INFANTS' BRAIN RESPONSES TO LOOMING DANGER: DEGENERACY OF NEURAL CONNECTIVITY PATTERNS

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Abstract— A fundamental property of most animals is the ability to see whether an object is approaching on a direct collision course and, if so, when it will collide. Using high-density electroencephalography in infants and a looming stimulus approaching under three different accelerations, we previously (van der Weel and van der Meer, 2009) found how the young human nervous system reflects visual information for impending collision. In the present study, using longitudinal data on 25 infants at 4-5 months and 12-13 months we showed that infants' looming related brain activity is clearly localized in the visual cortex (V1) following retinotopic mapping, but is highly adaptive in its organization otherwise. Analyzing the orientation of electrical source flow, we provided evidence for a high degree of variability, spread across a relatively large area of the visual cortex. The findings revealed a highly functional organization with connectivity patterns constantly emerging and changing in many different directions between trials. This indicates degeneracy of neural connectivity patterns through reentry principles where neurons temporarily assemble to enable an appropriate looming response with the necessary precision.

Keywords: Looming, Infants, High-density EEG, Source analysis, Tau-coupling, Timing in the brain, Neural reuse, Vicarious functioning, Degeneracy, Reentry

I. INTRODUCTION

How does the infant brain deal with information about imminent collisions? By simulating a looming object on a direct collision course towards infants, it is possible to investigate brain activities in response to looming information. Looming refers to the last part of the approach of an object that is accelerating toward the infant (Kayed and van der Meer, 2007). To prevent an impending collision with the looming object, infants must use a timing strategy that ensures

they have enough time to estimate when the object is about to hit them in order to perform the appropriate behavioral response. Defensive blinking is widely considered as an indicator for sensitivity to information about looming objects on a collision course. Infants must use time-to-collision information to precisely time a blinking response so that they do not blink too early and reopen their eyes before the object makes contact or blink too late when the object may have already made contact. An accurate defensive response helps to prevent injury to the infants. For a successful defensive response to avoid collisions, development of prospective control is important. Infants must use looming visual information to correctly time anticipatory responses to avoid impending collisions (Agyei, van der Weel, & van der Meer, 2016).

The timing strategies that infants use to determine when to make a defensive blink to a looming virtual object on a collision course were investigated using infants between 22 and 30 weeks of age in a cross-sectional behavioral study (Kayed and van der Meer, 2000). The youngest infants used a strategy based on visual angle to time their defensive blinks, causing them to blink too late when the looming object approached at high accelerations. The oldest infants, on the other hand, used a strategy based on time-to-collision that allowed them to blink in time for all the approach conditions of the virtual object. When precise timing is required, the use of the less advantageous strategy involving the approaching object's visual angle may lead to errors in performance compared to the use of a strategy based on the remaining time-to-collision that allows for successful performance irrespective of object size and speed.

With the presentation of a looming virtual object on a direct collision course, we also studied the developmental differences in infants longitudinally at 4 and 12 months using EEG. The looming stimulus was programmed to loom towards the infant with different accelerations, which finally came up to the infant's face to simulate a visual collision experience. Looming-related peak visual evoked potential (VEP) responses were analyzed using source dipoles in occipital areas indicating the 3D location and orientation of electrical current. Results showed a developmental trend in the prediction of a looming object's time-to collision in infants. With age, average VEP duration in infants decreased, with peak VEP responses closer to the loom's time-to-collision (van der Weel and van der Meer, 2009; van der Meer et al., 2012). In addition, infants around 12 months of age used the more sophisticated and efficient strategy based on time-to-collision to time their brain responses to the virtual collision. Their looming-

related brain responses occurred at a constant time-to-collision irrespective of visual loom speed, an indication of the development of prospective control at this age (Agyei et al., 2016). The use of such a timing strategy based on a fixed time-to-collision may reflect infants' levels of neural maturity and locomotion experience. Maturity and experience are important factors needed for accurate timing of prospective actions in response to looming objects to ensure successful evasive maneuvers during navigation.

