having to defend themselves from the avatar. Indeed, it has been established that carrying out a defensive behavior for a prolonged period of time can trigger a shrinkage of PPS. For instance, expert boxers exhibit an anomalous Hand Blink Reflex (HBR) compared to controls (Biggio et al., 2019). The HBR is a subcortical response at the brainstem level, elicited by the electrical stimulation of the median nerve at the wrist and recorded from the orbicularis oculi muscles. HBR dramatically increases when the stimulated hand is statically positioned inside the PPS surrounding the face (Sambo et al., 2012). However, when boxers assume the guard position, the HBR is heavily suppressed, even though the affected limb is stationarily positioned within the PPS. This might be because boxers perceive themselves as protected from danger while they are in the guard position, thus shrinking their PPS. Similarly, we might speculate that participants in Exp. 2 in which two kind of fight-related actions were involved (hammering and shooting), might have been prompted to activate a defensive behavior to be adequately defend themselves from the avatar, and this, in turn might have reduced the size of their PPS.

One of the key contributions of the present study is that it has successfully investigated PPS manipulations in a VR environment, as previous studies have questioned the possibility to do so. For instance, as mentioned in the Introduction, Ferroni et al. (2022) found that the same kind of training that triggered an expansion of PPS in a real life setting did not achieve the same result in VR, which prompted them to conclude that the PPS in VR might be characterized by different properties. One possible explanation to reconcile these findings might be in terms of the differences between the experimental paradigm implemented here and in Ferroni et al. (2022). In their paradigm, during the training phase participants had to move an object from point A to point B with both points being located in the EPS. This means that participants never had to move objects closer to or further away from them, with no transitions between PPS and EPS. On the other hand, in the Pull training of the present study, the only condition that was successful in inducing a significant enlargement of the PPS, objects were moved from EPS to PPS to establish a clear connection between the two spaces. Considering this, it is surprising that the opposite movement, Push, did not provide any significant result and even more interesting it's that, nevertheless, the tendency found was towards an enlargement of the PPS. If the direction of motion is crucial to the reshaping, one might have expected a constriction of the size of the PPS. Going back to the comparison between the present study with that of Ferroni et al. (2022), it is clear that the condition more similar across the two studies is the Hammer training, in which participants had "physical contact" with the targets but without moving the objects between the PPS and the EPS. Notably, in Ferroni et al. (2022) such training yielded a weak tendency to shrink the PPS, suggesting that the two kinds of training taken into account, might trigger similar PPS reshaping. These results, in combination with those from the present study, strongly suggest that the type of motor routine carried out during the training, plays a fundamental role in PPS reshaping.

From the current results it is clear that pulling objects towards oneself has a special role in the representation of PPS, which could possibly be derived from the evolutionary relevance of pulling objects closer in order to interact with them. Future studies should aim at investigating two main experimental questions. First, it should be determined whether it is possible to trigger a reshaping with any other kind of tool training while considering variables such as the cinematic of the training actions or the training duration. Subsequently it would also be crucial to test the lifespan of the expansion effect triggered by the tool training, to determine whether changes in the PPS are transient phenomena or are long lasting. Finally, as the present study revealed that reliable and accurate measurements of PPS can also be achieved in VR, future studies should take further advantage of this technology to investigate PPS in more ecological settings and situations.

# Chapter 8

# General Discussion

# 8. General Discussion

## 8.1 Overview of the findings

The general aim of this thesis was to test the validity of ATOM Theory from multiple point of views, by focusing, in particular, on the relationship between action and perception.

Several issues were investigated, such as the role of the task used to investigate cross-dimensional interactions, the effect on space perception induced by motor adaption, the characteristics of the interference between running and time and numerosity perception, the relationship between magnitude perception and Peripersonal space and the properties of Peripersonal space in virtual reality environments.

I first aimed to replicate the well-established influence of numerosity on duration judgments using different types of behavioral tasks. I found that, while the more widely used discrimination task allows us to detect the influence of stimulus numerosity on duration judgments, the same does not apply when participants are asked to perform an equality judgement or a reproduction task. This suggests that, while numerosity affects duration judgments at some stage of the decisional process, this phenomenon might not be purely perceptive. On the contrary, dedicated sensorimotor circuits in the brain might be dedicated for the interplay between the processing of quantitative perceptual information and the motor system. In line with that, it has been reported that a sequence of rapid up and down hand motion (tapping) is capable of adapting perception of both numerosity and duration. For this reason I aimed at extending this result to the third main magnitude appointed by ATOM theory: space. The results demonstrate that, albeit smaller in magnitude compared to duration and numerosity, rapid finger tapping induces a compression of perceived space. In order to investigate whether the influence of self-motion on magnitude perception is limited to the upper-limb effector or whether it also extends to the lower limbs, I employed a running paradigm and tested its interference with duration and numerosity perception. As already reported in previous literature, I found that running systematically interferes with duration perception and causes an overestimation of perceived time. However, in order to overcome some of the discrepancies in the existing literature that might be cause by methodological differences, I applied a standardized motor paradigm to different time ranges and sensory modalities. This allowed me to generalize the effect induced by running on duration perception. On the other hand, I found no distortion of numerosity judgments as a consequence of running, suggesting that this effect does not generalize across perceptual magnitudes.

One important issue intimately related to the planning and execution of actions is the portion of space in which we can actively manipulate the objects around us termed Peripersonal space. Indeed, action needs proximity with its target, and there is evidence of perceptual networks dedicated exclusively to Peripersonal space. As is often the case with magnitude perception, time has been the first domain investigated while taking into account the influence of stimulus distance. As I tried to extend this investigation to the study of other magnitudes as well, I found that numerosity perception relies less on stimulus distance than time does, with participants showing the same perceptual precision and accuracy in both Peripersonal and Extrapersonal space.

In the last chapter of this thesis i have explored the malleability of the border between peri-personal and extra-personal space via a innovative VR paradigm likely to become a stepping stone for future studies on magnitude perception and for the interaction between perception and action. This study was conducted in collaboration with the Center for Applied Neuroscience of the University of Cyprus. My aim was to validate in a VR environment a paradigm that has been replicated multiple times in real world settings to measure the exact size of participants' Peripersonal space. Following this, I also experimented for the first time in VR a tool-training method aimed at reshaping participants' Peripersonal space. My results show that, similarly to real world settings, a short period of tool-training is sufficient to cause a significant enlargement of the Peripersonal space.

## 8.2 Conclusions

The aim of this thesis was to fill in some of the gaps in the vast but controversial literature regarding ATOM Theory. Indeed, while an interaction between action and perception is undeniably present, its properties and ramification have proven difficult to pinpoint.

My results seem to suggest a prominent role of the effectors involved, with hand-movements proving able to distort all magnitudes. The lower limbs, on the other hand, have proven to be incapable of distorting space and numerosity. However, these findings are insufficient to exclude any potential effect of the lower limbs on magnitude perception given that, for example, in our paradigm the presentation of the stimuli were far way the location in which action was performed (the surface of the treamill) while the spatial proximity of between the location where action get performed and that in which perceptual stimuli are deployed has been demonstrated to play a key role in this sensorymotor interacion (Anobile, Domenici, et al., 2020) . Indeed, despite being a reliable and significant effect, the distortion induced by finger tapping on numerosity, for instance, has been shown to be highly spatially selective, requiring an almost perfect spatial correspondence between the effector and the stimulus in order to induce a distortion (Anobile et al., 2021). Future studies should then focus on developing new behavioral paradigms, in which a spatial correspondence between effector and stimulus is achieved. Another issue raised in this thesis was the task specificity of some cross-magnitude interactions: this result significant effect, the distortion induced by finger tapping on numerosity, for instance, has been shown to be highly spatially selective, requiring an almost perfect spatial correspondence between the effector and the stimulus in order to induce a distortion (Anobile et al., 2021). Future studies should then focus on developing new behavioral paradigms, in which a spatial correspondence between effector and stimulus is achieved. Another issue raised in this thesis was the task specificity of some cross-magnitude interactions, this result is of key importance, as it posits some methodological concerns. If some effects are task dependent, one might then argue that they are not the genuine result of a perceptual bias, but merely reflect a decisional bias. A possible tool to be used to extricate the two is the use of confidence measurements. Indeed, while having participants perform different tasks causes a significant lengthening of the experimental session, confidence judgments can be measured at no cost, and have proven before to be a reliable method to distinguish decisional biases from perceptual ones (Maldonado Moscoso et al., 2020). It would then be crucial to test whether the task-dependent influence of numerosity on duration observed in Chapter 2 is also reflected in confidence judgments. However, even if this were not the case, I would speculate that in case cross-magnitude interference only happened at a decisional level, rather than at a perceptual one, this would not necessarily disprove ATOM Theory, as the issue would just translate from the perceptual to the decisional domain and it might be asked why decisions about one magnitude should be influenced by another if they don't share the same neural resources.

Finally, the study using a virtual reality setting presented in Chapter 8 was designed as an exploratory attempt to validate methodologies developed in laboratories conditions within Virtual reality settings as it would open up to the possibility of keeping rigorous methodological manipulation as those typical of laboratory experiments but in much more ecological conditions. Virtual reality a relatively novel tool in psychophysics, but it has proven to be of primary importance, as it allows on the one hand to test participants in a much more ecological setting, and on the other to design experimental paradigms in which, for instance, perception and proprioception dissociated. For this reason, a preliminary and thorough validation of virtual reality is of paramount importance as it allows to generalize any future finding.

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