By localizing brain source activity, using source dipole models, for looming stimuli approaching at different speeds and using extrinsic tau-coupling analysis, the temporal dynamics of post-synaptic neuronal activity in the first year of life was further investigated (van der Weel and van der Meer, 2009). Tau-coupling analysis calculated tau of the peak-topeak source waveform activity and the corresponding tau of the approaching looms. Source dipoles that modeled brain activities within the visual areas of interest O1, Oz, and O2 were fitted around peak looming VEP activity to give a direct measure of brain source activities on a trial-by-trial basis. Using pre-locomotor infants at 4-7 and 8-9 months and crawling infants at 10–13 months of age, synchronized theta-band activity in response to the looming stimulus was found. This was consistent with other studies that identified oscillations in the theta range as important for registration and processing of visual perceptual information (e.g., Kahana et al., 2001). Extrinsic tau-coupling analysis on the source waveform activities showed evidence of strong and long tau-coupling in all infants. The oldest infants showed brain activity with a temporal structure that was consistent with the temporal structure present in the visual looming stimuli. Thus, in the course of development, the temporal structure of different looming stimuli may be sustained while progressing through the more mature infant brain. Sustaining the temporal structure of looming information in brain wave activity may provide increasingly accurate time-to-collision information about looming danger as infants become more mobile with age. Infants at 10-13 months differentiated well between the different loom speeds with increasing values of the tau-coupling constant, K, for the faster loom. For further details, see van der Weel and van der Meer (2009).

Resonance

The fact that changing patterns in the optical looming information were reflected in the changing patterns in the neurological flow through the infant brain in our results, may shed

some light on the concept of *resonance* introduced by Gibson in 1966: "We may suppose the orienting of the organs of perception is governed by the brain so the whole system of input and output resonates to the external information" (p. 5).

Unfortunately, Gibson has not been clear as to what the concept exactly entails or how it works, and because of this, Gibsonians argued that the concept is best used as a metaphor (e.g., Turvey et al. 1981; Michaels and Carello, 1981; Chemero, 2009). Therefore, to develop the concept further, moving it out of the metaphor stage, we propose to use our looming data to highlight possibilities to strengthen the concept's explanatory value. The variable tau (τ) and its rate of change specify the time-to-contact between an approaching object and the visual system (Lee, 2009). The same variable was found to be operating in the neural flow when looming-related activity was progressing through the infant brain. Thus, theta rhythm oscillatory activity in the visual cortex was tau-coupled to the approaching looms, that is, the change in the rhythm's temporal structure was linearly correlated with the value of tau of the looms. This, in our view, may indicate a process of resonance in which informational and electrical flow are successfully coupled in terms of the same variable tau via the coupling constant *K*.

Thus, by correlating the temporal dynamics of post-synaptic neuronal activity with the corresponding loom speeds using tau we were able to show how structural patterns in the optical loom information were maintained in the peak-to-peak source waveform activity. However, how are these intricate processes of resonance further organized in the infant brain? For this, we propose in the remainder of this study to re-examine our original looming data (van der Weel & van der Meer, 2009) in terms of localization and orientation of looming-related electrical source activity in the nervous system.

Neural reuse and vicarious functioning

Traditionally, it is assumed that there exists one-to-one mapping between brain structure and function implying some kind of modular organization of the brain (Fodor, 1981), involving a collection of specialized, encapsulated components –or modules– each dedicated to handling some well-defined aspect of information-processing. In the case of our looming experiments, this would involve a specific mapping procedure between the incoming looming information

and a specialized, encapsulated module in the brain dealing with looming-related neural activity.

Gibson (1966) suggested an alternative approach for this type of modular organization when he introduced Lashley's (1922) concept of *vicarious use* of brain tissue, explaining that the same neural tissue can be involved in different temporarily assembled structures suitable to a task. In other words, the functioning of the neurons depends on the context in which they are operating. Recently, Anderson (2014) elaborated on this idea by introducing the concept of *neural reuse*, which is the continual establishment of new patterns of functional connectivity between different regions of the brain at different moments in time (see also de Wit et al., 2017). In this view, neurons can change function completely when incorporated in different systems; they temporarily assemble to enable a given task.

Degeneracy of neural connectivity patterns: multiple realisability and the process of reentry

However, Reed (1996) introduced a different concept to stress the high degree of flexibility of organization of the nervous system, namely that of *degeneracy*. Degeneracy is the ability of elements that are structurally different to perform the same function or yield the same output. It is a term used by mathematicians to refer to ill-formed functions—functions of the form f(x) = y, where there is no unique y for a given x. Another way of saying this is that there is no one-to-one mapping from x to y, because for any function f(x) there are often two results for a given value of x. The relationship between neural processes and behavioral results is degenerate in just this way, and in both directions. That is, a given neural process, x, does not invariably produce a given behavior, y; nor, for a given behavior, y', is there invariably a unique neural process x' causing it (Reed, 1996, p. 74).

Edelman (2001) elaborated on this idea when he introduced the concept of *reentry*. He argued that in order to provide coordinated neural outputs in the brain, linkages of degenerate networks are achieved through a process called reentry. Reentry is a dynamic process of ongoing spatiotemporal correlation occurring between functionally segregated neural areas that are mediated by signaling through massively parallel, reciprocal fibers (Edelman, 1987). Thus, the functioning of neural models depends on the presence of a large number of

different, alternative reentrant circuits that dynamically yield a similar output, i.e., such circuits are degenerate.

These different concepts, discussed briefly here, express the highly flexible organization of the brain. Bullmore and Sporns (2009) refer to this type of flexible organization as functional connectivity as opposed to structural connectivity. It is this dichotomy between functional and structural connectivity that was in the back of our minds when we reanalyzed the data material we recorded in van der Weel and van der Meer (2009). The specific question was how is the flow of looming related information organized in the visual areas of the developing infant brain such that resonance can take place. A structural connectivity organization would be characterized by a rather fixed, non-variable localization of neural activity, while a functional connectivity organization would be characterized by a flexible and variable localization of neural activity in response to the various looms.

II. MATERIALS, METHODS AND ANALYSES

We analyzed a database of high-density EEG recordings from 25 infants, acquired between 2007 and 2011 in the Developmental Neuroscience Laboratory at the Norwegian University of Science and Technology (NTNU) in Trondheim, Norway. All infants were healthy and born full-term, as determined by parental report. The database corresponds to a longitudinal experiment on looming responses, consisting of 128-channel EEG recorded during two sessions. The first session was recorded when the infants were 5-6 months old and the second session was recorded when the infants were 12-13 months old, i.e., before and after the onset of self-produced locomotion. In the experiment, the infants were presented with a visual stimulus that created the illusion of an object approaching on a direct collision course (see Figure 1).



Figure 1. The experimental setup and diagram of stimulus configuration (**a**) and procedure (**b**). Each infant was shown a semi-randomized sequence of an image of a circular disc approaching on a collision course. As the virtual object approaches the eye, its image size on the screen grows. The looming stimulus simulated an object coming from far away (subtending 5° at the eye, θ) approaching for a duration of 2, 3 and 4 s under three different constant accelerations (21.1, 9.4 and 5.3 m/s², respectively) and finally 'hitting' the infants in the face ($\theta = 131^\circ$). Movement stopped when the image filled the entire screen.

The stimulus was programmed to loom towards the infant by increasing in size. The experiments were conducted in a dimmed room with the infants seated in a baby car seat facing a large projection screen. At all times, one of the infant's parents was seated next to the infant and one of the experimenters was present to monitor the recordings. Data collection was performed in one block, including pauses if the infant seemed to lose interest (e.g., looked away

from the stimulus). The experiment ended if no further interest could be obtained or if the infant showed distress.

High-density EEG was recorded at 500 Hz with a HydroCel Geodesic Sensor Net 200 (Electrical Geodesics) with 128 sensors evenly distributed across the scalp. During acquisition, low-pass and high-pass filters were applied (0.1 to 100 Hz). All impedances were kept under 50 k Ω , as recommended for high-impedance amplifiers (Ferree et al., 2001). The EEG data and event triggers (onset/offset of looming stimulus) were stored for offline analysis. The identification of looming responses was conducted with Brain Electrical Source Analysis (BESA) 6.1. Further details about the experiment and the methods can be found in van der Weel and van der Meer (2009) and van der Meer et al. (2012).

ANALYSES

The EEG recordings were band-pass filtered between 1 and 50 Hz and downsampled to 100 Hz. The number of channels was reduced to 78 channels by removing the channels corresponding to electrodes placed in close proximity of to the face and neck, as the majority of the noisy channels showed strong presence of muscle artifacts. Afterwards the EEG data were referenced to the common average. The data were inspected in two-second segments centered around the event markers (e.g., looming response). Data segments contaminated by muscle activity and movement artifacts were rejected by determining outliers (i.e., values exceeding the mean plus three times the standard deviation) based on amplitude, spectral power, and mean frequency. The total number of included trials from 25 infants tested longitudinally was 360 events in the first session at 5-6 months and 282 events in the second session at 12-13 months, more or less evenly distributed between infants and loom speeds.

The characteristics of the looming response were investigated by quantifying event-related potentials (ERPs), inter-trial phase coherence (ITC: Stapells et al. (1984)), and event-related (de)synchronization (ERD/ERS: Pfurtscheller and Lopes da Silva (1999); Makeig et al. (2004) from the annotated EEG data. The annotations on the EEG data indicate the occurrence of an event-related potential in the left and right visual cortex. Event-related potentials are characterized by phase locking of ongoing cortical activity (Klimesch et al., 2007; Sauseng et al., 2007) and can be unmasked by simply averaging over repetitions of the stimulus that elicits a response. Information about the contribution of specific cortical rhythms to an event-related

potential is better explained with analyses in the frequency or time-frequency domain (Pfurtscheller and Lopes da Silva, 1999; Makeig et al., 2004), such as inter-trial phase coherence or phase-locking value, which measure the phase consistency of neural oscillations across repetitions of a stimulus or event. To reveal changes in oscillatory dynamics that occur without phase-locking, it is necessary to quantify relative suppression or enhancement of intrinsic cortical rhythms (e.g., power changes) with an analysis of event-related (de)synchronization (Pfurtscheller and Lopes da Silva, 1999). The complete characterization of the looming response was carried out after preprocessing of the EEG data. Together, these analyses help to understand the physiological phenomena behind the looming response.

III. RESULTS

EVENT RELATED POTENTIALS

The looming responses were treated as evoked potentials although this differs from the classical definition. Every looming response occurs somewhere within a trial without explicit reference to an external event other than the infants' perception of the visual stimulus. The database included in this study was inspected by an expert to determine the presence of increased activity of the visual cortex (negative potential) under the assumption that it represents a looming response. Treating the recordings as an event-related potential and averaging across trials and across infants (due to the relative low number of trials per baby), indeed reveals characteristic components and phase-locking of cortical rhythms.

The looming response showed similar characteristics for infants at both ages (Figure 2). The ERPs displayed clear components at the latencies -70 and 20 ms, relative to the manual annotations included in the database. The scalp distribution of these components suggests that the looming response arises from the parieto-occipital cortices, in agreement with previous analyses of this database (van der Weel and van der Meer, 2009; van der Meer et al., 2012). The ERPs were significantly different from zero in the interval ± 200 ms at both infant ages and over all channels. In the parietal and occipital channels, late deviations from zero occurred in the interval between 200 and 500 ms, likely corresponding to the responses caused by the virtual collision with the looming stimulus. The average time between the looming response and the virtual collision, i.e., the time-to-collision, was 487 ± 345 ms (12-13 months) and 1071 ± 563 ms (5-6 months). The variability of the time-to-collision could cause the visual responses to spread

across several milliseconds. The effect of this variability is also seen in the time-frequency analyses.



Figure 2. Looming response: event-related potential. The grand average ERPs show similar characteristics in both groups of infants. The scalp maps (insets) show clear components at the latencies -70 and 20 ms, relative to the manual annotations included in the database (t = 0 ms), which suggest a parieto-occipital source location of the looming response. The colored lines show individual traces over the 78 EEG sensors included for analysis. Channel significance on the top of the traces indicates when a trace is significantly different from zero (α =0.05, bootstrap).

SOURCE ANALYSIS

In Figure 2, the ERP data were aligned in time, obscuring the precise location and orientation of brain electrical activity in response to the looms. To highlight the exact location and orientation of looming-related activity an additional source analysis was carried out.

In order to locate brain activity specifically in response to looming, we applied brain electrical source analysis (BESA 6.1, MEGIS software GmbH; Hoechstetter et al., 2004). The BESA algorithm estimates the location and the orientation of multiple equivalent dipolar sources by calculating the scalp distribution that would be obtained for a given dipole model (forward solution) and comparing it to the original visual evoked potential (VEP) distribution. Interactive changes in the location and orientation in the dipole sources lead to minimization of the residual variance between the model and the observed spatiotemporal VEP distribution (Scherg, 1990).

Here, we initially used a symmetrical VEP surrogate source model (Scherg, 2002) consisting of 10 regional sources and 7 dipoles (see Figure 3a), which we later for simplicity reduced to a three-dipole model of the visual areas consisting of standard 10–20 sites O1, Oz and O2 (see Figure 3b). Dipoles at these sites were fitted around peak looming VEP activity, providing source waveforms (SWF) of the modelled brain regions as a direct measure of their activities on a trial-by-trial basis.

Two dipoles, visual cortex radial left (VCrL in blue) and visual cortex radial right (VCrR in red), showed consistent symmetrical synchronized activity in response to the looming stimulus. However, brain activity at dipole visual cortex vertical midline (VCvM in green) was most prominent in the majority of all looming trials and was therefore used in subsequent analyses (see Figure 3c).



Figure 3. Dipole model. We used a symmetrical VEP surrogate source model consisting of 10 regional sources (colored squares) and seven dipoles (a), which we later for simplicity reduced to a three-dipole model of the visual areas consisting of standard 10–20 sites O1, Oz and O2 (b). However, brain activity at dipole VCvM (visual cortex vertical midline in green) was most prominent and was therefore used in subsequent analyses (c).

Thus, by following the same procedure as in Hoechstetter et al. (2004), a four-shell ellipsoidal head model was created for every trial, and dipole *VCvM* (see Figure 3c in green) was inserted into the head model. This model was then applied to the raw data transforming the EEG scalp signal to separate brain space signals resulting in a new EEG voltage sequence of the summed post-synaptic neuronal activity over time.



Figure 4. Dipole VCvM for a 2 s loom for one of our infant subjects at 12 months. A fourshell ellipsoidal head model was created for every trial, and dipole VCvM was inserted into the head model. This model was then applied to the raw data transforming the EEG scalp signal to separate brain space signals resulting in a new EEG voltage sequence of the summed post-synaptic neuronal activity over time. This way x, y, and z coordinates (see inset) could be obtained for both localization (x-loc, y-loc, and z-loc; body of dipole) and orientation (xori, y-ori, and z-ori; tail of dipole) of the resulting dipole.

Figure 4 shows the result of this technique for one 2 s loom trial of one of our infant subjects at 12 months. The resulting x, y, and z coordinates of both dipole location (x-loc, y-loc and z-loc; body of dipole) and orientation (x-ori, y-ori, and z-ori; tail of dipole) were obtained for all trials and used in subsequent analyses.



Figure 5. Average location of dipole VCvM for all individual subjects at 5-6 months (red) and at 12-13 months (blue). Note a slight shift in localization in y,z direction when infants get older.

Figure 5 shows the average location of dipole activity for each subject at 5-6 months (red dots) and at 12-13 months (blue triangles). Dipole body localization appears to be rather localized where activity sources of all subjects at both ages occurred within a surface area of a 1 cm³ die in the Oz region of the visual cortex. There was, however, a significant shift of 0.056 cm in y,z direction of dipole body localization between the infants at 5-6 months and 12-13 months, F(1,24)=4.85, p<0.04.



Figure 6. Location and orientation of dipole VCvM for six typical subjects at 5-6 months (red) and at 12-13 months (blue). Location (filled symbols) of dipole activity appears stable in a confined part of the visual cortex with a slight shift from younger to older age (see also Figure 5). Orientation (open symbols) of dipole activity, however, is much more variable, is spread over a substantially larger area of the visual cortex, and is very different for every looming trial.

Figure 6 shows location and orientation of source dipole VCvM for each trial for six typical infant subjects at 5-6 months and 12-13 months of age. Overall results, including all subjects, show that variability of orientation of dipole activity far exceeds the variability of dipole location and that it is spread over a substantially larger area of the visual cortex equivalent to a 2 cm³ die, F(1,24)=190.11, p<0.001).

III. DISCUSSION

The question we asked ourselves in this study was how the flow of electrical activity of looming-related information is organized in the visual areas of the infant brain such that resonance can take place. A traditional organization would be characterized by a rather fixed localization of neural activity, while a functional connectivity would be characterized by a flexible organization of neural activity in response to the various looms. Our results showed that both structural and functional organization principles were occurring in the infants' brain responses to the approaching looms. Location of dipole activity as indicated by the body of dipole VCvM was stable across all subjects and trials and occurred within a 1 cm³ area of the visual cortex. From 5-6 months to 12-13 months, there was only a slight but significant shift in dipole location. This may be due to relocation of looming-related activity or simply to natural head growth. These findings hint at a rather structural organization of brain activity in response to the different looms. However, these findings may be explained by the strict retinotopic organization of the visual system. Retinotopic organization is the mapping of visual input from the retina to neurons within the visual stream organization (Engal, Glover, & Wandell, 1997). This implies that within a small region of the visual cortex, all the cells deal with a local region of the field of view. Thus, localized visual cortical regions respond maximally to particular regions of the visual field, relative to the retina of the eye. This principle may explain the relatively small amount of variation of dipole VCvM localization found in our results on a trial-to-trial and subject-to-subject basis. Thus, our dipole location results show some structural principles of organization, but this may not be very surprising since they can be considered a direct result of the anatomy of the visual system.

However, when it comes to orientation of dipole activity, as indicated by the tail of dipole VCvM activity, the results tell an entirely different story. These results showed a high degree of variability of activity which in addition was spread across a relatively large area (ca 2 cm³) of the visual cortex. This reveals a much more functional form of organization with

connectivity patterns emerging in various directions and changing radically from trial to trial. This may indicate some type of reentry of degenerate neural circuits in which neurons temporarily assemble to enable an appropriate looming response (Edelman, 2001) as discussed in the introduction section.

Thus, from these results, it seems that looming-related electrical activity is finding its way through the visual system initially adhering to retinotopic principles. Then, when electrical activity is arriving in the visual cortex a more flexible type of organization takes over, informing the brain about the impending collision with precise time-to-collision information. Such a combination of both structural and functional organization of looming-related activity through the brain can be used to interpret our earlier developmental looming findings (van der Weel & van der Meer, 2009; van der Meer et al., 2012).

In these studies, we provided evidence of extrinsic tau-coupling of dipole activity showing strong and long tau-coupling in all infants. The oldest infants showed brain activity with a temporal structure that was consistent with the temporal structure present in the visual looming stimuli. Thus, the temporal structure of different looming stimuli was sustained while progressing through the more mature infant brain. In the light of our present results, this may indicate a two-fold principle of brain organization: (a) structural, electrical activity is flowing from the retina to the corresponding area in the visual cortex adhering to retinotopic principles and (b) functional, after arriving at the designated area in the visual cortex electrical activity is proliferating further into the subsequent parts of the visual cortex adhering to principles of reentry of degenerate neural circuits.

Analogous to a rocket in a fireworks display, the rocket is shot up to a particular location in space (structural) after which it explodes in various directions (c.f., orientation of the different looming trials), allowing for a more flexible and functional principle of organization. In the case of our looming trials, degeneracy of neural connectivity patterns entails the flow of electrical source activity across a number of arbitrary neurons in such a way that the temporal structure present in the visual looming information can be revealed, through resonance, to the brain. This way, while sustaining the temporal structure present in the looming information, increasingly accurate time-to-collision information about looming danger was provided to our infants. At 12-13 months, they differentiated well between the different loom speeds with increasing values of the tau-coupling constant, *K*, for the faster looms (van der Weel & van der Meer, 2009).

With this type of reentry of degenerate brain patterns, there is no need for a one-to-one mapping between brain structure and function as suggested by Fodor (1981). Instead, brain organization can be flexible in the sense that structurally different neural tissue can be involved in flexible temporarily assembled structures. The functioning of the neurons depends on the context in which they are operating. In this view, neurons adhere to reentry principles; they temporarily assemble to reveal the typical characteristics of the approaching looms to the brain.

These results may shed light on how the infant brain is informed about an impending collision using resonance. However, in order for the infants to be able to protect the eyes from injury, it is not enough to be able just to perceive the rapid approaching objects, but it is also important to be able to take an appropriate action. Exactly how a defensive blinking or withdrawing response is organized based on appropriate looming information resonating in the visual cortex, remains to be investigated. It may be that appropriate looming information resonates through larger parts of the brain reaching the motor cortex after which a tailored response is made. Alternatively, however, it may be that neural tissue involved in the perceptual resonance of the looming information is also involved in the providing of an appropriate defensive action. Namely, empirical evidence for such a functional type of organization has been reported not just at the level of neural regions large or small, but even at the level of single neurons. For example, certain neurons in the worm are capable of performing both motor and sensory functions (White et al., 1986).

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